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# Systematics and ecology of tonguefishes of the genus *Symphurus* (Cynoglossidae: Pleuronectiformes) from the western Atlantic Ocean*

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**Abstract.**—The 24 species of the cynoglossid genus *Symphurus* Rafinesque, 1810 occurring in the western Atlantic Ocean are revised. *Symphurus* species are found from the southern Scotian Shelf (ca. 45°N) southward to central Argentina (ca. 45°S). These small to medium-size, left-sided flatfishes inhabit diverse substrates ranging from shallow estuarine habitats to deepwater substrates on the outer continental shelf and upper continental slope. Thirty-four nominal species of symphurine tonguefishes have been described previously from this area. Twenty-four, including two new species, are considered valid: *S. arawak* Robins and Randall, 1965, in shallow sandy habitats adjacent to coral reefs from Alligator Reef, Florida, through the Caribbean Sea to Colombia; *S. billykrietei*, new species, on mud bottoms of the outer continental shelf from the southern Scotian Shelf (ca. 45°N) to the central Gulf of Mexico, differing from other species in meristic and morphometric characters, black peritoneum, relatively small eye without pupillary operculum, dark brown stripe covering fin rays and connecting membranes on basal one-third of dorsal and anal fins, and small, darkly pigmented spot on scaly portion of caudal fin; *S. caribbeanus* Munroe, 1991, on sandy and silty substrates in estuarine and neritic waters in the Caribbean, including the Greater Antilles and coastal waters off Central America to Colombia; *S. civitatium* Ginsburg, 1951, on sand substrates in nearshore and neritic waters from Cape Hatteras, North Carolina, to the Yucatan Peninsula, and rarely at Bermuda; *S. diomedeanus* (Goode and Bean, 1885), widespread on continental shelf calcareous muds and sands from Cape Hatteras, North Carolina, through the Gulf of Mexico and Caribbean Sea, south to Uruguay; *S. ginsburgi* Menezes and Benvegnú, 1976, on outer continental shelf mud bottoms from about Cabo Frio, Brazil (ca. 23°S), to Maldonado, Uruguay (ca. 35°S); *S. jenynsi* Evermann and Kendall, 1907, on mud bottoms in neritic waters from near Cabo Frio, Brazil (ca. 22°S), to northern Argentina; *S. kyaropterygium* Menezes and Benvegnú, 1976, on the inner continental shelf from Baia da Ilha Grande (ca. 23°S) to Rio Grande do Sul (ca. 31°S); *S. marginatus* (Goode and Bean, 1886), on outer continental shelf and upper continental slope mud bottoms from southern New Jersey (ca. 40°N) to central Brazil (21°34'S); *S. minor* Ginsburg, 1951, primarily on live-bottom habitats off the southeastern United States and eastern Gulf of Mexico westward to about DeSoto Submarine Canyon (ca. 29°87'W), rarely off southern Scotian Shelf to ca. 44°N; *S. nebulosus* (Goode and Bean, 1883), on the outer continental shelf and upper continental slope from near Long Island, New York (ca. 40°48'N), to the Blake Plateau off Fort Lauderdale, Florida (ca. 26°28'N); *S. oculellus* Munroe, 1991, on the inner continental shelf on mud bottoms from Guyana (57°W) to northeastern Brazil (2°S, 40°W); *S. ommaspilus* Böhlke, 1961, on shallow-water sandy substrates in the Caribbean Sea from the Bahamas, Lesser Antilles, and Belize; *S. parvus* Ginsburg, 1951, on inner continental shelf mud bottoms from off Cape Lookout, North Carolina (ca. 34°23'N), through the Gulf of Mexico and Caribbean Sea to Venezuela; *S. pelicanus* Ginsburg, 1951, on continental shelf soft mud bottoms from the western and central Gulf of Mexico and Caribbean Sea to Trinidad; *S. piger* (Goode and Bean, 1886), on the outer continental shelf and upper continental slope from southern Florida (ca. 30°N), the Gulf of Mexico, and throughout the Caribbean Sea to Suriname (ca. 7°N, 53'W); *S. plagiusa* (Linnaeus, 1766), on soft mud and silt substrates in estuarine and neritic habitats from Long Island Sound to the Campeche Peninsula, also the Bahamas and Cuba; *S. plagusia* (Schneider, in Bloch and Schneider, 1801), on sand and silt substrates in estuarine and neritic habitats from the Greater Antilles and Central America to about Rio de Janeiro, Brazil; *S. pusillus* (Goode and Bean, 1885), on the outer continental shelf from off Long Island, New York (ca. 40°N), to DeSoto Submarine Canyon in the eastern Gulf of Mexico (ca. 29°87'W); *S. rhytisma* Böhlke, 1961, from the Bahamas, Belize, Curaçao, and perhaps Brazil; *S. stigmosus*, new species, in deepwater areas of the Straits of Florida and Gulf Stream off southern Florida and in the Caribbean off Yucatan, Serrana Bank, and Dominica, differing from other species in its combination of meristic and morphometric features, black peritoneum, relatively large rounded contiguous eyes without pupillary operculum, and dorsal and anal fins with combination of 1) dark brown longitudinal stripe on basal one-third which covers fin rays and intervening membranes and 2) usually a series of distinct, darkly pigmented blotches alternating with unpigmented areas of somewhat larger size on posterior two-thirds of fins; *S. tessellatus* (Quoy and Gaimard, 1824), on sandy and silty substrates in estuarine and neritic habitats from the Greater Antilles and Central America to northern Argentina; *S. trewavasae* Chabanaud, 1948, on continental shelf mud bottoms from about Cabo Frio, Brazil (ca. 22°53'S), to central Argentina (ca. 45°S); and *S. urospilus* Ginsburg, 1951, on live-bottom habitats on the inner continental shelf from about Cape Hatteras, North Carolina, to Yucatan Peninsula, and Cuba. Seven species are synonymized. *Achirus ornata* Lacepède, 1802, and *Plagusia brasiliensis* Agassiz, in Spix and Agassiz, 1831, are synonyms of *Symphurus tessellatus* (Quoy and Gaimard, 1824); *Plagusia fasciata* DeKay, 1842, is a synonym of *Symphurus plagiusa* (Linnaeus, 1766); *Symphurus bergi* Thompson, 1916, is a synonym of *S. jenynsi* Evermann and Kendall; *Symphurus sumptuosus* Chabanaud, 1948, and *S. pterospilotus* Ginsburg, 1951, are synonyms of *S. diomedeanus* (Goode and Bean, 1885); and *Symphurus meridionalis* Lema and Oliveira, 1977, is a synonym of *S. jenynsi* Evermann and Kendall. Descriptions, differential diagnoses, an artificial key, and summaries of ecological information are provided for 24 species of western Atlantic symphurine tonguefishes.

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Symphurine tonguefishes belong to one genus (*Symphurus* Rafinesque, 1810) of approximately 75 species of small to medium-size, left-sided flatfishes (Munroe, 1992). Superficially, these flatfishes are recognized in having a small mouth with strongly curved and toothed jaws on the blind side, in having the caudal, dorsal, and anal fins united, and in having lost pectoral fins, lateral line, and left-side pelvic fin. The right pelvic fin has a reduced number of fin rays compared with that for other flatfishes, comprising only four rays, and it is situated along the midline of the body.

Symphurine tonguefishes are the most speciose and widely distributed members of the Cynoglossidae, which comprises approximately three genera and some 125 species. Within the Cynoglossidae, *Symphurus* forms a monophyletic taxon that is the sister group of the *Cynoglossus-Paraplagusia* lineage (Chapleau, 1988). Synapomorphies diagnosing this genus (Chapleau, 1988) include a greatly reduced, ocular-side, lateral ethmoid lacking an osseous attachment either to the interorbital complex dorsally or to the vomer ventrally, the lateral ethmoid with a long posterodorsal arm in contact with the anterior process of the supraoccipital, fusion between ocular- and blind-side anterior arms of the frontals, replacement of the anterior portion of the supraoccipital bone by a cranial fontanelle (a character perhaps unique among flatfishes), all proximal radials anterior to the first hemal spine of the caudal region of the body equally long and in contact with this spine, lack of a lateral line canal on the ocular side (unique among flatfishes), and only a single pterygiophore inserted in the first interneural space (Munroe, 1992).

Species of *Symphurus* have been reported from all temperate and tropical oceans (Chabanaud, 1955a, 1955b, 1956; Mahadeva, 1956; Ginsburg, 1951; Menezes and Benvegnú, 1976; Munroe, 1992) but are the only cynoglossids found in the New World. In fact, it is in these waters where the greatest diversity of species of *Symphurus* is found, with approximately 30 nominal species recorded from both coasts of the Americas (Ginsburg, 1951; Menezes and Benvegnú, 1976; Munroe, 1992). Compared with other flatfishes, *Symphurus* is the most diverse genus of flatfish occurring in the New World, and its species occupy the greatest variety of habitats within this region.

In the western Atlantic Ocean, tonguefishes occur from the Scotian Shelf (ca. 45°N; Scott and Scott, 1988) southward to central Argentina (ca. 45°S, Evermann and Kendall, 1907; Menezes and Benvegnú, 1976; Lazzaro, 1973, 1977; Lema et al., 1980; this study). Throughout this region, *Symphurus* species occur in diverse habitats including such shallow-water areas as muddy and silty substrates in turbid estuaries, sandy patches in seagrass beds in clear tropical waters, and sand substrates on, or adjacent to, coral reefs. In addition, species of *Symphurus* also inhabit a variety of different substrates in moderate depths on the continental shelf, and some species live even on deepwater substrates located on the outer continental shelf and upper continental slope. In fact, *S. nebulosus* and *S. marginatus*, collected as deep as 810 m and 750 m, respectively (see below), are among the deepest-dwelling flatfishes in the western Atlantic.

In some demersal fish communities, especially those on soft-bottom habitats in the western Atlantic Ocean (Wenner and Sedberry, 1989), symphurine tonguefishes can be abundant and probably account for a significant portion of the fish biomass. Although not usually targeted commercially, some tonguefishes, other small-size flatfishes (*Etropus*, *Citharichthys*), and juveniles of larger species of flatfishes (i.e. *Syacium* spp., etc.) may represent a significant proportion of bycatch in trawl fisheries for shrimps and commercially important demersal finfishes (Roithmayr, 1965; Anderson, 1968; Furnell, 1982; Pellegrin, 1982; Maharaj, 1989; Maharaj and Recksiek, 1991). Irrespective of limited commercial importance, these relatively small flatfishes, because of their abundance and diversity, play significant ecological roles as both predator and prey in trophic interactions within benthic communities of the western Atlantic (Yáñez-Arancibia and Sánchez-Gil, 1986).

Accurate identification of fauna in bycatch of commercial fisheries is important to determine environmental impacts of commercial fishing on both target and nontarget species (Villegas and Dragovich, 1984; Sheridan et al., 1984; Rothschild and Brunenmeister, 1984; Maharaj and Recksiek, 1991; Andrew and Pepperell, 1992; Murray et al., 1992; Murawski, 1994). Such impacts, along with other large-scale anthropogenic changes on the biosphere, have highlighted the urgency for careful evaluations of oceanic biodiversity in order to provide baseline information for researchers tasked with monitoring effects of such changes on the biotas. Meaningful estimates of biodiversity, as well as accurate estimates of the faunal composition of noncommercial bycatch in commercial fisheries, depend upon accurate identifications of the taxa involved.

Accurate identifications, however, require detailed systematic studies of the fauna. Uncertainties regarding the taxonomic status of several species of western Atlantic tonguefishes, concomitant with inadequate diagnoses, and until recently, the relative scarcity of representative size series for many deep-sea species, have precluded accurate identifications

for many western Atlantic *Symphurus*. Inherent difficulties with identifications have also prevented detailed comparative study of ecologies and life histories for many tonguefishes occurring in this region. Consequently, despite the fact that *Symphurus* is the most speciose western Atlantic flatfish genus, it has remained, both systematically and ecologically, one of the least known western hemisphere groups of flatfishes, particularly with respect to those species occurring in bathyal regions. Only in the last three decades has intensified study of fish communities inhabiting bathyal regions yielded larger samples of deepwater tonguefishes. However, this material has largely remained unidentified owing to a lack of adequate descriptions and identification keys for most Atlantic *Symphurus* species. Consequently, ecological information associated with these specimens has been minimally assessed.

Objectives of this study are to revise the species of symphurine tonguefishes occurring in the western Atlantic Ocean, including evaluation of all nominal species described previously; to present detailed descriptions, diagnoses, and an identification key for the 24 species herein considered valid; and to summarize available distributional and other ecological data for each species. Early life history stages of *Symphurus* are abundant in ichthyoplankton collections throughout the western Atlantic, but larval series of only a few species have thus far been identified (Olney and Grant, 1976; Kurtz and Matsuura, 1994). Meristic data in this paper, coupled with geographic information for the species, should facilitate identification of larval series for more species.

This work complements earlier revisionary studies on symphurine tonguefishes occurring in the Atlantic Ocean (Ginsburg, 1951; Menezes and Benvegnú, 1976; Munroe, 1990, 1991). Revisionary studies are being presented regionally because of the large number of species in the genus and need for analysis of each species before a phylogenetic study can be accomplished. No phylogenetic hypotheses of relationships for species of *Symphurus* have been proposed, precluding interpretation of geographical or ecological information for this taxon within an historical context. Munroe (1992) recognized nine species groups within *Symphurus* primarily on the basis of shared similarities in interdigitation (ID) patterns. Although some species groups are perhaps not monophyletic, tonguefishes possessing similar ID patterns were found to have additional shared features, thus supporting the hypothesis that species with the same ID pattern are more closely related than those possessing different ID patterns. Species descriptions and discussions of distributional and size-related life history information for the western Atlantic tonguefishes are presented below within the context of these species groups.

## Taxonomic history

At least 34 nominal species of western Atlantic symphurine tonguefishes (Table 1) have been described, commencing with the earliest descriptions of *Pleuronectes plagiusa* Linnaeus, 1766 (=*S. plagiusa*, this study), and *Pleuronectes plagusia* Schneider, in Bloch and Schneider, 1801 (=*S. plagusia*). From the early 1800's until collections were made in deepwater habitats during oceanographic surveys in the 1880's and early 1900's, literature dealing with western Atlantic *Symphurus* consisted almost entirely of nomenclatural rearrangements of previously described taxa with little new information. However, in the mid-1880's, exploration of New World deep-sea environments began in earnest, and major oceanographic expeditions recovered many new species of fishes. Among these were five tonguefishes: *Aphoristia* (=*Symphurus*) *nebulosa*, *A. diomedeana*, *A. pusilla*, *A. marginata*, and *A. pigra*, described in a series of papers by Goode and Bean (1883, 1885b, 1886) and which still represent the majority of deep-sea western North Atlantic tonguefish species.

In 1889, Jordan and Goss evaluated the validity of pleuronectiform species of Europe and the Americas. No new species of tonguefishes were described, but these authors proposed that *Aphoristia nebulosa* (=*S. nebulosus*) differed significantly enough from other tonguefishes to be placed in a separate genus or subgenus (*Acedia*). Also apparent in this and earlier works (Jordan, 1886a, 1886b) is that subtle variations in meristic and morphometric features, characteristic of members of this taxon, were not fully appreciated by these authors. Consequently, characters useful in properly diagnosing the species were not identified. Jordan and Goss, for example, concluded that the western Atlantic *S. pusillus* (Goode and Bean) and *S. diomedeanus* (Goode and Bean) were probably not distinct species but represented geographically variable populations of the common, abundant inshore species *S. plagiusa* (Linnaeus). Likewise, they also considered the eastern Pacific species *S. elongatus* (Günther) and *S. atricaudus* (Jordan and Gilbert) as probably being geographic variants of the tropical western Atlantic *S. plagusia* (Schneider, in Bloch and Schneider). These taxa are all now regarded as distinct species (Munroe, 1992).

Later, Jordan and Evermann (1898) reviewed published information and evaluated the status of tonguefishes occurring in northern and central re-

**Table 1**

Status of specific and subspecific names and new combinations assigned to western Atlantic species of *Symphurus* in chronological order. (Original authorship, generic placement, and spelling are maintained in the table.)

| Taxon | Status |
|---|---|
| *Plagusia* Browne, 1756 | nonbinomial (rejected) |
| *Pleuronectes plagiusa* Linnaeus, 1766 | *S. plagiusa* |
| *Pleuronectes plagusia* Browne, 1789 | (rejected) |
| *Pleuronectes plagusia* Schneider, in Bloch and Schneider, 1801 (after Browne) | *S. plagusia* |
| *Achirus ornatus* Lacepède, 1802 | nomen dubium |
| *Plagusia ornata* Cuvier, 1816 | *?S. tessellatus* |
| *Plagusia tessellata* Quoy and Gaimard, 1824 | *S. tessellatus* |
| *Plagusia brasiliensis* Agassiz, 1829 | *S. tessellatus* |
| *Plagusia fasciata* DeKay, 1842 | *S. plagiusa* |
| *Aphoristia ornata* Kaup, 1858 (n. comb.) | *?S. tessellatus* |
| *Glossichthys plagiusa* Gill, 1861 (n. comb.) | *S. plagiusa* |
| *Plagusia plagiusa* Gill, 1864 (n. comb.) | *S. plagiusa* |
| *Aphoristia nebulosa* Goode and Bean, 1883 | *S. nebulosus* |
| *Aphoristia diomedeana* Goode and Bean, 1885 | *S. diomedeanus* |
| *Aphoristia pusilla* Goode and Bean, 1885 | *S. pusillus* |
| *Aphoristia marginata* Goode and Bean, 1886 | *S. marginatus* |
| *Aphoristia pigra* Goode and Bean, 1886 | *S. piger* |
| *Acedia nebulosa* Jordan and Goss, 1889 (n. comb.) | *S. nebulosus* |
| *Aphoristia fasciata* (not DeKay) Goode and Bean, 1895 | *S. tessellatus* |
| *Symphurus jenynsi* Evermann and Kendall, 1907 | *S. jenynsi* |
| *Symphurus bergi* Thompson, 1916 | *S. jenynsi* |
| *Symphurus trewavasae* Chabanaud, 1948 | *S. trewavasae* |
| *Symphurus sumptuosus* Chabanaud, 1948 | *S. diomedeanus* |
| *Symphurus minor* Ginsburg, 1951 | *S. minor* |
| *Symphurus parvus* Ginsburg, 1951 | *S. parvus* |
| *Symphurus pelicanus* Ginsburg, 1951 | *S. pelicanus* |
| *Symphurus pterospilotus* Ginsburg, 1951 | *S. diomedeanus* |
| *Symphurus civitatum* Ginsburg, 1951 | *S. civitatium* |
| *Symphurus urospilus* Ginsburg, 1951 | *S. urospilus* |
| *Symphurus ommaspilus* Böhlke, 1961 | *S. ommaspilus* |
| *Symphurus rhytisma* Böhlke, 1961 | *S. rhytisma* |
| *Symphurus arawak* Robins and Randall, 1965 | *S. arawak* |
| *Symphurus kyaropterygium* Menezes and Benvegnú, 1976 | *S. kyaropterygium* |
| *Symphurus ginsburgi* Menezes and Benvegnú, 1976 | *S. ginsburgi* |
| *Symphurus meridionalis* Lema and Oliveira, 1977 | *S. jenynsi* |
| *Symphurus oculellus* Munroe, 1991 | *S. oculellus* |
| *Symphurus caribbeanus* Munroe, 1991 | *S. caribbeanus* |
| *Symphurus billykrietei* n. sp. | *S. billykrietei* |
| *Symphurus stigmosus* n. sp. | *S. stigmosus* |

gions of the New World. They described no new species, but contrary to Jordan and Goss (1889), *S. pusillus*, *S. diomedeanus*, *S. elongatus*, and *S. atricaudus* were recognized as distinct species. It is evident, however, that these authors were still influenced by earlier conclusions presented in Jordan and Goss (1889) because Jordan and Evermann hypothesized that *S. pusillus* and *S. diomedeanus* were closely related to *S. plagiusa* (Linnaeus). A more recent hypothesis (Munroe, 1992) indicates that *S. pusillus* belongs to a species group distinct from that including *S. diomedeanus* and *S. plagiusa*.

Four additional nominal species of *Symphurus* from western South Atlantic localities were described during the first half of this century. In 1907, Evermann and Kendall described *S. jenynsi* from Argentina, and Thompson (1916) described *S. bergi* (=*S. jenynsi*) from the same geographic area. Later, Chabanaud (1948a) described *S. trewavasae* and *S. sumptuosus* (=*S. diomedeanus*) from off Brazil and Uruguay, respectively.

In 1951, Ginsburg published the first revision of western Atlantic tonguefishes since that of Jordan and Evermann (1898). He recognized 15 nominal species of western Atlantic tonguefishes, including six previously undescribed. Five of the new species (*S. civitatum*, *S. minor*, *S. parvus*, *S. pelicanus*, and *S. urospilus*) were described on the basis of material

from the Caribbean Sea and more northern areas, whereas *S. pterospilotus* (=*S. diomedeanus*; see Menezes and Benvegnú, 1976; this study) was described from a single specimen taken off Uruguay. In addition to describing new species, Ginsburg diagnosed the genus, evaluated taxonomic characters considered important for identifying tonguefishes, and updated information on distributions and diagnostic features for all 15 nominal species that he recognized.

Despite these important contributions, Ginsburg's study was limited because his treatment (particularly of deep-sea, southern Caribbean Sea, and South Atlantic species) was constrained by insufficient material. In addition, Ginsburg relied almost exclusively on external characters (primarily fin-ray counts) to identify and diagnose his specimens and therefore was unable to resolve problems involving externally phenetically similar species that differ unambiguously in internal characters, such as interdigitation patterns and vertebral numbers (Munroe, 1987).

Soon after Ginsburg's revision, two species (*S. ommaspilus* and *S. rhytisma*) of shallow-water, dwarf tonguefishes were discovered in the Caribbean on patches of sand adjacent to coral reefs (Böhlke, 1961). In 1965, Robins and Randall described *S. arawak*, a third species of dwarf tonguefish collected in similar habitats.

The first significant revision of western South Atlantic tonguefishes was by Menezes and Benvegnú (1976), who studied primarily tonguefishes occurring along the eastern coast of South America, although including comparative material from elsewhere in the western Atlantic whenever possible. Two new species (*S. kyaropterygium* and *S. ginsburgi*), collected from moderate depths on the continental shelf off southern Brazil, were described in their work, and *S. pterospilotus* Ginsburg was placed in the synonymy of *S. diomedeanus* (Goode and Bean). Menezes and Benvegnú's study complemented that of Ginsburg (1951), but the regional nature and limited study material of this revision prevented resolution of the status of several nominal species of western Atlantic tonguefishes.

In 1977, Lema and Oliveira published a key to western Atlantic species of *Symphurus*, based almost entirely on information (primarily counts of fin rays) gathered from published literature accounts. In addition to their identification key, these authors discussed the distribution of symphurine tonguefishes in southern Brazilian waters and described *S. meridionalis* (=*S. jenynsi*, see below) from shallow waters on the inner continental shelf off southern Brazil.

The most recent systematic treatment of Atlantic symphurine tonguefishes is that of an unpublished dissertation (Munroe, 1987), in which 23 species, including three new ones, were recognized in the western Atlantic. Five of these 23, including two undescribed species (now *S. oculellus* and *S. caribbeanus*), represent the Atlantic members of the *S. plagusia* complex and were documented earlier (Munroe, 1991). The present study expands upon earlier research on this group of fishes. It includes one previously undescribed species in addition to those reported in Munroe (1987), and it provides additional information on Atlantic members of the *S. plagusia* complex.

Western Atlantic tonguefishes belong to the same species groups as eastern Atlantic and eastern Pacific tonguefishes, and several species pairs, comprising a western Atlantic species and another species from these areas, are hypothesized. No western Atlantic *Symphurus* species occur in these other areas; therefore, detailed comparisons distinguishing western Atlantic tonguefishes from species occurring in other geographic regions are provided only among phenetically similar species or hypothesized species pairs. Comparative information on eastern Atlantic tonguefishes is found in Munroe (1990, 1992), whereas Munroe and Mahadeva (1989), Mahadeva and Munroe (1990), Munroe and Nizinski (1990), Munroe et al. (1991), Munroe (1992), and Munroe et al. (1995) provide data for eastern Pacific tonguefishes. Among western Atlantic tonguefishes, only *S. nebulosus* has a pterygiophore interdigitation pattern (1-2-2) commonly found in Indo-West Pacific tonguefishes (Munroe, 1992). Therefore, all western Atlantic tonguefishes, except *S. nebulosus*, are readily distinguished from those of the Indo-West Pacific region by differences in ID patterns (Munroe, 1992), and no further comparisons between species from western Atlantic and Indo-Pacific regions are necessary to distinguish the species.

## Methods and materials

### Counts and measurements (Figs. 1–5)

Descriptions of pigmentation are based on formalin-fixed fishes stored in alcohol. In text and tables (whenever possible), species that share a common interdigitation pattern (Fig. 1, A–E) are grouped together and arranged alphabetically within this grouping. The order of presentation begins with *S. nebulosus*, the only western Atlantic species with a 1-2-2 interdigitation pattern; then follow species with the 1-3-2 pattern, unpigmented peritoneum, and four

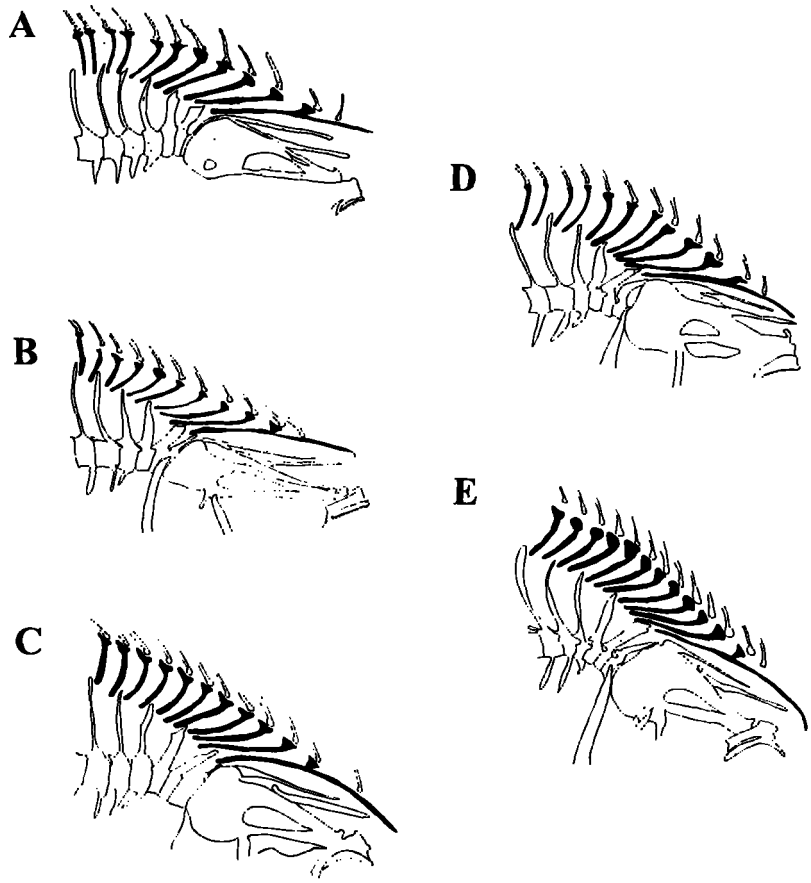


**Figure 1**

Blind-side view of five predominant interdigitation patterns of anterior proximal dorsal-fin pterygiophores (in black), and neural spines found in western Atlantic species of *Symphurus* (skull at right). (**A**) 1-2-2 pattern (only *S. nebulosus*). (**B**) 1-3-2 pattern (9 species). (**C**) 1-3-3 pattern (only *S. trewavasae*). (**D**) 1-4-2 pattern (4 species). (**E**) 1-4-3 pattern (9 species).

hypurals; species with 1-3-2 pattern, pigmented peritoneum, and four hypurals, with newly described species presented first; those with 1-3-2 pattern, pigmented peritoneum, and five hypurals; *S. trewavasae* with the 1-3-3 pattern; four species with a 1-4-2 pattern (three with shared pigmentation pattern followed by *S. ommaspilus*); and nine species with the 1-4-3 pattern, arranged alphabetically in subgroups of increasing numbers (10, 11, 12) of caudal-fin rays.

In the species accounts, only total ranges for meristic features are presented; modal counts can be found in the tables. Variation in meristic features of widely distributed species were examined for specimens collected throughout the geographic range of the species. Although statistically significant intraspecific differences were not apparent in features examined, meristic data, partitioned by geographic region, were tabulated to facilitate identifications. Some sympatric species have nearly complete overlap in meristic features when data are summarized for specimens collected throughout their entire ranges. However, when meristic data for specimens within smaller geographic regions are examined more closely, the amount of overlap in counts between some pairs of co-occurring species was found to be less, and thus counts of meristic features were more informative, thereby facilitating identifications.

Material examined for western Atlantic species is listed in the Appendix. Specimens of species occurring in other regions and used in comparative analyses were listed in Munroe (1990, 1992).

**Interdigitation pattern (ID)** Patterns of interdigitation of proximal dorsal pterygiophores and neural spines (Fig. 1, A–E) were counted and recorded (Table 2) according to the methods of Munroe (1992) for the

**Table 2**

Number of specimens with predominant interdigitation patterns (ID pattern) of dorsal pterygiophores and neural spines in western Atlantic species of *Symphurus*.

| | ID Pattern | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| Species | 1-2-2 | 1-3-2 | 1-3-3 | 1-4-2 | 1-4-3 | 1-5-2 | 1-5-3 | Other |
| *nebulosus* | 22 | — | — | — | — | — | — | 5 |
| *arawak* | 1 | 35 | 1 | — | — | — | — | 4 |
| *rhytisma* | — | 9 | — | — | — | — | — | 0 |
| *ginsburgi* | — | 56 | 1 | 1 | — | — | — | 2 |
| *billykrietei* | — | 89 | 3 | — | — | — | — | 0 |
| *stigmosus* | — | 12 | — | — | — | — | — | 0 |
| *pusillus* | — | 22 | 1 | — | — | — | — | 2 |
| *pelicanus* | — | 56 | 1 | — | — | — | — | 3 |
| *marginatus* | 2 | 77 | 11 | — | — | — | — | 9 |
| *piger* | 2 | 137 | 1 | — | — | — | — | 1 |
| *trewavasae* | — | 4 | 49 | 11 | 3 | — | — | 6 |
| *kyaropterygium* | — | — | 1 | 13 | — | — | — | 0 |
| *minor* | — | 2 | — | 74 | 1 | — | — | 1 |
| *parvus* | — | 1 | — | 33 | 6 | 35 | — | 5 |
| *ommaspilus* | — | — | — | 28 | — | — | — | 0 |
| *diomedeanus* | — | — | 9 | 13 | 160 | 6 | 13 | 17 |
| *jenynsi* | — | — | 4 | 2 | 62 | 2 | 6 | 10 |
| *plagiusa* | — | — | 22 | 24 | 85 | 4 | 1 | 5 |
| *urospilus* | — | — | 4 | 8 | 74 | 15 | 4 | 5 |
| *plagusia* | — | — | 5 | 2 | 33 | — | 1 | 3 |
| *civitatium* | — | — | 8 | 19 | 128 | 7 | 3 | 6 |
| *tessellatus* | — | — | 10 | 11 | 209 | 3 | 15 | 30 |
| *oculellus* | — | — | 2 | 2 | 55 | — | 3 | 2 |
| *caribbeanus* | — | — | 8 | — | 69 | 2 | — | 5 |

first three, or in unusual cases, the first five interneural spaces. Only data for occurrence of predominant patterns are reported here (additional information on variation in this character was presented in Munroe, 1992). The number of dorsal pterygiophores inserted into interneural spaces 1–3 was found to be diagnostic for species or groups of species of *Symphurus* (Munroe, 1987; 1992). Interdigitation patterns are recorded as a formula, such as 1-3-2 (Fig. 1B), indicating that one pterygiophore inserts into interneural space one, three into interneural space two, and two into interneural space three. The first neural spine abuts directly against the cranium so that there is no obvious space between it and the cranium. Therefore, the first interneural space reflected in the formula is that between the first and second neural spines.

**Caudal-fin rays (Table 3)** Previous authors (Ginsburg, 1951; Mahadeva, 1956; Menezes and Benvegnú, 1976; Munroe, 1987, 1990, 1991) have found that the caudal-fin ray count is extremely conservative within species of this genus. Previous studies have included the ultimate dorsal- and anal-fin rays, which lie on the same vertical plane as the caudal-fin rays (Fig. 4, B–C), in the caudal-fin ray counts. This method is followed in the present study. Counts are usually even numbers (10, 12, 14) and rarely odd numbers (11 in *S. urospilus*).

**Dorsal (Table 4) and anal-fin rays (Table 5)** These include all rays except the ultimate ray. The thick, muscular gonadal duct preceding the first anal-fin ray is not counted.

**Vertebral counts (Table 6)** All western Atlantic *Symphurus* consistently have nine abdominal vertebrae, three without and six with haemopophyses; abdominal vertebral counts are thus reported as (3+6). Counts of total vertebrae include the urostylar centrum.

**Hypural counts (Fig. 4, B–C)** These include all separate hypurals without any implied interpretation of the fate (fused or lost during ontogeny) of the fifth hypural, which may not always be present as a separate element.

**Scale counts (Fig. 2D)** Accurate, repeatable scale counts are difficult to make on species of *Symphurus*,

**Table 3**

Frequency distribution of numbers of caudal-fin rays for western Atlantic *Symphurus* species.

| | Number of caudal-fin rays | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Species | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 |
| *nebulosus* | — | — | — | — | — | 2 | 24 | — | 1 |
| *arawak* | — | — | — | 3 | 38 | 1 | 1 | — | — |
| *rhytisma* | — | — | — | — | 9 | — | — | — | — |
| *ginsburgi* | — | 1 | 2 | 2 | 49 | 1 | — | — | — |
| *billykrietei* | — | — | — | 6 | 84 | 1 | — | — | — |
| *stigmosus* | — | — | — | 1 | 11 | — | — | — | — |
| *pusillus* | — | — | — | — | 26 | — | — | — | — |
| *pelicanus* | — | — | 1 | 4 | 50 | 1 | — | — | — |
| *marginatus* | — | — | — | 3 | 98 | 1 | — | — | — |
| *piger* | — | — | 2 | 2 | 134 | 1 | — | — | — |
| *trewavasae* | — | — | 73 | — | — | — | — | — | — |
| *kyaropterygium* | — | — | 13 | 1 | — | — | — | — | — |
| *minor* | 1 | 1 | 74 | 3 | — | — | — | — | — |
| *parvus* | — | 3 | 70 | 3 | — | — | — | — | — |
| *ommaspilus* | — | — | 28 | — | — | — | — | — | — |
| *diomedeanus* | — | 9 | 202 | 1 | 1 | — | — | — | — |
| *jenynsi* | — | 3 | 78 | — | — | — | — | — | — |
| *plagiusa* | — | 5 | 132 | 2 | — | — | — | — | — |
| *urospilus* | — | 1 | 4 | 108 | — | — | — | — | — |
| *plagusia* | — | — | — | 2 | 41 | 1 | — | — | — |
| *civitatium* | — | — | — | 8 | 164 | — | — | — | — |
| *tessellatus* | — | — | 4 | 17 | 249 | 3 | — | — | — |
| *oculellus* | — | — | — | 4 | 59 | — | — | — | — |
| *caribbeanus* | — | — | 1 | 2 | 81 | 1 | — | — | — |

especially for those specimens collected by trawls at considerable depths, because scales are often abraded and lost. For specimens missing scales, approximate counts were based on partial scale counts, counts of scale pockets, or on a combination of the two whenever possible. Longitudinal scale count (Table 7) includes the total number of complete diagonal rows of scales along a hypothetical line starting immediately above the opercular angle and continuing posteriorly along the middle of the body to the end of the hypural plate (Fig. 2D, number 1); the few rows of scales along the caudal-fin base are not included, and the last scale to be included in the count must be at least half way in front of the hypural plate. The head scale count (Table 8) includes all oblique rows of scales on the head counted posteriorly from the first complete row of scales immediately behind the posterior border of the lower eye (Fig. 2D, number 2); it includes the last complete row of scales immediately anterior to the midpoint emargination on the posterior border of the operculum, but the few small rows of scales present on either the dorsal or ventral fleshy lobes of the operculum are not included. The transverse scale count (Table 9) is the number of scales in a diagonal row from the base of the dorsal fin at a point directly above the posterior margin of the operculum to the base of the anal fin (Fig. 2D, number 3). Scales extending out onto the dorsal- and anal-fin rays are not included.

Measurements were made either on ocular- or blind-side surfaces (Fig. 2, A–C). All measurements in the text refer to standard length, unless otherwise noted. Measurements less than 150 mm were taken to the nearest 0.1 mm with dial calipers or an ocular micrometer. Measurements over 150 mm were taken to the nearest mm with a steel ruler. Morphometric features are expressed either as measurements in thousandths of standard length (SL) or thousandths of head length (HL) and are defined as follows: Standard length (SL): distance from tip of fleshy snout to posterior end of hypural plate. Trunk length (TKL; not measured on all species): longitudinal distance from posterior angle of operculum to caudal-fin base. Body depth (BD): distance across body at the anus, exclusive of fins; measured on blind side. Preanal length (PAL): tip of fleshy snout to origin of anal fin; measured on blind side. Dorsal-fin length (DBL): base of anteriormost dorsal-fin ray to posterior end of hypural plate. Predorsal length (PDL): tip of fleshy snout to base of first dorsal-fin ray. Anal-fin length (ABL): base of anteriormost anal-fin ray to posterior end of hypural plate. Caudal-fin

## Table 4

**Frequency distributions of numbers of dorsal-fin rays for western Atlantic *Symphurus* species.**

| Species | Number of dorsal-fin rays | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 69 | 70 | 71 | 72 | 73 | 74 | 75 | 76 | 77 | 78 | 79 | 80 | 81 | 82 | 83 | 84 | 85 | 86 | 87 | 88 | 89 | 90 | 91 | 92 | 93 | 94 | 95 | 96 | 97 | 98 | 99 | 100 | 101 | 102 | 103 | 104 | 105 | 106 | 107 | 108 | 109 | 110 | 111 | 112 | 113 | 114 | 115 |
| *nebulosus* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | — | 2 | 8 | 7 | 6 | 2 | — | 1 | — | — |
| *arawak* | — | 2 | 5 | 7 | 11 | 15 | 5 | 1 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *rhytisma* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 4 | 2 | 2 | — | 1 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *billykrietei* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | 1 | 12 | 23 | 33 | 20 | 2 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *stigmosus* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | 5 | 6 | 1 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *ginsburgi* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | 2 | — | 4 | 10 | 13 | 21 | 5 | 3 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *pelicanus* | — | — | — | — | — | — | — | — | 1 | 4 | 4 | 18 | 15 | 9 | 7 | 1 | 1 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *pusillus* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | 1 | 5 | 9 | 7 | 6 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *marginatus* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 2 | 2 | 6 | 10 | 18 | 18 | 21 | 17 | 6 | 1 | 1 | 1 | — | — | — | — | — | — | — | — | — | — | — |
| *piger* | — | — | — | — | — | — | — | — | — | — | — | 1 | 1 | 1 | 8 | 16 | 41 | 45 | 24 | 4 | — | 1 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *trewavasae* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 2 | 8 | 17 | 20 | 18 | 2 | 4 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *kyaropterygium* | — | — | — | — | — | — | — | — | — | — | — | 1 | — | — | 1 | 6 | 2 | 3 | 1 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *minor* | 1 | 1 | 1 | 15 | 17 | 21 | 9 | 6 | 5 | — | 2 | — | 1 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *parvus* | — | — | — | — | — | — | 1 | 2 | 4 | 9 | 5 | 10 | 19 | 9 | 13 | 4 | 1 | 2 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *ommaspilus* | — | — | — | — | — | — | 4 | 6 | 11 | 6 | 1 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *diomedeanus* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | 3 | 10 | 26 | 43 | 59 | 45 | 24 | 5 | 1 | 1 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *jenynsi* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | 5 | 9 | 20 | 15 | 19 | 9 | 7 | 3 |
| *plagiusa* | — | — | — | — | — | — | — | — | — | — | — | — | 1 | — | 2 | 9 | 9 | 12 | 26 | 31 | 36 | 9 | 3 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *urospilus* | — | — | — | — | — | — | — | — | — | — | — | — | — | 2 | 5 | 16 | 29 | 24 | 22 | 10 | 5 | 1 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *caribbeanus* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | — | 2 | 13 | 29 | 25 | 9 | 6 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *civitatium* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 2 | 3 | 14 | 33 | 49 | 46 | 23 | 1 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *plagusia* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | — | 5 | 11 | 12 | 4 | 5 | 5 | 1 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *oculellus* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 2 | — | 4 | 12 | 21 | 13 | 9 | 2 | — | 1 | — | — | — | — | — | — | — | — | — |
| *tessellatus* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 2 | 2 | 7 | 18 | 44 | 34 | 60 | 45 | 39 | 21 | 9 | 1 | — | — | — | — | — | — | — | — | — | — | — | — | — |

## Table 5

Frequency distributions of the numbers of anal-fin rays for western Atlantic *Symphurus* species.

| Species | 55 | 56 | 57 | 58 | 59 | 60 | 61 | 62 | 63 | 64 | 65 | 66 | 67 | 68 | 69 | 70 | 71 | 72 | 73 | 74 | 75 | 76 | 77 | 78 | 79 | 80 | 81 | 82 | 83 | 84 | 85 | 86 | 87 | 88 | 89 | 90 | 91 | 92 | 93 | 94 | 95 | 96 | 97 | 98 | 99 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *nebulosus* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | — | 2 | 6 | 4 | 7 | 5 | 2 | — |
| *arawak* | 1 | 3 | 3 | 10 | 11 | 12 | 6 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *rhytisma* | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | 2 | 3 | 3 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *billykrietei* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | 10 | 20 | 30 | 20 | 8 | 2 | 1 | 1 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *stigmosus* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 4 | — | 4 | 4 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *ginsburgi* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | 1 | 5 | 11 | 12 | 18 | 8 | 2 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *pelicanus* | — | — | — | — | — | — | — | — | — | 6 | 8 | 13 | 18 | 7 | 5 | 1 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *pusillus* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 4 | 5 | 14 | 2 | 2 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *marginatus* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 5 | 6 | 9 | 21 | 24 | 20 | 11 | 3 | 2 | 2 | — | — | — | — | — | — | — | — | — | — |
| *piger* | — | — | — | — | — | — | — | — | — | — | — | — | — | 3 | 6 | 18 | 47 | 40 | 19 | 7 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *trewavasae* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 2 | 8 | 17 | 23 | 12 | 8 | 2 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *kyaropterygium* | — | — | — | — | — | — | — | — | — | — | — | — | 1 | 1 | 2 | 6 | 3 | 1 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *minor* | 1 | 3 | 7 | 22 | 22 | 11 | 4 | 4 | 2 | 3 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *parvus* | — | — | — | — | — | 1 | 1 | 4 | 7 | 17 | 11 | 19 | 12 | 3 | 2 | 2 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *ommaspilus* | — | — | — | — | — | 2 | 6 | 16 | 2 | 2 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *diomedeanus* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | — | 3 | 8 | 27 | 54 | 64 | 45 | 13 | 3 | — | 2 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *jenynsi* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 2 | 3 | 11 | 25 | 14 | 20 | 8 | 3 | 2 |
| *plagiusa* | — | — | — | — | — | — | — | — | — | — | — | 1 | 4 | 6 | 10 | 12 | 27 | 28 | 35 | 13 | 6 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *urospilus* | — | — | — | — | — | — | — | — | — | 1 | — | 1 | 4 | 20 | 25 | 27 | 24 | 9 | 2 | 1 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *caribbeanus* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | 3 | 6 | 24 | 40 | 6 | 4 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *civitatium* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | 2 | 6 | 34 | 49 | 58 | 20 | 3 | 1 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *oculellus* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | 4 | 5 | 18 | 15 | 14 | 6 | 1 | 2 | — | — | — | — | — | — | — | — | — | — |
| *plagusia* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | — | 5 | 8 | 16 | 6 | 6 | 1 | 1 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *tessellatus* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | 1 | — | 5 | 27 | 37 | 51 | 51 | 51 | 32 | 20 | 4 | 1 | — | — | — | — | — | — | — | — | — | — | — | — | — |

**Table 6**

Frequency distributions of numbers of total vertebrae for western Atlantic *Symphurus* species.

| Species | Number of vertebrae | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 39 | 40 | 41 | 42 | 43 | 44 | 45 | 46 | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 | 60 |
| *nebulosus* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | 9 | 15 | 2 |
| *arawak* | 1 | 17 | 21 | 6 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *rhytisma* | — | — | — | — | — | — | — | 1 | 6 | 2 | — | — | — | — | — | — | — | — | — | — | — | — |
| *billykrietei* | — | — | — | — | — | — | — | — | — | — | — | 9 | 49 | 33 | 2 | — | — | — | — | — | — | — |
| *stigmosus* | — | — | — | — | — | — | — | — | — | — | — | — | 5 | 7 | — | — | — | — | — | — | — | — |
| *ginsburgi* | — | — | — | — | — | — | — | — | — | — | — | 7 | 38 | 13 | — | — | — | — | — | — | — | — |
| *pelicanus* | — | — | — | — | 1 | 7 | 25 | 27 | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *pusillus* | — | — | — | — | — | — | — | — | 4 | 15 | 10 | — | — | — | — | — | — | — | — | — | — | — |
| *marginatus* | — | — | — | — | — | — | — | — | — | — | — | — | 1 | 17 | 35 | 41 | 2 | 2 | — | — | — | — |
| *piger* | — | — | — | — | — | — | 1 | 4 | 48 | 80 | 11 | — | — | — | — | — | — | — | — | — | — | — |
| *trewavasae* | — | — | — | — | — | — | — | — | 3 | 25 | 31 | 8 | 3 | — | — | — | — | — | — | — | — | — |
| *kyaropterygium* | — | — | — | — | — | — | — | 1 | 9 | 3 | 1 | — | — | — | — | — | — | — | — | — | — | — |
| *minor* | — | — | 11 | 45 | 19 | 4 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *parvus* | — | — | — | — | 1 | 13 | 23 | 34 | 7 | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *ommaspilus* | — | — | — | — | 10 | 16 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *diomedeanus* | — | — | — | — | — | — | — | — | 4 | 50 | 131 | 34 | — | — | — | — | — | — | — | — | — | — |
| *jenynsi* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 4 | 37 | 36 | 11 |
| *plagiusa* | — | — | — | — | — | 1 | 16 | 30 | 69 | 26 | 1 | — | — | — | — | — | — | — | — | — | — | — |
| *urospilus* | — | — | — | — | — | 3 | 54 | 49 | 7 | 1 | — | — | — | — | — | — | — | — | — | — | — | — |
| *caribbeanus* | — | — | — | — | — | — | — | — | — | 1 | 43 | 33 | 5 | — | — | — | — | — | — | — | — | — |
| *civitatium* | — | — | — | — | — | — | — | 2 | 34 | 109 | 28 | 2 | — | — | — | — | — | — | — | — | — | — |
| *oculellus* | — | — | — | — | — | — | — | — | — | — | — | — | — | 6 | 35 | 20 | 2 | — | — | — | — | — |
| *plagusia* | — | — | — | — | — | — | — | — | 1 | 4 | 21 | 13 | 5 | — | — | — | — | — | — | — | — | — |
| *tessellatus* | — | — | — | — | — | — | — | — | — | 1 | 3 | 52 | 97 | 89 | 37 | 3 | — | — | — | — | — | — |

length (CFL): base of articulations of middle caudal-fin rays to tip of longest middle rays. Pelvic-fin length (PL); (only blind-side pelvic fin present in adults): basal articulation to distal tip of longest ray. Pelvic to anal length (PA): shortest horizontal distance from base of most posterior pelvic-fin ray to anal-fin origin. Head length (HL): tip of fleshy snout to most posterior extension of upper fleshy lobe of operculum. Head width (HW): greatest distance across head at posterior portion of operculum. Postorbital head length (POL): posterior margin of lower eye to posterior extent of upper fleshy lobe of operculum. Upper head lobe width (UHL): distance at operculum from dorsal margin of body to dorsal origin of operculum. Lower head lobe width (LHL): distance at operculum from dorsal origin of operculum to most ventral part of operculum. Snout length (SNL): anterior rim of lower eye to tip of snout. Upper jaw length (UJL): shortest horizontal distance from bony tip of premaxilla to angle of mouth. Eye diameter (ED): greatest horizontal diameter of the cornea of the lower eye; does not include fleshy tissue surrounding eye. Chin depth (CD): vertical distance from angle of mouth to most ventral aspect of head. Upper opercular lobe (OPUL): vertical distance from midpoint of opercular indentation to dorsal origin of operculum. Lower opercular lobe (OPLL): vertical distance from midpoint of opercular indentation to ventral margin of operculum.

## Qualitative characters

The following qualitative characters are also important in identifying *Symphurus*, especially when used in combination with meristic and morphometric data.

**Pupillary operculum (Fig. 3A)** A triangular or rounded, pigmented structure on the upper part of the cornea. A presumed function of the pupillary operculum is to shade the retina from direct exposure to light. Chabanaud (1948a), Ginsburg (1951), and Menezes and Benvegnú (1976) did not use this character in their studies on Atlantic tonguefishes. Mahadeva (1956) and Munroe (1987), however, found this character useful for diagnosing some eastern Pacific and Atlantic species. For example, a pupillary operculum is not found in any eastern Atlantic tonguefish nor in any western Atlantic deepwater species, and its absence is useful in distinguishing these *Symphurus* from other western Atlantic species with similar meristic and morphometric features but which possess a well-developed pupillary operculum.

**Jaw position (Fig. 3, A–E)** Relative position of the posteriormost point of the jaws with respect to the lower eye is useful in diagnosing some species. Five different positions of the posterior margin of the jaws were evident among the species. Species with short jaws were those with the posterior margin of the jaws at the anterior margin of the eye. Those with moderately long jaws have the posterior margin at the mideye region or at the posterior margin of the pupil. Species with long jaws are those with the posterior margin of the jaws at, or beyond, the vertical through the posterior margin of the eye.

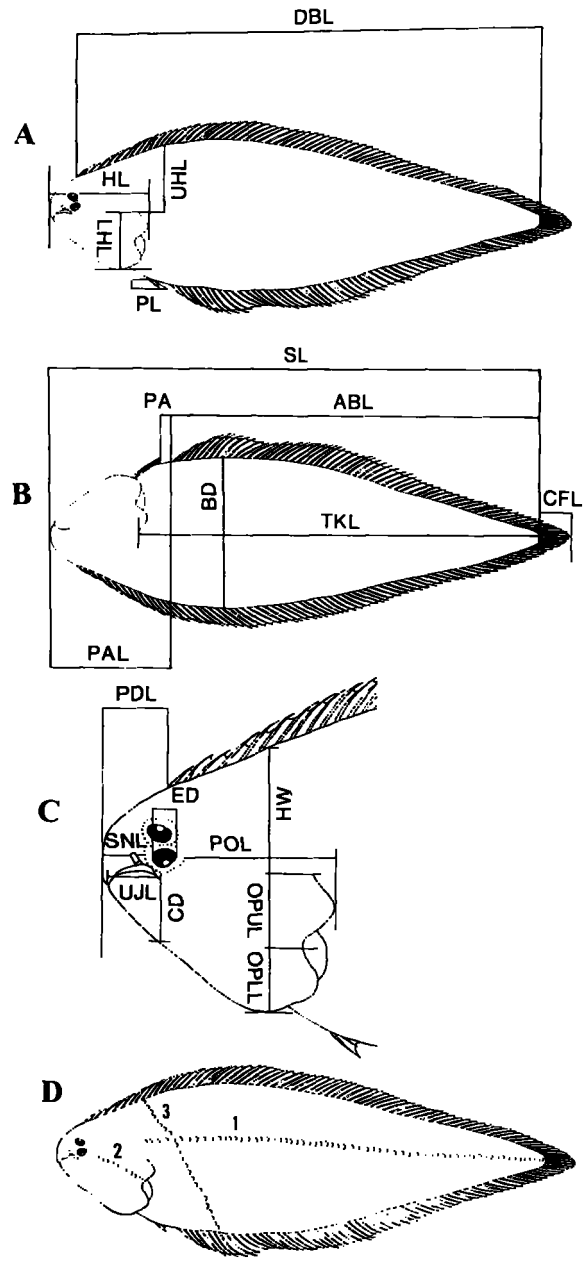


**Figure 2**

Body and head locations where measurements and scale counts (defined in text) were taken. Abbreviations are defined in "Counts and measurements" section. (**A**) Measurements made on ocular side of body. (**B**) Measurements made on blind side of body. (**C**) Measurements made on ocular side of head. (**D**) Scale count locations: 1 = longitudinal scale count; 2 = head scale count; 3 = lateral scale count.

**Dentition on ocular-side jaws** Degree of development of dentition on ocular-side jaws is useful in diagnosing some species. Some species have teeth along the entire margin of both jaws, others have only a partial row of teeth along the margin, and some lack teeth on the ocular-side jaws.

**Fleshy ridge on ocular-side lower jaw (Fig. 3D)** Presence or absence of a fleshy ridge on the ocular-side lower jaw is diagnostic for some species.

**Dorsal-fin origin (Fig. 3, A–F)** Relative position of the dorsal-fin origin with respect to the migrating (upper) eye is useful in identifying some species.

**Squamation on dorsal- and anal-fin rays (Fig. 4A)** Presence and approximate number of scales on dorsal- and anal-fin rays, especially on blind sides of the fin rays, is useful for identifying some species.

**Membrane ostia in dorsal and anal fins** Presence or absence of membrane ostia (small pores) in the basal part of the membranes of the dorsal and anal fins is useful for identifying some species.

**Body pigmentation** Numbers in parentheses refer to numbers on Figure 5, A and B. Ocular surface coloration is unique for some species. Frequently observed pigmentation patterns consist of uniform coloration with or without a bold caudal blotch (7), or patterns featuring a variable number of bold crossbands (2). Some species have the blind side of the body pigmented with a pepper-dot pattern (8) or with median dermal spots (i.e. those located internally along the vertebral column and visible externally (9), but most species usually have uniformly creamy-white or slightly yellowish coloration on the blind side.

**Fin pigmentation** Numbers in parentheses refer to Figure 5A. Pigment patterns on dorsal, anal, and caudal fins distinguish some species. Fin pigmentation showed the following variation: fins uniformly pigmented; fins with blotches (6); fins with rounded (5) or ocellated spots (4); and fins with a longitudinal stripe (3).

**Table 7**

Frequency distributions of the numbers of longitudinal scale rows for western Atlantic *Symphurus* species.

| | Number of scale rows | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | 55 | 56 | 57 | 58 | 59 | 60 | 61 | 62 | 63 | 64 | 65 | 66 | 67 | 68 | 69 | 70 | 71 | 72 | 73 | 74 | 75 | 76 | 77 | 78 | 79 | 80 | 81 | 82 | 83 | 84 | 85 | 86 | 87 | 88 | 89 | 90 |
| *arawak* | 1 | — | 1 | 3 | 4 | 6 | 3 | 7 | 7 | 3 | 1 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *pelicanus* | — | — | — | — | — | — | — | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 1 | 1 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *piger* | — | — | — | — | — | — | — | 1 | — | 3 | 1 | 9 | 9 | 10 | 13 | 13 | 9 | 10 | 6 | 1 | 1 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *trewavasae* | — | — | — | — | — | — | — | — | — | — | — | — | 1 | 1 | 1 | 2 | 4 | 3 | 5 | 12 | 1 | 5 | 3 | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *minor* | 2 | 1 | 3 | 3 | 6 | 9 | 8 | 8 | 6 | 3 | 1 | 1 | 2 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *ommaspilus* | — | — | — | 4 | 1 | 2 | 1 | 8 | 4 | 2 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *parvus* | — | — | — | — | 2 | 2 | 3 | 1 | 5 | 4 | 4 | 5 | 2 | 1 | 2 | 3 | 2 | — | 1 | 4 | 1 | — | — | 1 | — | — | — | — | — | — | — | — | — | — | — | — |
| *kyaropterygium* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 2 | — | 1 | 1 | 3 | — | — | — | 1 | — | — | — | — | — | — | — | — | — |
| *urospilus* | — | — | — | — | — | — | — | — | — | — | — | — | 1 | 2 | 2 | 3 | 5 | 6 | 3 | 5 | 5 | 11 | 5 | 4 | 5 | 4 | 2 | 1 | — | — | — | — | — | — | — | — |
| *civitatium* | — | — | — | — | — | — | — | — | — | — | — | 1 | — | — | — | 2 | — | — | 1 | 4 | 8 | 11 | 5 | 14 | 8 | 7 | 3 | 3 | 1 | — | — | — | — | — | — | — |
| *pusillus* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | 1 | — | 1 | — | — | 3 | 1 | — | — | 1 | — | — | — |
| *plagiusa* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | 2 | 1 | 4 | 2 | 6 | 4 | 2 | 7 | — | 1 | — | — | — | — |
| *plagusia* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | 3 | 2 | 3 | 2 | 2 | 1 | 3 | — | — | 2 | — |
| *caribbeanus* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 3 | — | 4 | 11 | 4 | 3 | 6 | 2 | 2 | 1 | 1 | 3 | — |

| | Number of scale rows | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | 79 | 80 | 81 | 82 | 83 | 84 | 85 | 86 | 87 | 88 | 89 | 90 | 91 | 92 | 93 | 94 | 95 | 96 | 97 | 98 | 99 | 100 |
| *billykrietei* | — | 1 | — | — | — | — | 3 | — | — | 4 | 1 | 1 | — | 4 | 1 | 2 | — | — | — | 2 | 1 | 2 |
| *ginsburgi* | — | — | — | — | — | — | — | — | 2 | 2 | — | 2 | 1 | — | 2 | 2 | — | — | — | — | — | — |
| *stigmosus* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 2 | 1 | 3 |
| *marginatus* | — | — | — | — | — | — | — | 3 | 3 | 5 | 5 | 6 | 6 | 8 | 5 | 6 | 5 | 3 | 1 | 1 | 2 | — |
| *rhytisma* | — | — | — | — | — | — | — | — | — | — | — | — | 1 | 1 | 1 | — | 1 | 1 | 1 | — | — | — |
| *diomedeanus* | 1 | — | — | 1 | 1 | 4 | 5 | 7 | 11 | 12 | 13 | 11 | 8 | 13 | 9 | 3 | 1 | 1 | — | — | — | — |
| *tessellatus* | — | — | 2 | 2 | 8 | 10 | 10 | 11 | 21 | 31 | 21 | 21 | 14 | 5 | 4 | 2 | — | 1 | — | — | — | — |
| oculellus | — | — | — | — | — | 1 | 3 | 1 | 7 | 5 | 2 | 6 | 4 | 2 | — | 1 | — | — | 1 | — | — | — |

| | Number of scale rows | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | 102 | 103 | 104 | 105 | 106 | 107 | 108 | 109 | 110 | 111 | 112 | 113 | 114 | 115 | 116 | 117 | 118 | 119 |
| *jenynsi* | 1 | — | 3 | 2 | 3 | 3 | 1 | 2 | 1 | 3 | 3 | 2 | 2 | 5 | 2 | 1 | — | 1 |

| | Number of scale rows | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | 120 | 121 | 122 | 123 | 124 | 125 | 126 | 127 | 128 | 129 | 130 | 131 | 132 | 133 | 134 | 135 |
| *nebulosus* | 1 | — | — | 1 | 1 | 2 | 2 | — | 4 | 1 | 4 | — | 1 | — | 1 | 1 |

**Peritoneum pigmentation** Relative intensity and coverage of pigmentation on the peritoneum is diagnostic for species especially when used in combination with other characters. Some species have an unpigmented peritoneum; some have a spotted peritoneum; and others have a black peritoneum.

**Opercular pigmentation** Degree of pigmentation on outer and inner surfaces of the opercle and isthmus, in combination with other characters, is useful for identifying some species. Some species have a prominent opercular blotch (Fig. 5A, number 1).

## Ecological assessment

Maturity was estimated by macroscopic examination of extent of posterior elongation of the ovary and presence of developing ova in the ovaries (ovaries of mature females are sometimes conspicuous through the body wall in transmitted light; in immature and large females, ovaries are best observed by dissection). Because no obvious differences in sizes of testes between immature and mature males were apparent, estimates of maturity were based entirely on females (see Figs. 6–9). Immature females were those with

## Table 8

Frequency distributions of the number of scales on the posterior head region for western Atlantic *Symphurus* species.

| | Number of scale rows | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | 28 |
| *nebulosus* | — | — | — | — | — | — | — | 1 | 2 | 4 | 8 | 3 | 1 | — | — | — | — |
| *arawak* | 2 | 6 | 14 | 16 | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *rhytisma* | — | — | — | — | — | — | 4 | 1 | 1 | — | — | — | — | — | — | — | — |
| *billykrietei* | — | — | — | — | 1 | 2 | 3 | 7 | 6 | 3 | 1 | — | — | — | — | — | — |
| *stigmosus* | — | — | — | — | — | — | — | 3 | 2 | 2 | 1 | — | — | — | — | — | — |
| *ginsburgi* | — | — | — | 1 | 2 | 2 | 4 | 5 | 3 | — | — | — | — | — | — | — | — |
| *pelicanus* | — | — | 4 | 2 | 1 | 1 | — | — | — | — | — | — | — | — | — | — | — |
| *pusillus* | — | — | — | — | — | 4 | 3 | 2 | — | — | — | — | — | — | — | — | — |
| *marginatus* | — | — | — | — | 6 | 32 | 25 | 5 | — | — | — | — | — | — | — | — | — |
| *piger* | — | — | — | — | 3 | 28 | 26 | 13 | 1 | 1 | — | — | — | — | — | — | — |
| *trewavasae* | — | — | — | 4 | 23 | 10 | 3 | — | 1 | — | — | — | — | — | — | — | — |
| *kyaropterygium* | — | — | — | — | 4 | 5 | 1 | — | — | — | — | — | — | — | — | — | — |
| *minor* | 2 | 13 | 23 | 12 | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *parvus* | — | 1 | 5 | 20 | 8 | 4 | 1 | — | — | — | — | — | — | — | — | — | — |
| *ommaspilus* | — | — | 5 | 9 | 6 | 3 | — | — | — | — | — | — | — | — | — | — | — |
| *diomedeanus* | — | — | — | — | 11 | 25 | 32 | 29 | 3 | 2 | — | — | — | — | — | — | — |
| *jenynsi* | — | — | — | — | — | — | — | — | — | 2 | 15 | 12 | 5 | 1 | — | — | — |
| *plagiusa* | — | — | — | 1 | 2 | 17 | 8 | 3 | — | — | — | — | — | — | — | — | — |
| *urospilus* | — | 2 | 11 | 25 | 26 | 3 | — | — | — | — | — | — | — | — | — | — | — |
| *caribbeanus* | — | — | — | — | — | 1 | 1 | 9 | 16 | 8 | 3 | — | — | — | — | — | — |
| *civitatium* | — | — | — | — | 3 | 18 | 32 | 16 | 3 | — | — | — | — | — | — | — | — |
| *oculellus* | — | — | — | — | — | — | — | 3 | 8 | 1 | 1 | 2 | — | — | — | — | — |
| *plagusia* | — | — | — | — | — | — | 8 | 4 | 8 | 2 | 1 | — | — | — | — | — | — |
| *tessellatus* | — | — | — | — | — | — | 1 | — | 8 | 8 | 4 | 1 | — | — | — | — | — |

## Table 9

Frequency distributions of the number of lateral rows of scales for western Atlantic *Symphurus* species.

| | Number of lateral scale rows | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 | 45 | 46 | 47 | 48 | 49 | 50 | 51 |
| *nebulosus* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | 1 | 1 | 1 | 1 | — | 3 | 1 | — |
| *arawak* | — | — | — | 1 | — | 1 | — | 1 | 9 | 9 | 5 | 4 | 8 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *rhytisma* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 2 | 2 | 1 | — | — | — | — | — | — |
| *billykrietei* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | — | 1 | 1 | — | — | — | 1 | 1 | — | — | 1 | — | — |
| *stigmosus* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | — | — | — | — | 2 | 1 | — | — | 1 | — | — |
| *ginsburgi* | — | — | — | — | — | — | — | — | 1 | — | — | 1 | — | 2 | 1 | 2 | 1 | 4 | 1 | — | 1 | — | — | — | — | — | — | — |
| *pelicanus* | 2 | 1 | 5 | — | 1 | 1 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *pusillus* | — | — | — | — | — | — | — | — | — | 1 | 1 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *marginatus* | — | — | — | — | — | — | 3 | 1 | 1 | — | 2 | 3 | — | 1 | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *piger* | — | — | — | — | — | — | — | — | 1 | 2 | 2 | 5 | 3 | 2 | 2 | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *trewavasae* | — | — | — | — | — | — | — | 1 | 2 | 8 | 11 | 9 | — | 2 | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *kyaropterygium* | — | — | — | — | — | — | — | — | — | — | — | — | 4 | 3 | — | 2 | — | — | — | — | — | — | — | — | — | — | — | — |
| *minor* | 1 | 2 | 2 | 1 | 3 | 6 | 7 | 7 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *parvus* | — | — | 2 | — | 1 | 2 | 5 | 4 | 5 | 2 | 2 | 1 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *ommaspilus* | — | — | — | 1 | — | 6 | 5 | 5 | 2 | 1 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *diomedeanus* | — | — | — | — | — | — | — | — | — | — | 2 | 2 | 3 | 4 | 12 | 15 | 16 | 7 | 3 | 4 | 4 | 1 | 1 | 1 | — | — | — | — |
| *jenynsi* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | 1 | 1 | 3 | 6 | 6 | 7 | 5 | 2 | — | 1 |
| *plagiusa* | — | — | — | — | — | — | 1 | — | — | 2 | 2 | 5 | 4 | 6 | 6 | 4 | — | — | — | — | — | — | — | — | — | — | — | — |
| *urospilus* | — | — | — | 1 | — | 1 | 2 | 8 | 15 | 11 | 13 | 3 | 3 | 1 | 8 | 7 | 8 | — | — | — | — | — | — | — | — | — | — | — |
| *caribbeanus* | — | — | — | — | — | — | — | — | — | — | — | — | 2 | 3 | 6 | 10 | 3 | 6 | 2 | 1 | 1 | — | — | — | — | — | — | — |
| *civitatium* | — | — | 2 | 1 | 2 | — | 2 | 5 | 4 | 6 | 2 | 11 | 5 | 6 | 6 | 1 | — | — | — | — | — | — | — | — | — | — | — | — |
| *oculellus* | — | — | — | — | — | — | — | — | — | — | — | — | 1 | 1 | 6 | 2 | 2 | 1 | 1 | — | — | — | — | — | — | — | — | — |
| *plagusia* | — | — | — | — | — | — | — | — | — | — | — | 1 | — | — | 2 | 3 | 7 | 3 | 3 | 1 | — | — | — | — | — | — | — | — |
| *tessellatus* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | 2 | 4 | 5 | 2 | 1 | 3 | 2 | — | — | — | — | — | — |

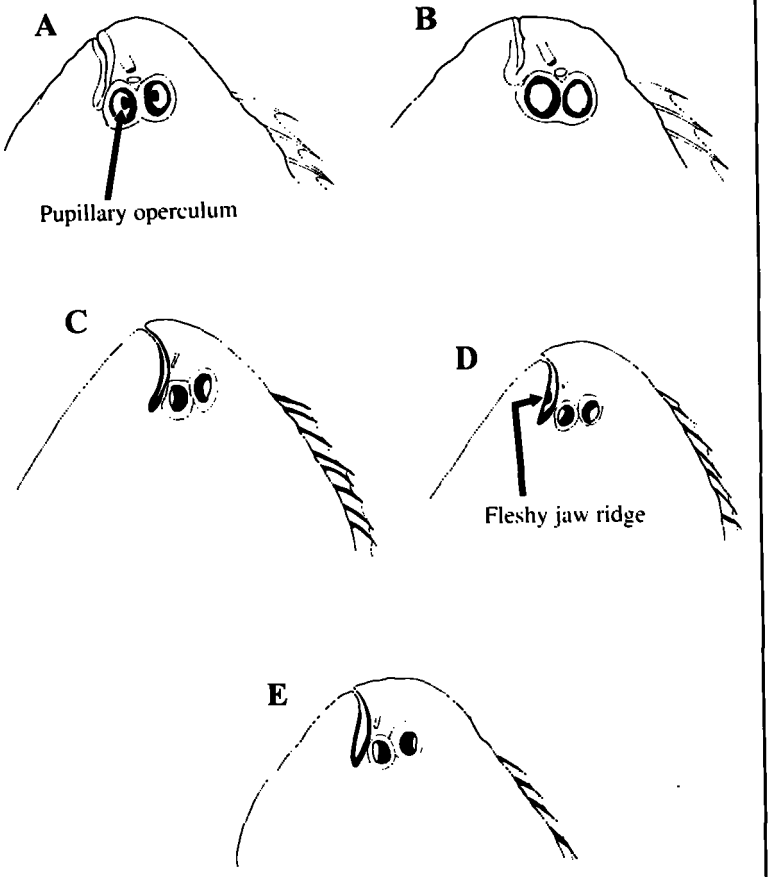


**Figure 3**

Eye structures, lower jaw positions , dorsal-fin positions, and jaw structures observed in western Atlantic *Symphurus*. (**A**) Eyes with well-developed pupillary operculum. (**B**) eyes without pupillary operculum. (**A–E**) Position of lower jaw relative to nonmigrating (lower) eye: (A) mideye; (B) anterior margin of eye; (C) posterior margin of eye; (D) posterior margin of pupil; and (E) posterior to eye. (**A–F**) Position of dorsal-fin origin in relation to eye: (A and C) at mideye; (B) at anterior margin of eye; (D) anterior to eye; and (E) posterior to eye. (**A–E**) Jaw structures: (A–C, E) lower jaw without fleshy ridge; (D) lower jaw with fleshy ridge.

nonelongate or only partially elongate ovaries. Mature females had fully elongate ovaries. Gravid females were those with enlarged ovaries filled with large, macroscopically visible ova.

When available, depth-of-capture information (converted and rounded to the nearest meter) was recorded and summarized (Table 10) for specimens listed in the Appendix. If depth of capture comprised a range of depths over which the nets were towed, a mean depth for that particular trawl was calculated and used in analyses. Evaluations of bathymetric distribution were not based on random-stratified sampling but on information from available material, supplemented with depth information from the literature. There exists, therefore, a potential for bias with respect to depth-of-capture information.

Statistical analyses (SPSS, 1975; SPSS-X, 1986) were conducted on the Primos computer system at the Virginia Institute of Marine Science. All statistical analyses of morphometric and meristic data were conducted on log-transformed data.

Synonymies appearing in accounts for *S. plagusia*, *S. tessellatus*, and *S. civitatium* (see below) are selective and abbreviated from the more detailed list compiled by Munroe (1991) for these species. The synonymy for *S. plagiusa* complements the compilation of detailed literature for *S. plagiusa* presented in Topp and Hoff (1972).

Abbreviations for institutions providing study material, or in which type material is deposited, follow Leviton et al. (1985). Additional collections are as follows: CAS-SU: California Academy of Sciences,

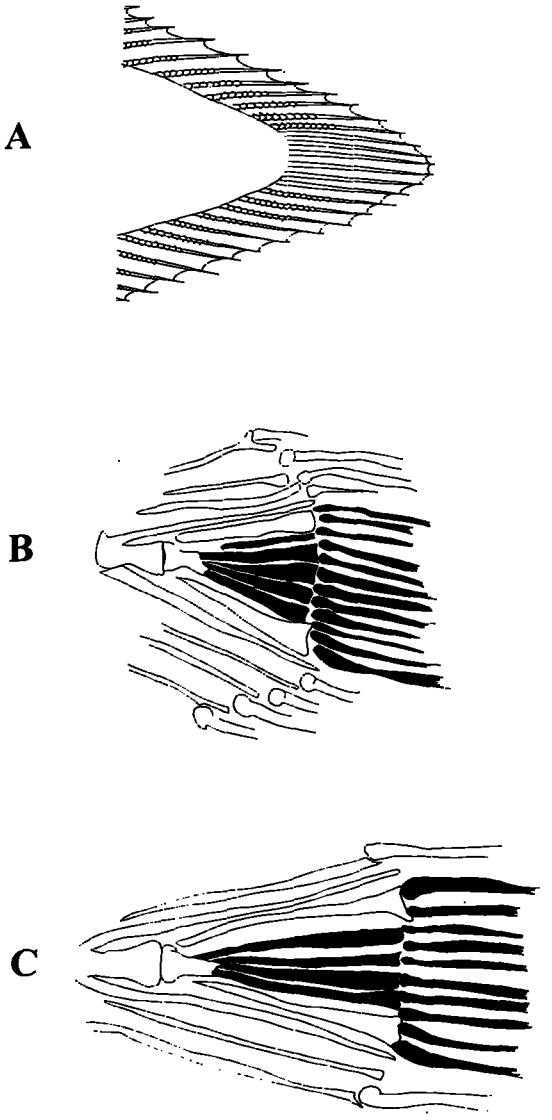


**Figure 4**

Degree of development of scales on blind sides of dorsal- and anal-fin rays and method of counting caudal-fin rays and hypurals for western Atlantic species of *Symphurus*. (**A**) Dorsal- and anal-fin rays with small ctenoid scales along their lengths. (**B**) Species with 12 caudal-fin rays and five hypurals (in black). (**C**) Species with 10 caudal-fin rays and four hypurals (in black).

San Francisco (collections formerly at Stanford University); IBUNAM: Instituto de Biología, Universidad Nacional Autonoma de Mexico, México, DF; IMS: Marine Sciences Institute, University of Texas at Austin, Port Aransas; INIDEP: Instituto Nacional de Investigacion y Desarrollo Pesquero, Mar del Plata; UFPB: Departamento de Sistematica e Ecologia, Universidade Federal da Paraíba, Joao Pessoa; UMML: Rosenstiel School of Marine and Atmospheric Sciences, University of Miami, Miami (now part of University of Florida (UF) collections; add 200,000 to original UMML catalog number); USU: Universidade Santa Ursula, Rio de Janeiro; ZMA: Zoologisch Museum, Universiteit van Amsterdam, Amsterdam (now Institute for Systematics and Population Biology, Zoologisch Museum).

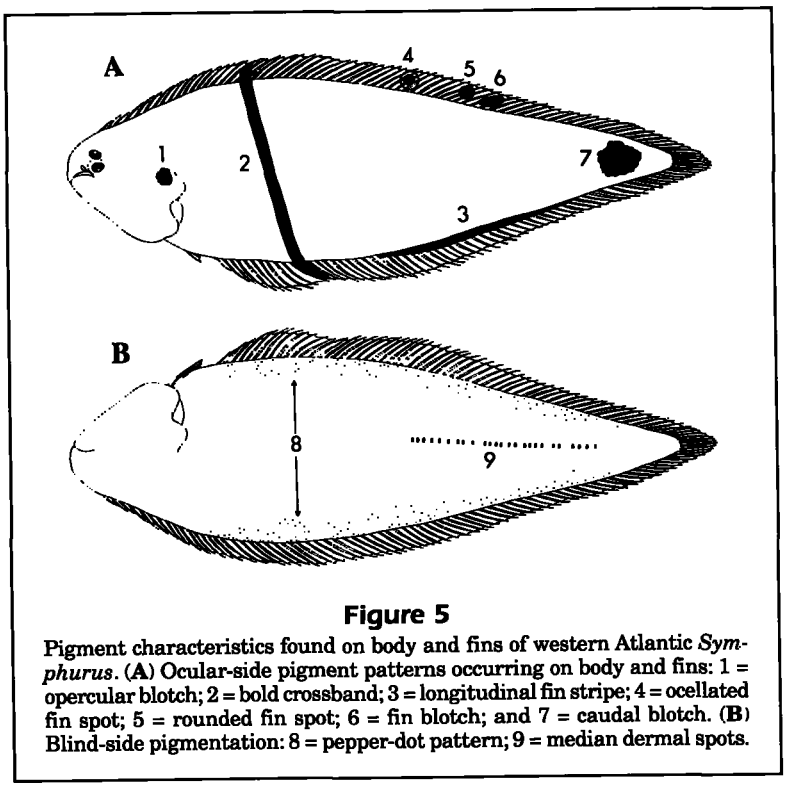


**Figure 5**

Pigment characteristics found on body and fins of western Atlantic *Symphurus*. (**A**) Ocular-side pigment patterns occurring on body and fins: 1 = opercular blotch; 2 = bold crossband; 3 = longitudinal fin stripe; 4 = ocellated fin spot; 5 = rounded fin spot; 6 = fin blotch; and 7 = caudal blotch. (**B**) Blind-side pigmentation: 8 = pepper-dot pattern; 9 = median dermal spots.

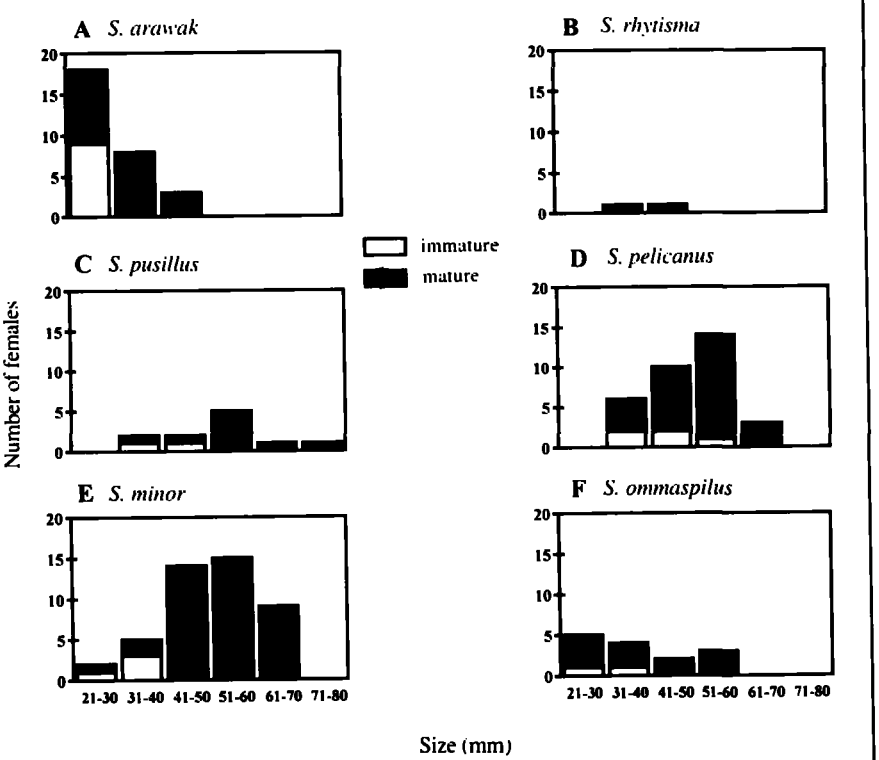


**Figure 6**

Frequency histograms indicating relative sizes (mm standard length) of immature and mature females, and sizes at sexual maturity for females of western Atlantic dwarf species (defined in text) of *Symphurus*.

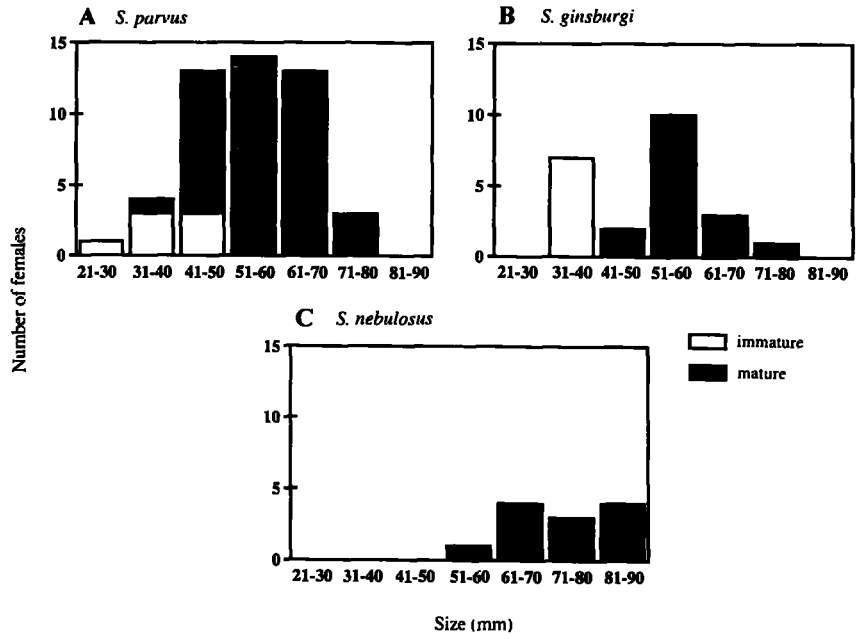


**Figure 7**

Frequency histograms indicating relative sizes (mm standard length) of immature and mature females, and sizes at sexual maturity for females of diminutive species (defined in text) of western Atlantic *Symphurus*.

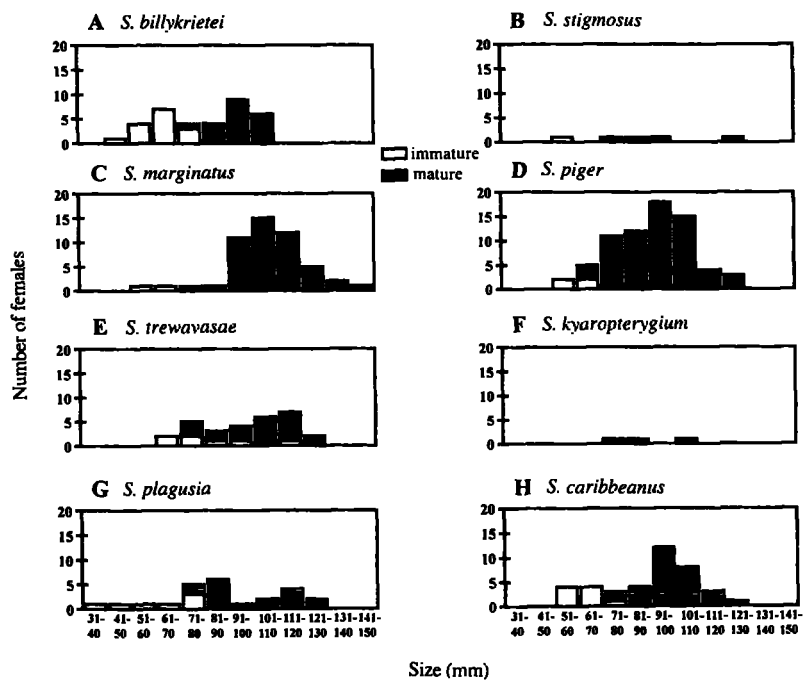


**Figure 8**

Frequency histograms indicating relative sizes (mm standard length) of immature and mature females, and sizes at sexual maturity for females of medium-size species (defined in text) of western Atlantic *Symphurus*.

## Table 10

Summary of bathymetric data (depth in meters) for western Atlantic *Symphurus* species. Abbreviations: plagi = *plagiusa*; di = *diomedeanus*; je = *jenynsi*; ur = *urospilus*; ca = *caribbeanus*; plagu = *plagusia*; ci = *civitatium*; te = *tessellatus*; oc = *oculellus*; om = *ommaspilus*; mi = *minor*; pa = *parvus*; ky = *kyaropterygium*; tr = *trewavasae*; ar = *arawak*; rh = *rhytisma*; pe = *pelicanus*; pu = *pusillus*; gi = *ginsburgi*; bi = *billykrietei*; st = *stigmosus*; pi = *piger*; ma = *marginatus*; ne = *nebulosus*.

| | Species | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Depth | plagi | di | je | ur | ca | plagu | ci | te | oc | om | mi | pa | ky | tr | ar | rh | pe | pu | gi | bi | st | pi | ma | ne |
| 1–10 | 116 | 1 | 5 | 11 | 49 | 21 | 130 | 49 | 2 | 13 | — | — | — | 1 | 9 | 3 | 1 | — | — | — | — | — | — | — |
| 11–20 | 173 | 2 | 22 | 32 | 30 | — | 56 | 91 | 12 | 10 | 8 | 1 | — | 3 | 22 | 2 | — | — | — | — | — | — | — | — |
| 21–30 | 20 | 25 | 12 | 57 | 16 | — | 77 | 13 | 12 | 1 | 14 | 4 | — | 7 | 7 | 1 | 1 | — | — | — | — | — | — | — |
| 31–40 | 5 | 93 | — | 22 | — | 4 | 58 | 87 | 17 | — | 24 | 5 | 2 | — | 3 | — | 5 | — | — | — | — | — | 1 | — |
| 41–50 | 5 | 65 | 12 | 1 | — | — | 13 | 67 | 6 | — | 21 | 18 | 1 | 14 | — | — | 6 | — | — | — | — | — | 3 | — |
| 51–60 | 1 | 54 | — | 1 | — | 1 | 8 | 17 | 2 | — | 6 | 39 | 3 | 12 | — | — | 22 | — | — | — | — | — | — | — |
| 61–70 | 2 | 24 | — | — | — | — | 1 | 28 | 27 | — | 3 | 18 | 6 | 17 | — | — | 16 | — | — | — | — | — | 1 | — |
| 71–80 | — | 23 | — | — | — | — | 1 | 21 | — | — | — | 6 | — | 17 | — | — | 1 | — | — | — | — | — | 1 | — |
| 81–90 | — | 10 | — | — | — | — | — | 1 | 2 | — | — | 12 | — | — | — | — | 1 | — | — | — | — | — | — | — |
| 91–100 | — | 13 | — | — | — | — | — | — | — | — | — | 3 | — | 9 | — | — | 1 | — | — | — | — | 3 | — | — |
| 101–110 | — | — | — | — | — | — | — | — | 1 | — | — | 6 | — | — | — | — | 1 | 2 | 3 | — | — | 4 | — | — |
| 111–120 | 1 | 2 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 7 | 4 | 2 | 1 | — | — | — | — |
| 121–130 | — | 1 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | — | — | — | — | — | — |
| 131–140 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 3 | 3 | 1 | 1 | — | 4 | — | — |
| 141–150 | — | 2 | — | — | — | — | — | — | — | — | — | 1 | — | — | — | — | — | — | — | — | — | 12 | — | — |
| 151–160 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | — | 5 | — | — |
| 161–170 | — | — | — | — | — | — | — | — | — | — | 3 | — | — | — | — | — | — | 2 | — | — | — | 13 | — | — |
| 171–180 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 11 | 2 | — | — | — | — |
| 181–190 | 1 | 1 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 3 | — | 4 | — | 36 | — | — |
| 191–200 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 2 | 15 | 1 | 1 | — | — | — |
| 201–210 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 2 | 1 | 2 | 1 | — | — |
| 211–220 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 221–230 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 3 | — | 6 | — | 24 | — | — |
| 231–240 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | — | 4 | — | 3 | — | 2 |
| 241–250 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 4 | — | — | — | — |
| 251–260 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 11 | — | 4 | — | — |
| 261–270 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | 8 | — | 2 | — | — |
| 271–280 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 7 | 1 | 36 | — | — |
| 281–290 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 5 | 3 | 1 | 2 | — |
| 291–300 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | 3 | — | 6 | 1 | — |
| 301–310 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 5 | — | 1 | 1 | — |
| 311–320 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 7 | — | — | 1 | — |
| 321–330 | — | — | — | 2 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 4 | — | 1 | 10 | — |
| 331–340 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 2 | — | 3 | 1 | — |
| 341–350 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | — | 2 | 10 | — |
| 351–360 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 4 | 3 | — | 2 | 1 |
| 361–370 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | 1 | 2 | 7 | — |
| 371–380 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 4 | 1 | 2 | 4 | — |
| 381–390 | — | — | — | — | — | — | — | — | — | — | — | 1 | — | — | — | — | — | — | — | — | — | 1 | 15 | 1 |
| 391–400 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | — | — | — | 2 |
| 401–410 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | 7 | — |
| 411–420 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | — |
| 421–430 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 |
| 431–440 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 2 | — | — |
| 441–450 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | 1 |
| 451–460 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 2 | 3 | — |
| 461–470 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 4 | — |
| 471–480 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 5 | — |
| 481–490 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 |
| 491–500 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 10 |
| 501–510 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | — |
| 511–520 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 2 | 1 |

*continued*

**Table 10 (continued)**

| | Species | | | | | | | | | | | | | | | | | | | | | | |
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| Depth | plagi | di | je | ur | ca | plagu | ci | te | oc | om | mi | pa | ky | tr | ar | rh | pe | pu | gi | bi | st | pi | ma | ne |
| 521–530 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 |
| 531–540 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 2 | — |
| 541–550 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 4 | 10 | — |
| 551–560 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 561–570 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 571–580 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 581–590 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 591–600 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 3 | — |
| 601–610 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 611–620 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 621–630 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 631–640 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 2 | — |
| 641–650 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | — | — | — | — |
| 651–660 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 |
| 661–670 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 2 | — |
| 671–680 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 1 | — |
| 681–690 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 2 |
| 691–700 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 701–810 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 4 | 3 |

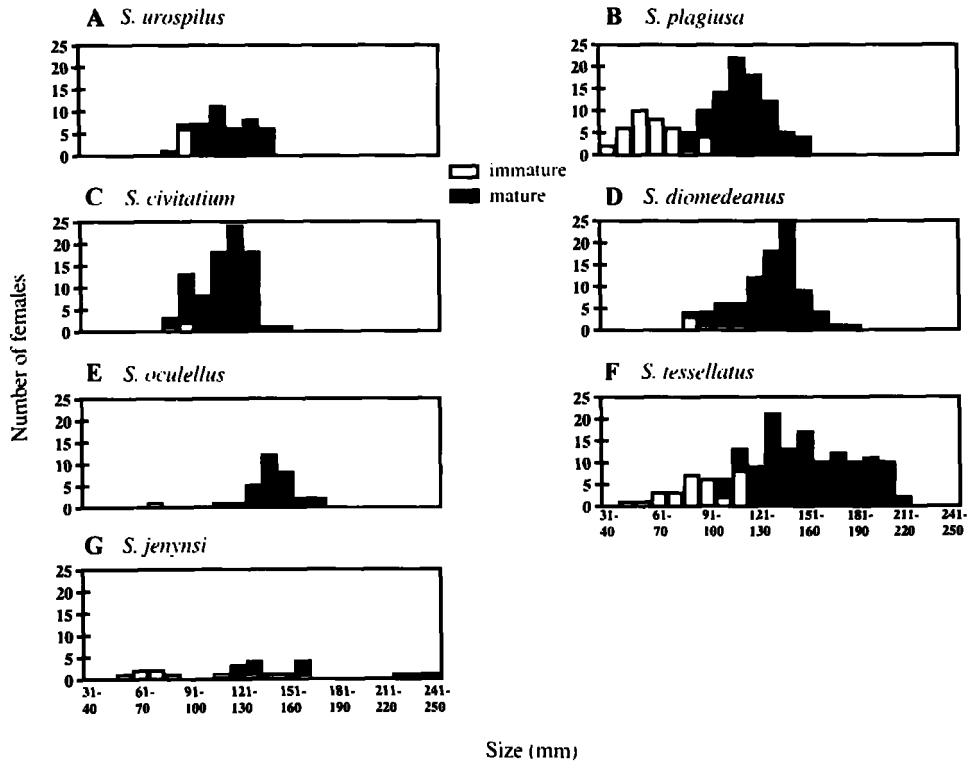


**Figure 9**

Frequency histograms indicating relative sizes (mm standard length) of immature and mature females, and sizes at sexual maturity for females of large-size species (defined in text) of western Atlantic *Symphurus*.

## Artificial key to western Atlantic *Symphurus*

**1a** Caudal-fin rays 14 (rarely 13); dorsal-fin rays more than 104; anal-fin rays 91–98; peritoneum black, usually visible through abdominal wall on both sides of body; body elongate, of nearly uniform width throughout most of its length (Fig. 10); total vertebrae 57–60; ID pattern usually 1-2-2 (Fig. 1A) ..... ***S. nebulosus***

**1b** Caudal-fin rays less than 13 (rarely 13); dorsal-fin rays usually less than 104; anal-fin rays less than 91; peritoneum black or unpigmented; body usually deeper in anterior one-third of length and tapering noticeably posteriorly; total vertebrae less than 57; ID pattern with 3 or 4 pterygiophores inserted into second interneural space (usually 1-3-2, 1-3-3, 1-4-2, or 1-4-3) (Fig. 1, B–E) ..... **2**

**2a** Peritoneum black, usually visible through abdominal wall on both sides of body; caudal-fin rays usually 12; pupillary operculum absent (Fig. 3B); teeth present on entire margins of ocular-side jaws; ID pattern usually 1-3-2 (see Fig. 1B) ..... **3**

**2b** Peritoneum unpigmented; caudal-fin rays 10–12; pupillary operculum present (Fig. 3A) or absent (Fig 3B); teeth present or absent over entire margins of both ocular-side jaws; ID pattern usually 1-3-2 (Fig. 1B), 1-3-3 (Fig. 1C), 1-4-2 (Fig. 1D), or 1-4-3 (Fig. 1E) ..... **9**

**3a** Blind side of body with pepper-dot pattern of melanophores (usually heaviest along bases of dorsal and anal fins) (Fig. 5B, number 8); dorsal-fin rays 77–85; anal-fin rays 64–70; 70 or fewer scales in longitudinal series; dorsal-fin origin in posterior position, usually only reaching vertical through posterior margin of upper eye or occasionally not reaching that point; dorsal and anal fins without pigmented blotches or stripes; total vertebrae 43–46 ..... ***S. pelicanus***

**3b** Blind side of body without pepper-dot pattern of melanophores; dorsal-fin rays usually greater than 85; anal-fin rays usually greater than 69; usually more than 70 scales in longitudinal series; dorsal-fin origin in more anterior position, usually at point between verticals through middle of pupil and anterior margin of upper eye; dorsal and anal fins either uniformly pigmented, or with series of alternating pigmented blotches and unpigmented regions, or with stripe along basal margin of fin; total vertebrae usually greater than 46 ..... **4**

**4a** Dorsal-fin rays 93–104; anal-fin rays 80–89; ocular-surface usually with a large, dark brown diamond-shaped blotch on caudal region of body (see Fig. 32), but otherwise uniformly pigmented and without pattern of distinct crossbands; basal margins of dorsal and anal fins with dark brown stripe, but without blotches; total vertebrae 51–56, usually 52–54 ..... ***S. marginatus***

**4b** Dorsal-fin rays usually less than 95; anal-fin rays usually 84 or fewer; ocular-surface of body without dark brown, diamond-shaped blotch on caudal region, with or without distinct pattern of crossbands; dorsal and anal fins with or without pigmented blotches; total vertebrae 47–53, usually 52 or less ..... **5**

**5a** Scales fewer, 62–75 in a longitudinal series; 5 hypurals; anal-fin rays 68–74; inner opercular linings and both sides of isthmus usually lightly pigmented; total vertebrae 45–49, usually 47–49 ..... ***S. piger***

**5b** Scales more numerous, usually 77–100 in a longitudinal series; 4 hypurals; anal-fin rays 71–84; inner opercular linings and isthmus unpigmented; total vertebrae 47–52, usually greater than 48 ..... **6**

**6a** Dorsal-fin rays 83–88; anal-fin rays 71–75; total vertebrae 47–49; scales in longitudinal series 77–87; ocular surface usually yellowish or lightly straw-colored, with one to two prominent, complete crossbands immediately posterior to opercular opening (Fig. 28); dorsal and anal fins without stripe along basal margin; (adult size relatively small, usually not exceeding 80 mm SL) ..... ***S. pusillus***

**6b** Dorsal-fin rays 87–95; anal-fin rays 74–84; total vertebrae 50–53; scales in longitudinal series 85–99; ocular surface usually dark brown, straw-colored or yellowish, with series of mostly incomplete crossbands posterior to opercular opening, or ocular surface uniformly pigmented without crossbands; dorsal and anal fins frequently with dark brown stripe along basal margins, sometimes in combination with series of large, pigmented blotches alternating with un pigmented areas on dorsal and anal fins ..... **7**

**7a** Dorsal and anal fins usually with alternating series of prominent, darkly pigmented blotches (see Fig. 22); blotches usually wider than intervening unpigmented areas; no pigmented spot on scaly base of caudal fin; eyeballs round, usually contiguous, or nearly contiguous, within fleshy orbital sac (see Fig. 21A) ..... ***S. stigmosus* n. sp.**

**7b** Dorsal and anal fins usually without alternating series of prominent, darkly pigmented blotches; if blotches present, then as wide as, or only slightly narrower than, width of intervening unpigmented areas; pigmented spot present on scaly base of caudal fin; eyeballs longer than wide, separated by small space within fleshy orbital sac (see Fig. 21B) ..... **8**

**8a** Eye diameter relatively large (see Fig. 20), ratio of ED to TKL [ED:TKL] = 3.2–4.7 (usually exceeding 3.5% of trunk length) ..... ***S. ginsburgi***

**8b** Eye diameter relatively small (see Fig. 20), ED:TKL = 2.5–4.0 (usually less than 3.4% of trunk length) ..... ***S. billykrietei* n. sp.**

**9a** Caudal-fin rays usually 12; pupillary operculum absent (Fig. 3B); ID pattern usually 1-3-2 (Fig. 1B) or 1-4-3 (Fig. 1E) ..... **10**

**9b** Caudal-fin rays usually 10 or 11; pupillary operculum present (Fig. 3A) or absent (Fig. 3B); ID pattern usually 1-3-3 (Fig. 1C), 1-4-2 (Fig. 1D), or 1-4-3 (Fig. 1E) ..... **16**

**10a** Dorsal-fin rays 70–76; anal-fin rays 55–61; 55–65 scales in longitudinal series; pattern of pepper-dots (Fig. 5B, number 8) on blind side of body (usually); some specimens with darkly pigmented, triangularly shaped caudal blotch; total vertebrae 39–42; ID pattern usually 1-3-2 (Fig. 1B); adult sizes usually less than 50 mm SL ..... ***S. arawak***

**10b** Dorsal-fin rays usually more than 80; anal-fin rays 68 or more; 66–97 scales in longitudinal series; no pepper-dots on blind side of body; caudal blotch present or absent; total vertebrae 46 or more; ID patterns usually 1-3-2 (Fig. 1B) or 1-4-3 (Fig. 1E); small (<45 mm SL) or large (>70 mm SL) adult sizes ..... **11**

**11a** Body whitish or pallid, occasionally with faint crossbands; a darkly pigmented blotch on caudal region of ocular side of body in some specimens; dorsal-fin rays 83–87; anal-fin rays 68–71; total vertebrae 46–48; teeth well-developed along margins of both ocular-side jaws; inner opercular linings and isthmus on both sides of body unpigmented; eye relatively large, ED 11.6–15.8% of HL; ocular-side lower jaw without fleshy ridge (Fig. 3E); ID pattern usually 1-3-2 (Fig. 1B); adults usually less than 45 mm SL ..... ***S. rhytisma***

**11b** Body usually darkly pigmented, straw-colored to dark brown, with prominent crossbands or uniformly pigmented; no darkly pigmented caudal blotch on ocular side of body; dorsal-fin rays 86–107; anal-fin rays 70–89; total vertebrae 47–55; teeth usually absent or only poorly developed on margins of ocular-side jaws (especially upper jaw); inner opercular lining and isthmus on ocular side of body heavily pigmented; eye relatively small, ED 6.4–11.4% of HL; fleshy ridge present or absent on ocular-side lower jaw; ID patterns usually with 4 or more pterygiophores inserted into interneural space two; adults exceeding 70 mm SL ..... **12**

**12a** Large black spot on outer surface of ocular-side operculum; dorsal-fin rays 91–106; anal-fin rays 74–89; total vertebrae 48–54 ..... **13**

**12b** Ocular-side operculum without obvious black spot; dorsal-fin rays 86–97; anal-fin rays 70–81; total vertebrae 46–51 ..... **14**

**13a** From 4 to 8 small ctenoid scales on blind sides of posterior rays of dorsal and anal fins (Fig. 4A); ocular-side lower jaw without fleshy ridge on posterior portion (Fig. 3E); posterior extension of ocular-side jaws reaching only to point between verticals through posterior margin of pupil and posterior margin of eye; ocular surface usually with nine, or fewer, wide crossbands; posterior one-third of dorsal and anal fins becoming progressively darker (black in mature males); dorsal and anal fins without blotches; dorsal-fin rays 91–102; anal-fin rays 74–86; total vertebrae 48–54, usually 50–53 ..... ***S. tessellatus***

**13b** No ctenoid scales on blind sides of posterior rays of dorsal and anal fins; ocular-side lower jaw with pronounced fleshy ridge on posterior portion (Fig. 3D); posterior extension of ocular-side jaws reaching vertical at posterior margin of lower eye or reaching vertical slightly posterior to posterior margin of lower eye; ocular surface with 10–14 narrow crossbands; posterior one-third of dorsal and anal fins usually without progressive posterior darkening, but with alternating series of blotches and unpigmented areas; dorsal-fin rays 97–106; anal-fin rays 81–89; total vertebrae 52–55, usually 53–54 ..... ***S. oculellus***

**14a** Dorsal and anal fins with alternating series of pigmented blotches and unpigmented areas; lower jaw on ocular-side without fleshy ridge (Fig. 3E); snout pointed; distance between upper eye and dorsal-fin base only slightly greater than eye diameter; ocular surface usually with 9–15, prominent, narrow crossbands; eye relatively large, usually 9.0–10.0% of HL ..... ***S. caribbeanus***

**14b** Dorsal and anal fins without alternating series of pigmented blotches and unpigmented areas; lower jaw on ocular-side with fleshy ridge (Fig. 3D); snout squarish; distance from upper eye to dorsal-fin base much greater than eye diameter; ocular surface uniformly pigmented or with faint crossbands occasionally present; eye relatively small, usually only 6.4–9.4% of HL ..... **15**

**15a** Total vertebrae 47–51, usually 49–51; dorsal-fin rays 89–97; anal-fin rays 73–81; 79–89 scales in longitudinal series; eye relatively small, usually only 6.4–9.4% of HL ..... ***S. plagusia***

**15b** Total vertebrae 46–50, usually 47–49; dorsal-fin rays 86–93; anal-fin rays 70–78; 66–83 scales in longitudinal series; eye relatively large (7.0–11% of HL) ..... ***S. civitatium***

**16a** Caudal-fin rays usually 11; large ocellated spot on caudal fin; dorsal and anal fins without spots; pupillary operculum well developed (Fig. 3A) ..... ***S. urospilus***

**16b** Caudal-fin rays usually 10; no ocellated spot on caudal fin; if spot present on caudal fin (occasionally in *S. diomedeanus)*, then spots also present on posterior dorsal and anal fins; pupillary operculum present or absent ..... **17**

**17a** Dark brown blotch on caudal region of ocular surface of body (see Figs. 38, 40, and 42) or single ocellated spot on posterior dorsal and anal fins (see Fig. 44); pupillary operculum present (Fig. 3A); no fleshy ridge on ocular-side lower jaw (Fig. 3E); ostia present in bases of membranes of dorsal and anal fins; ID patterns usually 1-4-2 (Fig. 1D) or 1-5-2 ..... **18**

**17b** No dark brown blotch on caudal region of ocular surface of body; no ocellated spots on posterior dorsal and anal fins; pupillary operculum and fleshy ridge on ocular-side lower jaw present or absent; no ostia in membranes at bases of dorsal and anal fins; ID patterns usually 1-3-3 (Fig. 1C) or 1-4-3 (Fig. 1E) ..... **21**

**18a** Single ocellated spot on posterior region of dorsal and anal fins (see Fig. 44); ocular surface whitish or yellowish-white without dark brown blotch in caudal region ..... ***S. ommaspilus***

**18b** No ocellated spots on dorsal and anal fins; ocular surface straw-colored to dark brown with dark brown blotch on caudal region (see Figs. 38, 40, 42) ..... **19**

**19a** Dorsal-fin rays 80–87; anal-fin rays 67–72; total vertebrae 46–49, usually 47–48; scales in longitudinal series 73–81; (continental shelf off southern Brazil) ..... ***S. kyaropterygium***

**19b** Dorsal-fin rays 69–86, usually less than 83; anal-fin rays usually less than 68; total vertebrae usually less than 47; scales in longitudinal series usually less than 78; (continental shelf off eastern United States, Gulf of Mexico, and Caribbean Sea) ..... **20**

**20a** Dorsal-fin rays 69–81, usually 72–77; anal-fin rays 55–64, usually 56–64; total vertebrae 41–44, usually 41–43; 55–67 scales in a longitudinal series ..... ***S. minor***

**20b** Dorsal-fin rays 75–86, usually 77–84; anal-fin rays 60–70, usually 62–67; total vertebrae 43–47, usually 44–46; 59–78 scales in longitudinal series ..... ***S. parvus***

**21a** Posterior dorsal and anal fins spotted (usually); pupillary operculum present (Fig. 3A) ..... ***S. diomedeanus***

**21b** Dorsal and anal fins without spots; pupillary operculum absent or only weakly developed (Fig. 3B) ..... **22**

**22a** Dorsal-fin rays 107–115; anal-fin rays 91–99; scales on head posterior to lower eye 21–25; scales in longitudinal series 102–119; total vertebrae 57–60 ..... ***S. jenynsi***

**22b** Dorsal-fin rays less than 95; anal-fin rays 79 or fewer; scales on head posterior to lower eye 20 or fewer; scales in longitudinal series 86 or fewer; total vertebrae 51 or fewer ..... **23**

**23a** From 4 to 8 small ctenoid scales on blind sides of posterior rays of dorsal and anal fins (Fig. 4A); fleshy ridge usually present on ocular-side lower jaw (Fig. 3D); inner opercular linings and both sides of isthmus heavily pigmented; prominent black spot usually present on outer surface of ocular-side opercle; dorsal-fin rays 81–91; anal-fin rays 66–75; 76–86 scales in longitudinal series; total vertebrae 44–49, usually 45–48; eye relatively small (8.3–12.6% of HL); ID pattern usually 1-4-3 (Fig. 1E) ..... ***S. plagiusa***

**23b** No ctenoid scales on blind sides of posterior rays of dorsal and anal fins; ocular-side lower jaw without fleshy ridge (Fig. 3E); inner opercular lining and isthmus on ocular side of body lightly pigmented, those of blind side unpigmented; no black spot on outer surface of ocular-side opercle; dorsal-fin rays 88–94; anal-fin rays 73–79; 67–77 scales in longitudinal series; total vertebrae 47–51, usually 48–49; eye relatively large (11.4–16.2% of HL); ID pattern usually 1-3-3 (Fig. 1C) ..... ***S. trewavasae***

## Species accounts

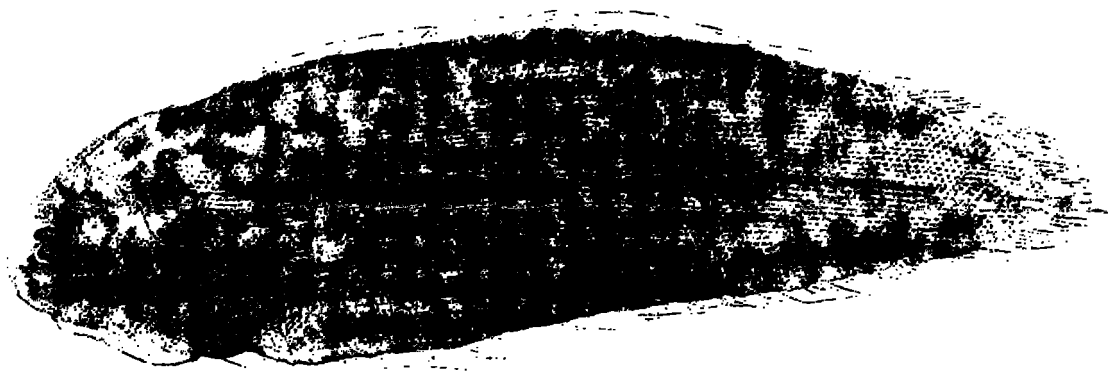

**Figure 10**
*Symphurus nebulosus* (Goode and Bean), UMO 311.8, 76.7 mm SL, North Atlantic 40°48'N, 66°36'–38'W.

### *Symphurus nebulosus* (Goode and Bean, 1883) (Figs. 1A, 7, 10C, 11; Tables 1–11)
### Freckled tonguefish

*Aphoristia nebulosa* Goode and Bean, 1883:192 (original description, counts, measurements; 421 m; Gulf Stream, 32°07'N, 78°37'30"W). Günther, 1887:167 (based on Goode and Bean, 1883). Goode and Bean, 1896:458 (redescription, figure of holotype).

*Aphoristia marginata* (not of Goode and Bean, 1886). Goode and Bean, 1886:154 (in part; specimen from *Fish Hawk* Station 1154 is *S. nebulosus*).

*Symphurus* (*Acedia*) *nebulosus*. Jordan and Goss, 1889:321–323, 326–327 (new subgenus; redescription based on Goode and Bean, 1883; in key). Jordan and Evermann, 1898:2712 (in key; redescription of holotype; counts, measurements, color description). Evermann and Marsh, 1900:332 (in key).

*Symphurus nebulosus*. Chabanaud, 1939:26 (Atlantic coast of Carolinas). Chabanaud, 1952:5 (brief comparison with *S. ligulatus*). Ginsburg, 1951:200 (redescription, counts, measurements for three specimens; off Long Island, New York, to northern Florida). Munroe, 1990:475 (comparison with *S. ligulatus*). Munroe, 1992:367, 374 (ID pattern; geographic, bathymetric distributions).

**Diagnosis** *Symphurus nebulosus* is the only western Atlantic tonguefish with the combination of a 1-2-2 ID pattern and 14 caudal-fin rays. The following combination of characteristics distinguishes *S. nebulosus* from all congeners, except the eastern Atlantic *S. ligulatus*: predominant 1-2-2 ID pattern; 14 caudal-fin rays; 5 hypurals; 57–60 (modally 58–59) total vertebrae; 105–113 dorsal-fin rays; 91–98 anal-fin rays; 120–135 scales in longitudinal series; black peritoneum; absence of pupillary operculum; absence of fleshy ridge on ocular-side lower jaw; complete row of teeth along margins of ocular-side jaws; absence of scales on blind sides of dorsal- and anal-fin rays; elongate body with relatively uniform and narrow depth (165–282 SL, usually 225–240 SL); uniformly pigmented ocular surface without caudal blotch; and uniformly pigmented dorsal, anal, and caudal fins lacking spots or blotches. *Symphurus nebulosus* is distinguished from *S. ligulatus* by modal differences in total vertebral counts, relatively longer head and wider lower head lobe, longer postorbital length, somewhat deeper body, and ocular-side upper lip usually lacking a prominent pigmented band (lightly pigmented band occasionally present).

**Description** A diminutive species attaining maximum sizes of ca. 87 mm SL. ID pattern usually 1-2-2

(22/27 specimens), rarely 2-2-2 or 1-2-3 (Table 2). Caudal-fin rays 14 (24/27), infrequently 13 or 16 (Table 3). Dorsal-fin rays 105–113, usually 107–111 (Table 4). Anal-fin rays 91–98, usually 93–98 (Table 5). Total vertebrae 57–60 (25/27), usually 58–59 (Table 6). Hypurals usually 5 (19/20 individuals), rarely 4 (1/20). Longitudinal scale rows 120–135, usually 125–130 (Table 7). Scale rows on head posterior to lower orbit 19–24, usually 21–22 (Table 8). Transverse scales 43–50 (Table 9).

Proportions of morphometric features presented in Table 11. Body notably slender; of nearly uniform width for most of length with gradual taper in posterior one-fourth of body. Preanal length slightly smaller than body depth. Head long and narrow; usually slightly narrower than body depth. Head length slightly shorter than head width (HW: HL=1.00–1.28, $\bar{x}$=1.20). Upper head lobe notably narrow and usually slightly smaller than postorbital length. Lower head lobe wide, slightly less than postorbital length; usually projecting posteriorly beyond upper head lobe. Snout moderately short, somewhat rounded; with scaleless area on dorsal portion. Dermal papillae well developed on blind-side snout and chin; papillae usually not extending posteriorly to vertical equal with dorsal-fin origin. Anterior nostril on ocular side short when depressed posteriorly, not reaching anterior margin of lower eye. Jaws short, slightly arched; maxilla usually extending posteriorly to vertical through anterior margin of pupil of lower eye; less frequently, extending posteriorly to point between verticals through middle and anterior margin of lower eye. Ocular-side lower jaw without fleshy ridge. Teeth well developed on jaws. Margins of ocular-side dentary and premaxilla usually with complete row of slender teeth; less frequently, with teeth only on anterior two-thirds of premaxillary margin. Chin depth usually just slightly larger than snout length. Lower eye small; subelliptical; eyes usually equal in position or upper eye slightly in advance of lower eye. Anterior and medial surfaces of eyes usually without scales; 1–3 small scales usually in narrow interorbital space. Pupillary operculum absent. Dorsal-fin origin posteriorly placed, usually almost equal with vertical through middle of upper eye; less frequently reaching vertical through anterior margin of pupil, or occasionally reaching vertical through posterior margin of upper eye; predorsal length moderate. Anteriormost dorsal-fin rays shorter and with wider separation between bases than more posterior fin rays. Scales absent on blind sides of dorsal- and anal-fin rays. Pelvic fin moderately long; longest pelvic-fin ray, when extended posteriorly, usually reaching base of first, sometimes second, anal-fin ray. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anus, or occasionally extending posteriorly almost to anal-fin origin (membrane torn in specimens examined). Caudal fin short. Scales small, numerous, strongly ctenoid on both sides of body.

**Table 11**

Morphometrics for holotype (MCZ 27966) and 22 other specimens of *Symphurus nebulosus*. (Abbreviations defined in methods section; SL is expressed in mm; characters 2 to 14 are expressed in thousandths of SL; 15 to 21 in thousandths of HL; *n* = no. of specimens measured.)

| Character | Holotype | *n* | Range | Mean | SD |
|---|---|---|---|---|---|
| 1. SL | 76.6 | 23 | 45.0–86.2 | 72.6 | 10.18 |
| 2. BD | 243 | 23 | 165–282 | 233.5 | 23.92 |
| 3. PDL | 54 | 23 | 33–69 | 50.3 | 9.41 |
| 4. PAL | 236 | 23 | 163–246 | 223.2 | 17.73 |
| 5. DBL | 946 | 23 | 931–967 | 949.7 | 9.41 |
| 6. ABL | 739 | 23 | 708–790 | 757.0 | 19.44 |
| 7. PL | 57 | 20 | 46–81 | 65.4 | 8.30 |
| 8. PA | 63 | 21 | 37–67 | 49.3 | 9.06 |
| 9. CFL | — | 21 | 80–116 | 102.4 | 10.42 |
| 10. HL | 187 | 23 | 159–208 | 186.7 | 12.40 |
| 11. HW | 215 | 23 | 186–239 | 216.4 | 13.45 |
| 12. POL | 127 | 23 | 110–133 | 124.0 | 6.44 |
| 13. UHL | 124 | 23 | 64–144 | 122.4 | 16.20 |
| 14. LHL | 91 | 23 | 82–129 | 103.6 | 10.85 |
| 15. POL | 678 | 23 | 620–711 | 665.6 | 26.87 |
| 16. SNL | 189 | 23 | 160–248 | 208.7 | 22.91 |
| 17. UJL | 182 | 22 | 169–248 | 206.9 | 20.23 |
| 18. ED | 133 | 23 | 94–133 | 114.2 | 11.50 |
| 19. CD | 147 | 23 | 141–308 | 210.0 | 38.56 |
| 20. OPLL | 329 | 23 | 233–479 | 358.4 | 49.47 |
| 21. OPUL | 126 | 23 | 126–253 | 188.7 | 35.64 |

**Pigmentation (Fig. 10)** Body coloration generally similar for both sexes. Ocular surface of head and body almost always uniformly straw-colored to dark brown, sometimes with overlying pattern of ill-defined dark brown cloudy areas, but otherwise without distinctive markings. Abdominal area immediately posterior to opercular opening, sometimes darker than general body color. Individual scales on ocular side have underlying longitudinal streak of black pigment; about 40–60 longitudinally continuous pigmented streaks along ocular-side length. Outer surface of ocular-side opercle generally with similar background coloration as on body; inner linings of opercles and isthmus on both sides of body yellowish-white. Slight pigment band occasionally present on ocular-side upper lip (not in most specimens examined). Blind side off-white; usually with median line of internal black spots showing through skin along axis of vertebral column. Smaller speci-

mens typically with single longitudinal series of dark, internal spots on blind side of body at proximal ends of dorsal- and anal-fin pterygiophores. Peritoneum dark black, showing through abdominal wall on both sides, especially prominent in lightly pigmented and smaller specimens.

Fin rays of dorsal and anal fins uniformly light brown along length of fins with little, if any, pigment on fin membranes and without obvious pigmented blotches or spots. Proximal one-third of caudal fin with diffuse brown pigment similar to that on body; distal portion of caudal-fin rays usually unpigmented.

Goode and Bean (1883) described the holotype as grayish, everywhere mottled with brown. Ginsburg (1951) described three specimens he examined as partly faded and having almost uniformly reddish or yellowish-brown coloration.

**Size and sexual maturity (Fig. 7C)** *Symphurus nebulosus* is a diminutive species that attains a maximum size of ca. 87 mm. Ten males (64.3–86.2 mm), 12 females (54.9–83.8 mm), and two immature fish (36.4–45.0 mm) of indeterminate sex were examined for life history information. No size differences between sexes were apparent. Sexual maturity, based on females, occurs at ca. 60–65 mm (Fig. 7C). Females 63.8–83.8 mm were gravid; two others (54.9 and 68.1 mm) had elongate ovaries without evidence of ripening ova. Of 10 specimens taken in a single trawl (now divided between UNC 4951 and USNM 285758), six were gravid females (69.5–83.8 mm) and four were adult males (78.3–86.2 mm), indicating that adults of both sexes occupy similar habitats.

Gravid females were present in collections from lat. 40°N to 28°N and from 239 to 800 m depth, indicating spawning probably occurs throughout the entire geographic and bathymetric ranges of the species. The two smallest specimens examined (36.4 and 45.0 mm) were taken near the northern end of the geographic range (39°40'N and 39°55'N, respectively). The only other specimen (UMO 311.8; 76.7 mm) from this region (at 40°48'N) is a gravid female. Capture of both juveniles and adults at the north of the range indicates that this region has an adult population of *S. nebulosus* and is likely not populated only by larvae that have been transported by the Gulf Stream from more southern regions, as reported for *S. minor* (Markle et al., 1980) and other *Symphurus* species (Evseenko, 1982; Scott and Scott, 1988).

**Geographic distribution (Fig. 11)** Western North Atlantic in outer continental shelf and upper continental slope deep waters from the region just south of Long Island, New York (40°48'N), to the Blake Plateau off Fort Lauderdale, Florida (26°28'N).

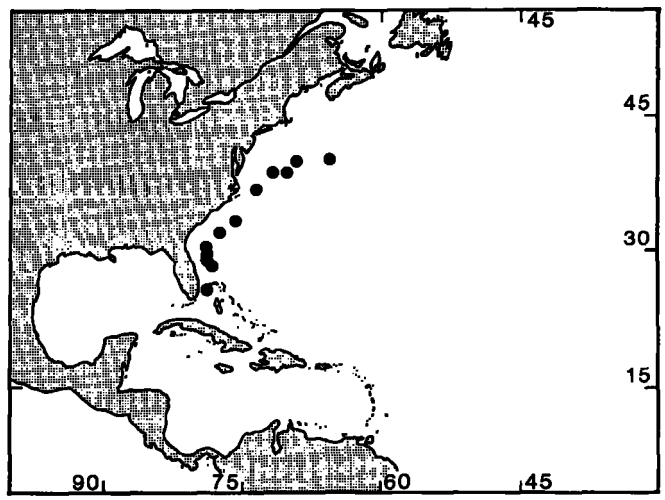


**Figure 11**

Geographic distribution of *Symphurus nebulosus* based on material examined (discussion of geographic distribution appears in species account).

**Bathymetric distribution** This species has rarely been collected (only 27 specimens located). Specimens were captured on soft mud substrates at depths ranging from 239 (USNM 291326, two individuals) to 810 m (UMML 20746, two specimens); most between 400–600 m. Six of 27 specimens were taken deeper than 530 m (Table 10). Because of its rarity in collections, little is known about the biology of *S. nebulosus*. Most captures (8/12) were of single specimens. The largest collection of 10 specimens occurred east of Cape Fear, North Carolina, at 495 m. Whether rarity in collections reflects natural low abundance or difficulties in sampling such relatively small fishes at depths where this species occurs is unknown.

**Remarks** Historically, comparisons of *S. nebulosus* have been made with *S. ligulatus* (Chabanaud, 1952; Munroe, 1987, 1990), a deepwater species of the Mediterranean Sea and eastern North Atlantic, which, as first noted by Chabanaud (1952) in a brief footnote, has meristic features similar to those of *S. nebulosus*. On the basis of similarities in meristic and morphological features (Munroe 1987, 1990), shared osteological characters (Munroe, unpubl. data), and similarities in pigmentation, it is hypothesized that *S. nebulosus* and *S. ligulatus* represent a closely related species pair with distributions in bathyal depths of temperate waters on opposite sides of the northern Atlantic. Both belong to a larger species group characterized by several features including a 1-2-2 ID pattern (Munroe, 1992). Members of this group occur primarily at bathyal depths throughout the Indo-Pacific Ocean.

**Comparisons** Among western Atlantic tonguefishes, *S. nebulosus* overlaps only *S. jenynsi* in some meristic features but can easily be distinguished from the latter by its 14 caudal-fin rays (vs. 10 in *S. jenynsi*), black peritoneum, and ocular-side pigmentation without pattern of crossbanding (vs. unpigmented peritoneum and ocular surface usually with pattern of crossbanding in *S. jenynsi*), in having complete dentition on both ocular-side jaws (reduced dentition on ocular-side premaxilla and teeth absent on ocular-side dentary in *S. jenynsi*), more numerous scales in longitudinal series (120–135 vs. 102–119 in *S. jenynsi*), its different ID pattern (1-2-2 vs. 1-4-3 in *S. jenynsi*), its larger eye (94–113 vs. 74–95 in *S. jenynsi*), in having 5 hypurals (vs. 4 in *S. jenynsi*), and by its much narrower (BD 165–282 SL in *S. nebulosus* vs. 231–328 SL in *S. jenynsi*) and smaller body (maximum sizes ca. 87 mm in *S. nebulosus* vs. >300 mm in *S. jenynsi*).

Body depth measurements in *S. nebulosus* approximate those in juvenile and small adult *S. marginatus*, another deepwater western Atlantic species (see below). However, *S. nebulosus* lacks the conspicuous dark brown blotch on the ocular-side caudal region of the body and posterior dorsal and anal fins and also lacks the stripe along basal margins of the dorsal and anal fins (both features present in *S. marginatus*). In addition, *S. marginatus* differs in having 12 caudal-fin rays, fewer total vertebrae (51–56), dorsal-fin rays (93–104), anal-fin rays (80–89), and fewer scales in a longitudinal series (86–99), its larger eye (125–248 HL), and ID pattern (1-3-2 in *S. marginatus*).

Of tonguefishes occurring outside the western Atlantic Ocean, *S. nebulosus* most closely resembles two deepwater species: *S. variegatus*, known only from two specimens taken in the western Indian Ocean off South Africa; and *S. ligulatus*, a species in the eastern Atlantic and Mediterranean Sea that possibly forms an amphi-Atlantic species pair with *S. nebulosus*. All three species have similar numbers of caudal-fin rays, slender bodies, and possess a 1-2-2 ID pattern. *Symphurus nebulosus* is distinguished from *S. variegatus* in having more vertebrae (57–60, usually 58–59 vs. 56 in *S. variegatus*). Within the genus, *S. nebulosus* is most similar to *S. ligulatus*. Comparisons of *S. ligulatus* and *S. nebulosus* revealed subtle but significant differences between these two species in 8 of 14 morphometric characters examined (Munroe, 1990). According to results from a discriminant function analysis (DFA), notable differences occur in postorbital and head lengths (both longer in *S. nebulosus*), lower head lobe width (wider in *S. nebulosus*), and body depth, which is somewhat deeper in *S. nebulosus* (BD 16.5–28.2% SL, but usually 22.5–24.0% SL vs. 19.4–23.8%, but usually 21.0–22.0% SL in *S. ligulatus*). *Symphurus nebulosus*, despite having a more darkly pigmented body in general, has only a slight band of pigment, if any, on the ocular-side upper lip. In contrast, *S. ligulatus* specimens generally have a well-developed band of pigment on both ocular-side lips. The species also differ in modal counts of total vertebrae (58–59 in *S. nebulosus* vs. 59–60 in *S. ligulatus*).

*Symphurus nebulosus* is readily distinguished from *S. vanmelleae*, a deepwater tropical eastern Atlantic species, in caudal-fin rays (14 vs. 12 in *S. vanmelleae*), vertebrae (9 abdominal vertebrae, 57–60, modally 58–59, total vertebrae vs. 10–11 abdominal and 56–58 total vertebrae in *S. vanmelleae*), modally higher meristic features (dorsal-fin rays 105–113 in *S. nebulosus* vs. 101–108 in *S. vanmelleae*; anal-fin rays 91–98 vs. 86–93), and ID patterns (1-2-2-2-2 vs. 1-2-2-1-2 or 1-2-2-2-1 in *S. vanmelleae*).

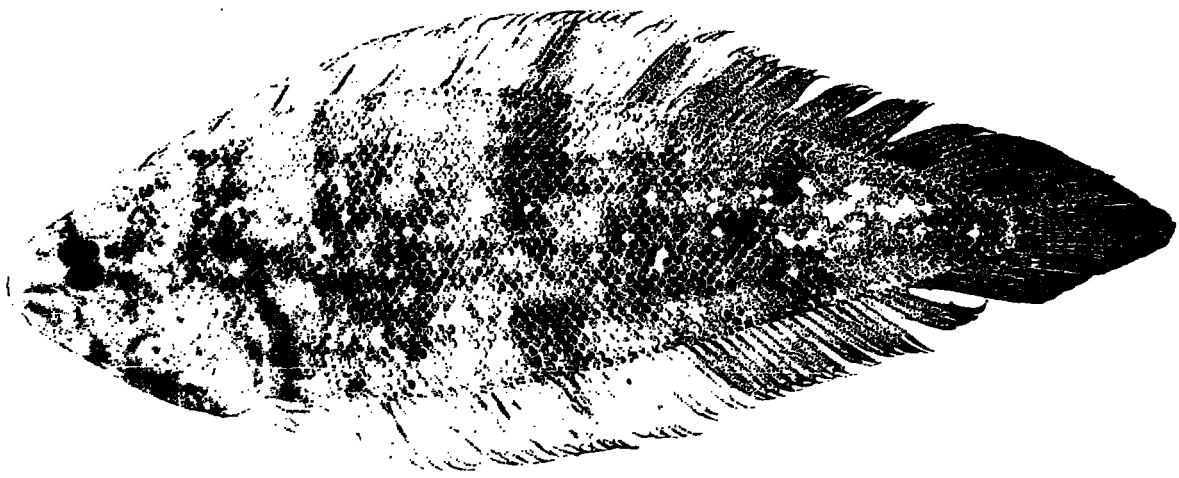

**Figure 12**
*Symphurus arawak* Robins and Randall, USNM 267784, 29.3 mm SL, off Belize 16°48'N, 88°04'W.

### *Symphurus arawak* Robins and Randall, 1965 (Figs. 6A, 12, 13; Tables 1–10, 12) Caribbean tonguefish

*Symphurus arawak* Robins and Randall, 1965:331 (original description with photograph; Curaçao). Böhlke and Chaplin, 1968:223 (Bahamas; diagnosis, counts, figure, distribution). Randall, 1968:166 (Caribbean distribution). Starck, 1968:31 (Alligator Reef, Florida). Topp and Hoff, 1972:107 (distribution). Garzon and Acero, 1983:106 (Caribbean Sea, Colombia; counts, measurements, photograph). Munroe, 1990:509 (maximum size and size at maturity). Munroe, 1992:368, 377 (ID pattern; geographic, bathymetric distributions). Cervigón et al., 1993:306 (Venezuela).

**Diagnosis** *Symphurus arawak* is a distinctive species characterized by a predominant 1-3-2 ID pattern; 12 caudal-fin rays; 39–42 total vertebrae; 70–76 dorsal-fin rays; 55–61 anal-fin rays (the lowest vertebral and fin-ray counts of any species in the genus); 55–65 scales in longitudinal series; unpigmented peritoneum; teeth along entire margin of ocular-side jaws; without pupillary operculum; without scales on blind sides of dorsal- and anal-fin rays; without fleshy ridge on ocular-side lower jaw; without membrane ostia in dorsal and anal fins; ocular surface pigmentation consisting of crossbands and, in some adults, of a darkly pigmented caudal blotch; with pepper-dots (Fig. 5B, number 8) on blind side of body (especially prominent on larger adults); dorsal, anal, and caudal fins without spots, but some adults with darkly pigmented blotch on posterior dorsal and anal fins; and small adult size (usually <50 mm).

**Description** *Symphurus arawak* is a dwarf species reaching maximum sizes of only ca. 50 mm SL. ID pattern usually 1-3-2 (35/41 specimens), rarely 1-2-2 or 1-3-3 (Table 2). Caudal-fin rays usually 12 (38/43), rarely 11, 13, or 14 (Table 3). Dorsal-fin rays 70–76 (Table 4). Anal-fin rays 55–61 (Table 5). Total vertebrae 39–42, usually 40–41 (38/45) (Table 6). Hypurals 4 (45/45). Longitudinal scale rows 55–65, usually 58–64 (Table 7). Scale rows on head posterior to lower orbit 12–15, usually 14–15 (Table 8). Transverse scales 27–36, usually 32–36 (Table 9).

Proportions of morphometric features presented in Table 12. Body relatively deep, of stocky build with greatest depth in anterior one-third of body; body depth tapering rapidly posterior to midpoint. Preanal length slightly smaller than body depth. Head long and wide; somewhat shorter than body depth. Head length usually slightly shorter than head width (HW:HL 0.9–1.3, $\bar{x}$=1.1). Postorbital length considerably smaller than body depth. Lower head lobe width nearly equalling postorbital length; slightly smaller than width of upper head lobe. Lower opercular lobe of ocular side considerably wider than upper opercular lobe. Snout long and pointed; cov-

**Table 12**

Morphometrics for holotype (ANSP 101985) and 39 other specimens of *Symphurus arawak*. (Abbreviations defined in methods section; SL is expressed in mm; characters 2 to 14 are expressed in thousandths of SL; 15 to 21 in thousandths of HL; *n* = no. of specimens measured.)

| Character | Holotype | *n* | Range | Mean | SD |
|---|---|---|---|---|---|
| 1. SL | 33.1 | 40 | 11.7–49.3 | 28.2 | 8.18 |
| 2. BD | 254 | 40 | 254–377 | 317.2 | 24.98 |
| 3. PDL | 94 | 39 | 49–145 | 93.1 | 15.12 |
| 4. PAL | 302 | 40 | 188–350 | 300.2 | 30.96 |
| 5. DBL | 909 | 40 | 649–941 | 903.3 | 44.33 |
| 6. ABL | 695 | 40 | 495–776 | 687.0 | 39.75 |
| 7. PL | 76 | 36 | 60–100 | 83.6 | 9.88 |
| 8. PA | 66 | 40 | 43–99 | 66.4 | 10.53 |
| 9. CFL | 160 | 34 | 120–204 | 169.6 | 17.99 |
| 10. HL | 275 | 40 | 182–299 | 265.8 | 20.58 |
| 11. HW | 299 | 40 | 225–316 | 282.0 | 17.04 |
| 12. POL | 169 | 40 | 114–188 | 156.6 | 15.96 |
| 13. UHL | 184 | 40 | 109–192 | 153.3 | 15.23 |
| 14. LHL | 130 | 40 | 110–174 | 140.0 | 14.73 |
| 15. POL | 615 | 40 | 500–660 | 588.7 | 34.46 |
| 16. SNL | 198 | 40 | 163–307 | 224.2 | 32.90 |
| 17. UJL | 231 | 40 | 200–333 | 235.6 | 23.42 |
| 18. ED | 132 | 40 | 97–200 | 144.1 | 19.71 |
| 19. CD | 165 | 40 | 132–347 | 204.8 | 36.14 |
| 20. OPLL | 253 | 39 | 229–379 | 288.5 | 34.64 |
| 21. OPUL | 220 | 39 | 159–303 | 230.8 | 30.17 |

ered to tip with small ctenoid scales; scales not embedded, but rather deciduous. Dermal papillae well developed on snout and chin of blind side. Anterior nostril on ocular side moderately long, almost reaching anterior margin of lower eye when depressed posteriorly. Jaws moderately long; maxilla usually extending posteriorly to vertical through middle, or sometimes only to vertical through anterior margin of pupil of lower eye, rarely only reaching vertical through anterior margin of lower eye. Ocular-side lower jaw without fleshy ridge. Teeth well developed on all jaws. Ocular-side dentary usually with complete row of slender teeth; less frequently teeth present only on anterior three-fourths of dentary. Ocular-side premaxilla with single row of teeth on anterior three-fourths of margin of upper jaw. Chin depth nearly equal to length of snout. Lower eye large; eyes usually equal in position. Anterior and medial surfaces of eyes not covered with scales; usually with 1 or 2, occasionally 3, small scales in narrow interorbital region. Pupillary operculum absent. Dorsal-fin origin usually reaching point between verticals through anterior margin and midpoint of upper eye; predorsal length long. No scales on blind sides of dorsal- and anal-fin rays. Pelvic fin long; longest pelvic-fin ray, when extended posteriorly, usually reaching base of first anal-fin ray. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anal-fin origin (membrane torn in many specimens). Caudal fin long. Scales large, strongly ctenoid on both sides of body.

**Pigmentation (Fig. 12)** Coloration similar for both sexes. Ocular surface usually off-white or pale yellowish, with about one-half of individuals with 2–7 (usually 4–5), conspicuous, dark brown, complete crossbands on body that sometimes extend onto fin rays. Other specimens with short, incomplete crossbands forming 6–10 large, and variably positioned, dark brown blotches on body; blotches best developed on caudal one-third of body. Blotches (rarely large ovoid spots) in midbody region somewhat offset, best developed on body in dorsal and ventral regions at bases of dorsal and anal fins. Each scale on body and head with numerous small melanophores, but background coloration pale in contrast to dark crossbands or blotches on body. Melanophores more heavily concentrated on scales in caudal one-third of body, forming dark caudal patch in some specimens. Crossbands on body, relatively wide, usually 4–8 scale rows wide, and beginning immediately posterior to opercular opening and continuing to base of caudal fin. Posteriormost pair of crossbands usually conjoined, forming darkly pigmented, M- or Y-shaped mark near point approximately one-third distance between caudal-fin base and opercular opening. Most specimens with narrow, dark, vertical bar extending from upper eye to dorsal profile, otherwise head with same background coloration as found on body. Dorsal margin of outer surface of ocular-side opercle with small dark spot near opercular opening, but otherwise with same general background pigmentation as body. Inner linings of both opercles and isthmus on both sides of body unpigmented. Band of pigmentation of variable intensity usually developed on ocular-side upper lip; lower lip on ocular side without pigmented band. Dark spot usually present in posterior angle of ocular-side jaws. Blind side of body in approximately one-half of specimens (mostly those larger than ca. 20 mm) with small pepper-dots extending variable distances along trunk, but usually best developed and most heavily concentrated in region overlying proximal pterygiophores of dorsal- and anal-fin rays and covering entire caudal one-third of body (Fig. 5B). Peritoneum unpigmented.

Anteriormost dorsal and anal fins without obvious pattern of spots or blotches, but with dark brown melanophores along length of each finray; melanophores becoming increasingly darker, almost dark brown or black, and more heavily concentrated in

posterior one-third of body. Posteriorly progressive increase in density of melanophores on fin rays throughout length of dorsal and anal fins, sometimes forming small blotches in area of fins proximate to body regions with blotches or crossbands. Melanophores particularly dense on dorsal- and anal-fin rays in caudal one-third of body, making posterior fin rays usually strikingly darker than those in anterior regions of fins. Caudal fin dark brown or black throughout entire length.

**Size and sexual maturity (Fig. 6A)** *Symphurus arawak* attains a maximum size of only ca. 50 mm (Fig. 6A) and is among the smallest of flatfishes (see "Discussion" section below). Most individuals were 25–40 mm, and only 3/42 exceeded 40 mm. Maximum size of females (49.3 mm) was somewhat larger than that of males (38.0 mm). Diminutive size is reflected in this species' ontogeny, as juveniles 11.7, 13.2, and 13.9 mm had already metamorphosed and assumed a benthic existence.

Specimens examined included 7 immature fish (sex undetermined, 11.7–28.0 mm), 10 males (23.3–38.0 mm), and 29 females (24.0–49.3 mm). Sexual maturity of females occurs at ca. 25–30 mm. Most females 24–30 mm had elongate ovaries, but only some had developing ova. Females larger than 30 mm had elongate ovaries that were either gravid or contained developing ova. The smallest gravid female was 30 mm. Nine females between 21–30 mm were immature with ovaries undergoing posterior elongation without visible ova.

**Geographic distribution (Fig. 13)** Throughout the Caribbean Sea, extending south and west to Isla de Tierra Bomba, Colombia; and a single capture at Alligator Reef, Florida (Starck, 1968). The majority of specimens were collected in the Bahamas and insular Caribbean regions including Curaçao, Dominica, Haiti, Jamaica, Puerto Rico, Providencia Island, and Cayman Islands. Robins and Randall (1965) reported this species at St. John, Virgin Islands. In addition to capture at Alligator Reef, other specimens were collected at continental reef areas at Belize and Cabo de la Aguja (one specimen) and Bahía de Gayraca (three specimens), Colombia (Garzon and Acero, 1983).

**Bathymetric distribution** The majority of *S. arawak* have been captured on sandy bottoms in clear wa-

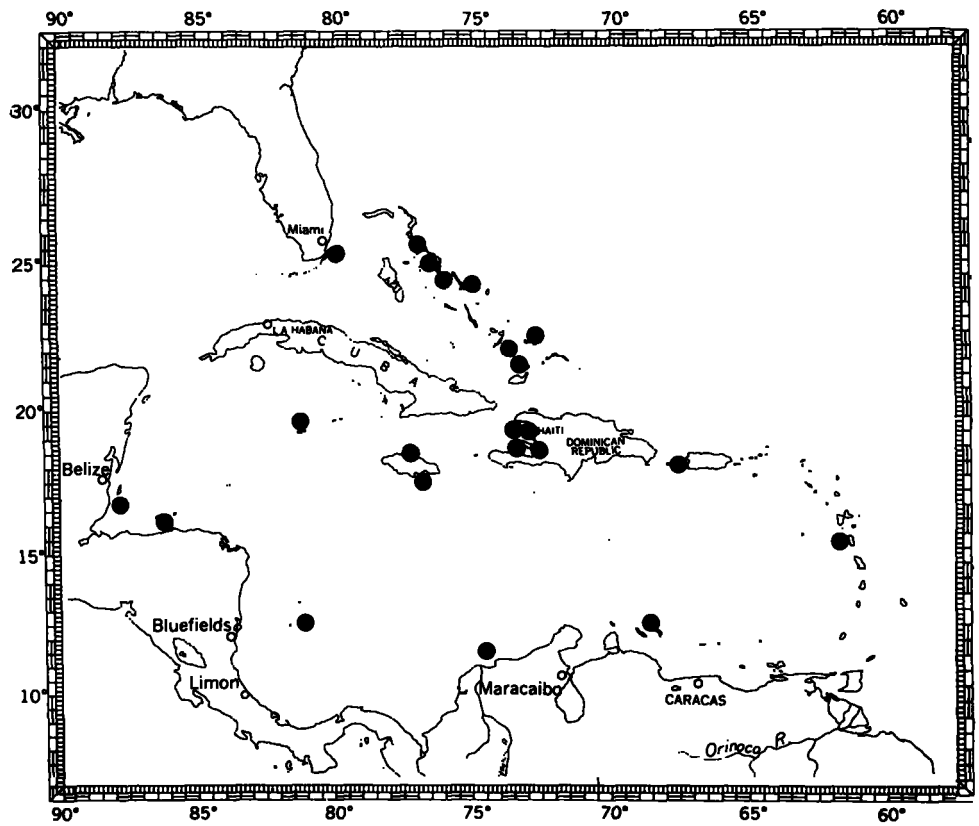


**Figure 13**

Geographic distribution of *Symphurus arawak* based on material examined (discussion of geographic distribution appears in species account).

ters adjacent to coral reefs at depths of 6–39 m, most between 6 and 30 m (Table 10). Only three specimens were taken deeper than 30 m (one each at 31, 34, and 39 m). Little else is known concerning the life history of this diminutive flatfish.

**Remarks** Robins and Randall (1965) tentatively proposed that *S. arawak* and *S. minor* are a north–south species pair occurring in tropical and warm temperate regions of the western Atlantic that may have differentiated because of repeated latitudinal fluctuations in the fish fauna during glacial and interglacial periods in the western Atlantic. This hypothesis is not supported by information presented in Munroe (1987; 1992), who has hypothesized that *S. arawak* and *S. minor* belong to different species groups within the genus. *Symphurus arawak* is a member of the species group characterized by a 1-3-2 ID pattern, 12 caudal-fin rays, lack of a pupillary operculum, and lack of ostia in basal portions of the dorsal- and anal-fin membranes. *Symphurus minor*, in turn, belongs to the species group characterized by a 1-4-2 ID pattern, 10 caudal-fin rays, and possessing a well-developed pupillary operculum and membrane ostia. Similarities between *S. arawak* and *S. minor* in meristic features and in small adult sizes do not appear to be synapomorphies that reflect a common ancestry but, rather, are probably convergently evolved traits.

**Comparisons** *Symphurus arawak* has the lowest counts for any species in the genus (Munroe, 1992). Among tonguefishes, only the western Atlantic *S. minor* and the sympatrically occurring *S. ommaspilus* approach the ranges in meristic features and small size of *S. arawak*. However, *S. arawak* differs significantly from these species in caudal-fin ray counts (12 vs. 10 in the others), absence of a pupillary operculum and membrane ostia (both present in *S. minor* and *S. ommaspilus*), a pepper-dot pattern of melanophores on the blind side of the body (absent in *S. minor* and *S. ommaspilus*), and *S. arawak* has modally fewer vertebrae (40–42 vs. 41–43 in *S. minor* and 43–44 in *S. ommaspilus*), and a different ID pattern (1-3-2 vs. 1-4-2 in *S. minor* and *S. ommaspilus*, respectively). *Symphurus arawak* differs further from *S. ommaspilus* in having body crossbands or a darkly pigmented blotch on the ocular side and no spots on the dorsal and anal fins (vs. uniformly whitish body without crossbands or pigmented blotch but having a single ocellated spot on dorsal and anal fins of *S. ommaspilus*).

*Symphurus arawak* is similar to three other Atlantic dwarf species, the sympatric *S. rhytisma* and two dwarf species, *S. lubbocki* Munroe and *S. reticulatus* Munroe, occurring on shallow-water substrates at midocean and eastern Atlantic islands. *Symphurus arawak* is easily separated from these others because of its lower counts (dorsal-fin rays 70–76 vs. 82–89; anal-fin rays 55–61 vs. 68–75, and total vertebrae 39–42 vs. 46–49 in these others). *Symphurus arawak* also has considerably larger and fewer (55–65) scales in a longitudinal series compared with those of *S. rhytisma* (91–97), *S. lubbocki* (107–109), and *S. reticulatus* (101–109). None of the other dwarf *Symphurus* have pepper-dot pigmentation on the blind side, and for each of these other species the pattern of pigmentation on the ocular surface also differs significantly from that of *S. arawak*. In *S. rhytisma*, ocular-side pigmentation consists of crossbands on the trunk, with usually the two posteriormost crossbands coalesced and forming a heavily pigmented caudal patch. *Symphurus lubbocki* has a cream-colored ocular surface with several, mostly incomplete, crossbands, whereas the ocular-side pattern of *S. reticulatus* is dark, chocolate-brown with alternating X- and Y-shaped markings, and in this species the dorsal and anal fins also have an alternating series of blotches and unpigmented areas (vs. uniformly pigmented areas and intensified pigmentation in caudal region in *S. arawak*).

*Symphurus pelicanus* is a diminutive (usually <70 mm), relatively deepwater, western Atlantic tonguefish that, reminiscent of *S. arawak*, also has a pepper-dot pattern of melanophores on the blind side of the body, 12 caudal-fin rays, and a 1-3-2 ID pattern. *Symphurus arawak* is easily distinguished from *S. pelicanus* by its unpigmented peritoneum (vs. black in *S. pelicanus*), lower meristic features (vs. dorsal-fin rays 77–85, anal-fin rays 64–70, and total vertebrae 43–46 in *S. pelicanus*), in having unpigmented inner opercular linings and isthmus (vs. inner opercular linings and isthmus sprinkled with melanophores in *S. pelicanus*), and *S. pelicanus* lacks the pigmented blotch on the ocular side of the body that is present on some adult *S. arawak*.

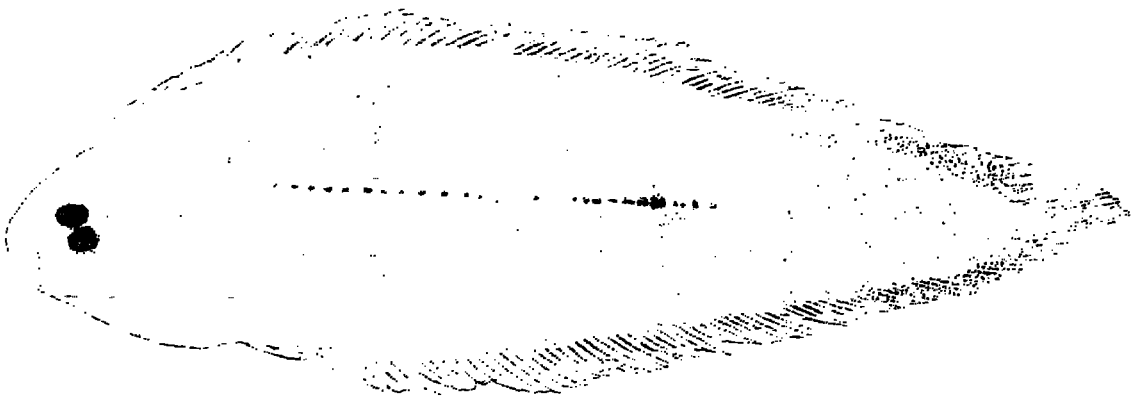

**Figure 14**
*Symphurus rhytisma* Böhlke, FMNH 94821, 21.7 mm SL, Belize at Glovers Reef.

### *Symphurus rhytisma* Böhlke, 1961 (Figs. 6B, 14, 15; Tables 1–10, 13) Patchtail tonguefish

*Symphurus rhytisma* Böhlke, 1961:3 (original description with photograph; Bahamas). Robins and Randall, 1965:334 (Curaçao, Lagoen; counts, measurements). Böhlke and Chaplin, 1968:224 (distribution, redescription, counts, figure). Munroe, 1990:485, 488 (comparison with eastern and mid-Atlantic species of *Symphurus*). Munroe, 1992:368, 377 (ID pattern; geographic, bathymetric distributions).

*Symphurus plagusia* (not of Schneider, in Bloch and Schneider, 1801). Andreata and Séret, 1995:590 (two specimens; inner continental shelf Brazil).

**Diagnosis** *Symphurus rhytisma* is readily distinguished from all congeners by the combination of 1-3-2 ID pattern; 12 caudal-fin rays; 83–87 dorsal-fin rays; 68–71 anal-fin rays; 46–48 total vertebrae; 91–97 scales in longitudinal series; unpigmented peritoneum; absence of pupillary operculum; absence of fleshy ridge on ocular-side lower jaw; teeth along entire margin of ocular-side jaws; absence of scales on blind sides of dorsal- and anal-fin rays; absence of membrane ostia in dorsal and anal fins; unpigmented blind side; ocular surface pigmentation generally consisting of several incomplete, dark brown crossbands contrasting against pallid background and of darkly pigmented blotch covering posterior one-third of ocular side of body (in all but largest specimens); with dorsal and anal fins unpigmented anteriorly, with pigmented blotches in midbody region, and heavy pigmentation on both sides of fins in caudal region; and small adult size (<50 mm).

**Description** *Symphurus rhytisma* is a dwarf species, attaining maximum size of only ca. 45 mm SL. ID pattern 1-3-2 (Table 2). Caudal-fin rays 12 (Table 3). Dorsal-fin rays 83-87 (Table 4). Anal-fin rays 68–71 (Table 5). Total vertebrae 46–48, usually 47 (Table 6). Hypurals 4 (9/9). Longitudinal scale rows 91–97 (Table 7). Scale rows on head posterior to lower orbit 18–20, usually 18 (Table 8). Transverse scales 43–45 (Table 9).

Proportions of morphometric features of specimens from Caribbean and Brazilian localities appear separately in Table 13 (description is based on Caribbean material only because the Brazilian specimens were in poor condition and measurements were imprecise and unreliable). Body moderately deep, maximum depth in anterior one-third of body; body depth tapering fairly moderately posterior to anus. Preanal length slightly shorter than body depth. Head long and narrow; head width considerably narrower than body depth. Head length usually just slightly shorter than head width (HW:HL 1.0–1.3, $\bar{x}$=1.09). Postorbital length considerably shorter than body depth. Lower head lobe moderately wide, less than postorbital length; narrower than upper head lobe. Lower opercular lobe of ocular side considerably wider than

**Table 13**

Morphometrics for holotype (ANSP 93812) and seven other specimens of *Symphurus rhytisma*. Data for Caribbean specimens ($n$=6) listed above those for Brazilian specimens ($n$=2). (Abbreviations defined in methods section; SL is expressed in mm; characters 2 to 14 are expressed in thousandths of SL; 15 to 21 in thousandths of HL; $n$ = no. of specimens measured.)

| Character | Holotype | $n$ | Range | Mean | SD |
|---|---|---|---|---|---|
| 1. SL | 25.6 | 6 | 21.7–45.1 | 31.5 | 8.71 |
| | | 2 | 26.7–27.0 | 26.8 | — |
| 2. BD | 297 | 6 | 295–333 | 302.4 | 17.46 |
| | | 2 | 243–266 | 254.5 | — |
| 3. PDL | 78 | 6 | 69–78 | 72.0 | 3.44 |
| | | 2 | 64–67 | 65.5 | — |
| 4. PAL | 262 | 6 | 262–295 | 274.1 | 13.25 |
| | | 2 | 262–307 | 284.5 | — |
| 5. DBL | 938 | 6 | 929–960 | 937.2 | 11.66 |
| | | 2 | 933–936 | 934.5 | — |
| 6. ABL | 738 | 6 | 719–767 | 737.0 | 17.70 |
| | | 2 | 730–772 | 751.0 | — |
| 7. PL | 78 | 6 | 70–83 | 78.2 | 4.60 |
| | | 1 | 82 | — | — |
| 8. PA | 66 | 6 | 35–66 | 54.2 | 12.19 |
| | | 2 | Not available | | |
| 9. CFL | 113 | 6 | 104–143 | 119.4 | 13.32 |
| | | 1 | 139 | — | — |
| 10. HL | 262 | 6 | 203–262 | 235.1 | 21.75 |
| | | 2 | 243–262 | 252.5 | — |
| 11. HW | 262 | 6 | 241–264 | 256.3 | 11.00 |
| | | 2 | 236–277 | 256.5 | — |
| 12. POL | 160 | 6 | 126–160 | 148.0 | 11.92 |
| | | 2 | 150–157 | 153.5 | — |
| 13. UHL | 152 | 6 | 134–166 | 154.0 | 11.04 |
| | | 2 | 161–176 | 168.5 | — |
| 14. LHL | 125 | 6 | 108–131 | 117.2 | 8.78 |
| | | 2 | 112–120 | 116.0 | — |
| 15. POL | 612 | 6 | 588–773 | 633.2 | 69.29 |
| | | 2 | 600–615 | 607.5 | — |
| 16. SNL | 224 | 6 | 206–250 | 228.0 | 15.92 |
| | | 2 | 200–231 | 215.5 | — |
| 17. UJL | 224 | 6 | 175–250 | 214.8 | 27.30 |
| | | 2 | 231–243 | 237.0 | — |
| 18. ED | 119 | 6 | 108–165 | 136.2 | 22.47 |
| | | 2 | 123–157 | 140.0 | — |
| 19. CD | 239 | 6 | 213–277 | 238.3 | 22.82 |
| | | 2 | 171–200 | 185.5 | — |
| 20. OPLL | 269 | 6 | 238-325 | 280.0 | 34.76 |
| | | 2 | 229–262 | 245.5 | — |
| 21. OPUL | 194 | 6 | 159–268 | 209.2 | 38.35 |
| | | 2 | 154–171 | 162.5 | — |

upper opercular lobe. Snout moderately long and pointed; mostly naked. Scales, when present on snout, deciduous and only in areas where dermal papillae absent. Dermal papillae dense, large and obvious on snout regions of both sides of body; extending onto chin region of blind side. Anterior nostril on ocular side long, usually reaching anterior margin of lower eye when depressed posteriorly. Jaws moderately long; maxilla usually extending posteriorly to vertical through anterior margin of pupil of lower eye; occasionally reaching vertical through midpoint of lower eye. Ocular-side lower jaw without fleshy ridge. Teeth well developed on all jaws. Blind-side jaws with small band of teeth on both upper and lower jaws. Ocular-side jaws usually with single row of teeth along complete margin of jaw; occasionally with teeth present only on anterior three-fourths of ocular-side premaxilla and dentary. Chin depth slightly shorter than snout length. Lower eye moderate in size; eyes usually equal in position, or with upper eye slightly in advance of lower eye. Anterior and medial surfaces of eyes usually not covered with scales; 0–4 small ctenoid scales in narrow interorbital region. Pupillary operculum absent. Dorsal-fin origin usually equal with vertical through midpoint of upper eye; predorsal length long. Scales absent on blind sides of dorsal- and anal-fin rays. Pelvic fin moderately long; longest pelvic-fin ray, when extended posteriorly, usually reaching base of first anal-fin ray. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anus, or occasionally extending posteriorly almost to origin of anal fin (membrane torn in some specimens). Caudal fin moderately long. Scales ctenoid, relatively small.

**Pigmentation (Fig. 14)** Coloration similar for both sexes. Ocular surface generally pallid, usually with traces of 2–8 (usually 8) incomplete, narrow, brown crossbands on head and body. Smaller individuals with conspicuous dark blotch on caudal region of body. Larger individuals with more diffuse and less well-defined caudal blotch; therefore this pigmentation feature may be better developed and more characteristic of juveniles. Crossbands usually beginning on head about at level equal with fifth dorsal-fin ray, and continuing at irregular intervals to base of caudal fin. Two anteriormost crossbands often incomplete and faintly pigmented, barely perceptible without magnification. Third crossband at, or slightly posterior to, anal-fin origin, most often across entire body and usually darkest of anteriormost crossbands. Posteriormost two crossbands on trunk usually conjoined, forming caudal blotch. Only crossbands in middle of body (usually fifth, sixth, and eighth), if any, extending onto fin rays of dorsal and anal fins. Head usually with two faintly pigmented crossbands about 3–4 scale rows wide; anteriormost crossband immediately posterior to eyes; posterior pigment band crossing distal margin of operculum. Ocular-side outer opercle usually with same background coloration as body. Inner linings of opercles and isth-

mus on both sides of body unpigmented. No pigment evident on ocular-side lips. Blind side uniformly pale, off-white. Some specimens with single, median line of black dermal spots showing through skin along axis of vertebral column on blind side (Fig. 5B, number 9). Peritoneum unpigmented.

Dorsal and anal fins unpigmented anteriorly, fins in midregion of body with pigmented blotches (extensions of body crossbands onto fins); dorsal and anal fins becoming increasingly pigmented in caudal region. In smaller specimens, especially, fin rays and membranes on both sides of vertical fins in region of caudal blotch heavily pigmented. Posteriormost dorsal- and anal-fin rays with pigment concentrated on proximal one-half of finrays forming a diffuse dark blotch on fins. Proximal one-third of caudal fin usually covered with dark melanophores; posterior two-thirds of fin unpigmented.

**Size and sexual maturity (Fig. 6B)** Of nine specimens studied, five were males (25.7–36.6 mm), two females (32.7, 45.1 mm), and two juveniles (21.7, 25.6 mm) of indeterminate sex. Males and females are somewhat similar in size. The largest female was gravid with obvious ova present throughout the elongate ovary. A second female (32.7 mm) was mature, or was approaching maturity, because its ovaries were elongate, but without any obvious ova. The small sizes (ca. 33–45 mm) at which this species reaches sexual maturity indicate that *S. rhytisma* is a dwarf species (Fig. 6B).

**Geographic distribution (Fig. 15)** Known mostly from Caribbean region of western North Atlantic with two specimens tentatively identified as *S. rhytisma* (see "Remarks" section below) collected off Espirito Santo, Brazil (between 20°S and 21°S latitude). This species has not been collected very frequently (only nine specimens located for this study). Of six Caribbean collections, three were made in the Bahamas, and the others at Glovers Reef, Belize, and Curaçao.

**Bathymetric distribution** All but one collection of *S. rhytisma* from the Caribbean region were made at stations treated with rotenone on sandy substrates adjacent to coral reefs. For six specimens with depth of capture information, two were from 6 m, and single specimens were collected at each of the following depths: 3, 14, 16, and 25 m (Table 10). Two specimens captured off Brazil (reported as *S. plagusia*) were taken by trawling at 37 and 97 m (Andreata and Séret, 1995).

**Remarks** Two specimens (USU 1054 and 1079) collected off Brazil are tentatively identified as *S. rhytisma*. Both are small (26.7 and 27.0 mm) males. Meristic features, including ID pattern (both 1-3-2), total vertebral counts (47; 47), dorsal-fin rays (83; 83), and anal-fin rays (70; 71) lie within ranges reported for *S. rhytisma* (see Tables 4–9), as do most morphometric features (Table 13). Scale counts or counts of scale pockets could not be taken from either specimen because scales were missing and the skin was abraded in many places. Coloration of both specimens is uniformly yellowish-whitish on the ocular surface, in agreement with most other specimens studied. However, neither has any trace of the pigmented caudal patch found on some other *S. rhytisma* specimens. One specimen (USU 1079) has some dark pigment on the posteriormost regions of the dorsal and anal fins that may be the remnants of a caudal blotch. Both specimens have a series of dermal melanophores along the vertebral column in the body midregion that is also found in other *S. rhytisma* specimens.

A 25.7-mm specimen (USNM 324677, from 15°42'N, 63°38'W near Isla de Aves in the Lesser Antilles) included in the material examined listed for *S. pelicanus* in Munroe (1992:402) is actually *S. rhytisma*.

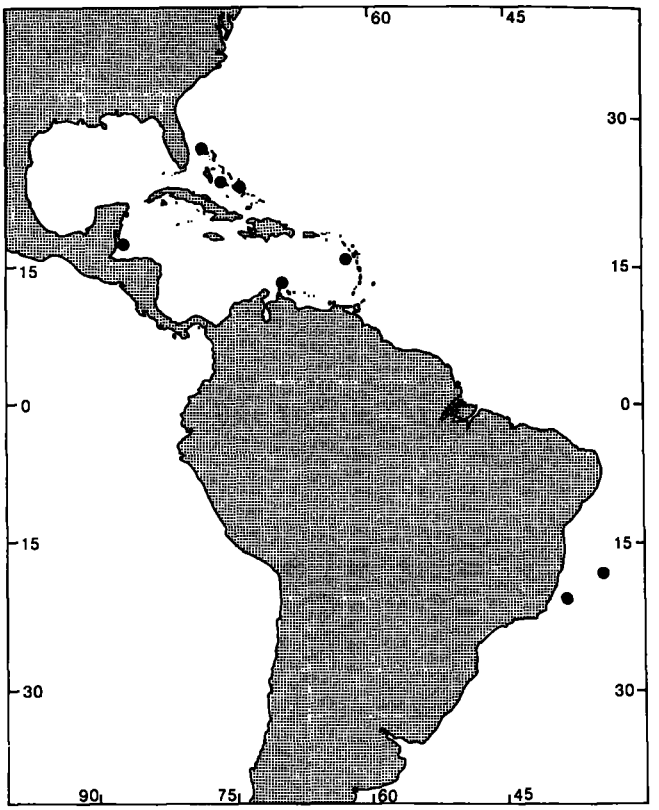


**Figure 15**

Geographic distribution of *Symphurus rhytisma* based on material examined (discussion of geographic distribution appears in species account).

**Comparisons** In the western Atlantic and Caribbean region, only *S. rhytisma* and *S. arawak* possess the combination of a 1-3-2 ID pattern, 12 caudal-fin rays, unpigmented peritoneum, and small adult size. *Symphurus rhytisma* is readily diagnosed from *S. arawak* by differences outlined in the "Comparisons" section of the account for *S. arawak*.

*Symphurus rhytisma* has some meristic features that overlap those of two deepwater, western Atlantic species, *S. pusillus* and *S. piger*. Although both have a 1-3-2 ID pattern and 12 caudal-fin rays as does *S. rhytisma*, they are easily separated from *S. rhytisma* in having a black peritoneum (unpigmented in *S. rhytisma*) and by lacking a pigmented blotch on the caudal region of the ocular side of the body (present in *S. rhytisma*). *Symphurus rhytisma* has much smaller and more numerous scales in a longitudinal series than does either of the other species (91–97 in *S. rhytisma* vs. 62–75 in *S. piger* and 77–87 in *S. pusillus*). *Symphurus rhytisma* also has fewer anal-fin rays (68–71) than does *S. pusillus* (71–75). *Symphurus rhytisma* differs further from *S. piger* in having an unpigmented isthmus and inner opercular linings (vs. lightly pigmented in *S. piger*), 4 hypurals (vs. 5 in *S. piger*), and in its much smaller size (45 mm vs. ca. 130 mm in *S. piger*).

Other Atlantic species most closely resembling *S. rhytisma* are *S. lubbocki* and *S. reticulatus*, dwarf species of tonguefishes collected in shallow-water habitats in insular locations in the central and eastern Atlantic. *Symphurus rhytisma* may be distinguished from both species by its lower meristic features (dorsal-fin rays 83–87 vs. 87–89 in *S. lubbocki* and *S. reticulatus*; anal-fin rays 68–71 vs. 74–75; total vertebrae 46–48 vs. 48–49 in these other species), somewhat larger scales (91–97 scales in a longitudinal series vs. 101–109 in the other two species), and by differences in pigmentation. In *S. rhytisma*, all but the largest specimens have a dark blotch across the posterior one-third of the body (vs. no blotch in these other species), and the ocular surface of the body of *S. rhytisma* generally has a series of incomplete, dark brown crossbands contrasting against a pallid background. This combination of features contrasts with that observed in *S. reticulatus*, which has a dark, chocolate-brown body with X- and Y-markings and a series of alternating blotches and unpigmented areas in the dorsal and anal fins, and that observed in *S. lubbocki*, which has a cream-colored background, lacks a caudal blotch, and which has dorsal and anal fins uniformly and lightly pigmented.

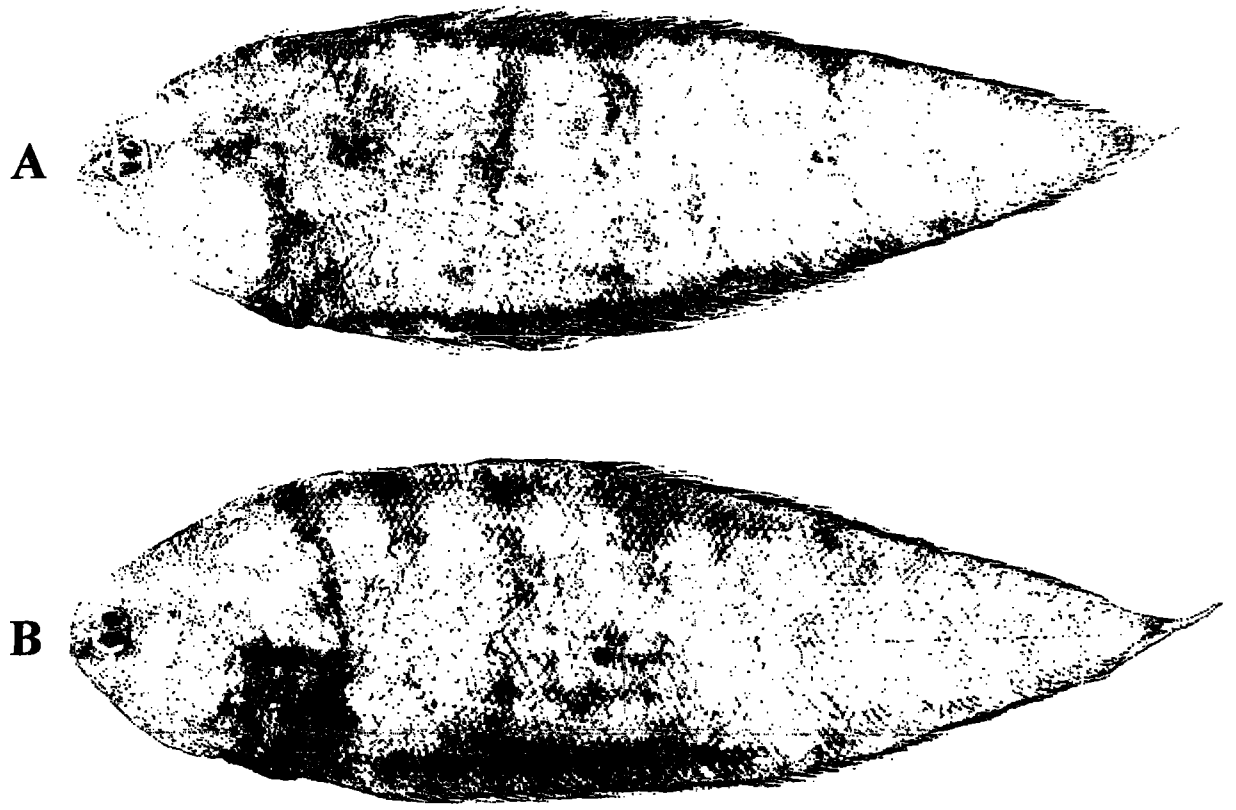


**Figure 16**

*Symphurus billykrietei* new species. (**A**) Holotype, USNM 326637, 112.2 mm SL, western Atlantic 36°41.4'–41.8'N, 74°40'–39.7'W. (**B**) Paratype, MCZ 91580, 108.1 mm SL, western Atlantic 39°32'N, 72°25'W.

## *Symphurus billykrietei*, new species (Figs. 8A, 16–21; Tables 1–10, 14–15) Kriete's tonguefish

*Symphurus pterospilotus* (not of Ginsburg, 1951). Scott and Scott, 1988:561 (Canadian Atlantic region; photograph).

*Symphurus* species C. (in part). Munroe, 1992:368, 377 (ID pattern; geographic, bathymetric distributions; data for *S. stigmosus* also included in account of *S. billykrietei*).

**Holotype** USNM 326637; (112.2 mm); off Virginia, 36° 41.4'–41.8'N, 74°40.1'–39.7'W; 275 m; 17 Sep 1975. Collection information for 69 paratypes listed in Appendix.

**Diagnosis** *Symphurus billykrietei* is a deepwater species distinguished from all congeners, except the western South Atlantic *S. ginsburgi*, by the following combination of characters: predominant 1-3-2 ID pattern; 12 caudal-fin rays; 4 hypurals; 89–95 dorsal-fin rays; 76–84 anal-fin rays; 50–53 total vertebrae; 80–100 scales in longitudinal series; black peritoneum; relatively small eye without pupillary operculum; small space between eyeballs within orbital sac; teeth along entire margin of ocular-side jaws; ocular-side lower jaw without fleshy ridge; absence of scales on blind sides of dorsal- and anal-fin rays; ocular-surface light to dark brown with bold crossbanding, but without darkly pigmented blotch across caudal region of body; blind side uniformly yellowish, without pepper-dots; with dark brown stripe, covering both fin rays and connecting membranes, on basal one-third of dorsal and anal fins; and with small darkly pigmented spot on scaly portion (proxi-

mal one-third) of caudal fin, but without distinct spots or blotches on distal two-thirds of caudal fin. *Symphurus billykrietei* is distinguished from *S. ginsburgi* by its smaller eye, longer trunk length, shorter head and postorbital lengths, shorter snout, and shorter upper jaw.

**Description** A medium-size species attaining maximum sizes of ca. 119 mm SL. ID pattern usually 1-3-2 (89/92 specimens), rarely 1-3-3 or 1-4-2 (Table 2). Caudal-fin rays usually 12 (84/91), rarely 11 (Table 3). Dorsal-fin rays 89–95, usually 91–94 (Table 4). Anal-fin rays 76–84, usually 77–81 (Table 5). Total vertebrae 50–53, usually 51–52 (82/92) (Table 6). Hypurals 4 (92/92). Longitudinal scales 80–100, usually 85–94 (Table 7). Scale rows on head posterior to lower orbit 16–22, usually 18–21 (Table 8). Transverse scales 38–49 (Table 9).

Proportions of morphometric features presented in Table 14. Body relatively deep, maximum depth in anterior one-third of body; body depth tapering rapidly posterior to midpoint. Trunk relatively long. Preanal length smaller than body depth. Head moderately short and relatively wide, narrower than body depth. Head length slightly smaller than head width (HW:HL 0.99–1.4, $\bar{x}$=1.1). Postorbital length considerably smaller than body depth. Lower head lobe width slightly smaller than postorbital length; narrower than upper head lobe. Lower opercular lobe of ocular side considerably wider than upper opercular lobe. Snout short, somewhat rounded; covered with small ctenoid scales. Dermal papillae well developed on blind-side snout; frequently also on ocular-side snout. Anterior nostril on ocular side usually reaches anterior margin of lower eye when depressed posteriorly. Jaws short; maxilla extending posteriorly almost to vertical through anterior margin of lower eye pupil. Ocular-side lower jaw without a fleshy ridge. Teeth well developed on blind-side jaws. Ocular-side dentary with row of teeth along complete margin of jaw. Ocular-side premaxilla with single row of slender teeth, or occasionally with only anterior three-fourths of margin of bone bearing teeth. Chin depth usually equal to or slightly larger than snout length. Lower eye moderately large; eyes usually equal in position and with small space between eye balls within orbital sac. Anterior and medial surfaces of eyes partially covered with 3–5 rows of small ctenoid scales; 1–2 scales in narrow interorbital region. Pupillary operculum absent. Dorsal-fin origin reaching vertical through midpoint of upper eye, occasionally only reaching vertical through anterior margin of pupil of upper eye; predorsal length long. Scales absent on blind sides of dorsal- and anal-fin rays. Pelvic fin moderately long; longest pelvic-fin ray reaching base of first anal-fin ray when depressed. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anus, or occasionally extending posteriorly almost to anal-fin origin (membrane torn in most specimens). Caudal fin moderately long. Scales moderate in size, ctenoid on both sides of body.

**Table 14**

Morphometrics for holotype (USNM 326637) and 69 additional specimens of *Symphurus billykrietei*. (Abbreviations defined in methods section; SL is expressed in mm; characters 2 to 15 are expressed in thousandths of SL; 16 to 22 in thousandths of HL; *n* = no. of specimens measured.)

| Character | Holotype | *n* | Range | Mean | SD |
|---|---|---|---|---|---|
| 1. SL | 112.2 | 69 | 49.6–112.2 | 75.3 | 17.49 |
| 2. BD | 324 | 36 | 251–328 | 294.2 | 18.56 |
| 3. TKL | 812 | 69 | 774–891 | 795.8 | 8.61 |
| 4. PDL | 46 | 36 | 35–58 | 48.3 | 5.56 |
| 5. PAL | 201 | 36 | 200–249 | 224.7 | 13.14 |
| 6. DBL | 954 | 36 | 942–965 | 951.7 | 5.56 |
| 7. ABL | 782 | 36 | 736–815 | 767.7 | 16.58 |
| 8. PL | 57 | 32 | 45–84 | 64.3 | 8.74 |
| 9. PA | 36 | 35 | 34–88 | 54.8 | 11.70 |
| 10. CFL | 117 | 35 | 100–147 | 121.2 | 8.98 |
| 11. HL | 188 | 69 | 187–226 | 204.3 | 8.66 |
| 12. HW | 238 | 36 | 207–270 | 234.3 | 16.39 |
| 13. POL | 120 | 69 | 116–201 | 133.9 | 10.07 |
| 14. UHL | 152 | 36 | 113–174 | 154.9 | 12.49 |
| 15. LHL | 97 | 35 | 93–128 | 107.3 | 9.21 |
| 16. POL | 640 | 69 | 600–728 | 651.7 | 25.32 |
| 17. SNL | 194 | 69 | 157–240 | 198.1 | 18.48 |
| 18. UJL | 213 | 69 | 179–253 | 206.8 | 15.70 |
| 19. ED | 123 | 69 | 98–143 | 119.8 | 9.94 |
| 20. CD | 251 | 36 | 166–289 | 222.2 | 26.60 |
| 21. OPLL | 261 | 36 | 232–352 | 298.4 | 31.88 |
| 22. OPUL | 237 | 36 | 164–315 | 219.5 | 33.85 |

**Pigmentation (Fig. 16)** Coloration similar for both sexes. Ocular surface light to dark brown, usually with 5–8 irregular, darker brown crossbands on head and body. Crossbands on body variable in intensity, usually 3–6 scales wide, and not continued onto dorsal and anal fins. Anteriormost crossband on opercular region of head faintly pigmented. All crossbands on body, except second anteriormost, usually incomplete and more intensely shaded on dorsal and ventral regions of body, rather diffuse in midsection of body. Some older, faded specimens with dark blotches along body only at bases of dorsal and anal fins (remnants of bands?). Second crossband, located immediately posterior to operculum, almost always continuous across abdominal region of body and the most intensely pigmented. Ocular-side outer opercle usually with similar background coloration as body. Some

specimens with dark spot at upper angle of ocular-side opercle. Inner linings of both opercles and isthmus on both sides of body usually unpigmented. Ocular-side lips almost always pigmented; upper lip usually with well-defined band of pigment, occasionally only lightly spotted; lower lip usually spotted, occasionally with dark pigment band. Specimens lacking scales uniformly yellowish to light brown with pattern of melanophores forming distinct V-shaped pigmentation on head region, dorsal and anterior to eyes. Blind side uniformly yellowish; some specimens (especially those without scales and faded in color) with median series of conspicuous dark black melanophores in dermis along axis of vertebral column (Fig. 5B, number 9) on both sides of body (most obvious in middle and posterior regions of body). Peritoneum black, showing through abdominal wall on both sides.

Dorsal and anal fins lightly pigmented anteriorly. Posterior to region of anteriormost crossband on body, basal portions of dorsal and anal fins usually darker, forming continuous narrow dark brown stripe on proximal portions of fin rays and connecting membranes; stripe not continuing across base of caudal fin. Specimens missing scales with series of black, dermal melanophores evident at bases of anteriormost dorsal-fin rays. Caudal fin with irregularly shaped spot on scaly portion of fin base; distal two-thirds of caudal fin generally unpigmented, occasionally speckled with melanophores to distalmost tips of fin rays.

**Size and sexual maturity (Fig. 8A)** *Symphurus billykrietei* is a medium-size tonguefish attaining lengths to ca. 119 mm, although most specimens were smaller (56–105 mm). The largest fish, a female measuring 119.0 mm, was slightly larger than the largest male (112.2 mm). Among 92 specimens for which sex was determined, 37 were females (49.6–119.0 mm) and 55 males (50.1–112.2 mm). Sexual maturity occurs at a relatively large size (ca. 80 mm) in females. Of 37 females, 21 (80.9–119.0 mm) were mature with elongate and gravid ovaries. The smallest mature females were 80.9, 83.9, 85.0, and 87.4 mm. Sixteen immature females (49.6–75.5 mm) had ovaries just undergoing elongation.

**Etymology** This species is named in honor of Billy Kriete, a former marine scientist at VIMS, and a friend whose great sense of humor and friendship are sadly missed.

**Geographic distribution (Fig. 17)** On the continental shelf in the western North Atlantic primarily from off southern Nova Scotia (ca. 43°N) and southward along the continental shelf of the United States to approximately Cape Hatteras, North Carolina (ca. 35°N latitude). Records south of Cape Hatteras, although few and infrequent, include a single specimen each from just south of Cape Hatteras (USNM 327180 at 34°46'N), from the eastern Gulf of Mexico in the Straits of Florida south of Dry Tortugas (USNM 158310), and from the southcentral Gulf of Mexico north of the Yucatan Peninsula (FMNH 88815).

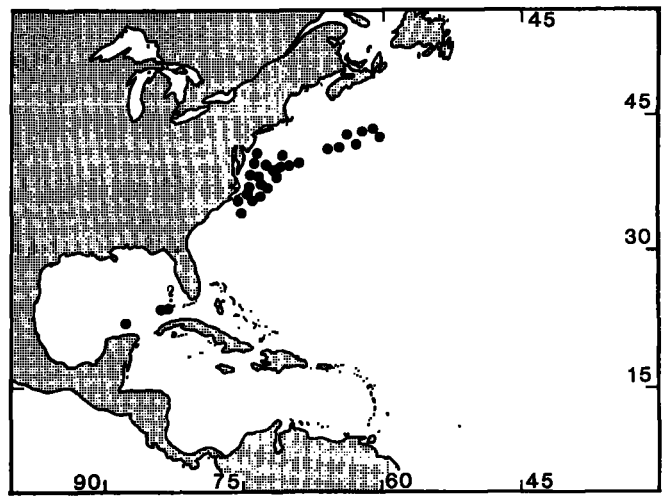


**Figure 17**
Geographic distribution of *Symphurus billykrietei* based on material examined (discussion of geographic distribution appears in species account).

Although the majority of specimens have been collected off southern New England and the mid-Atlantic Bight, *S. billykrietei* is captured frequently off the southern Scotian Shelf. In fact, this may be the only *Symphurus* species to occur commonly on the outer continental shelf in this region. It is interesting to note that among fish collected on the Scotian Shelf were several gravid females, indicating that spawning may occur even in northern portions of the species range.

*Symphurus billykrietei* has occasionally been captured in the Gulf of Mexico, although this species is apparently not abundant in deep waters of that region. Extensive trawling surveys of deep-sea fishes from north, central, and western areas of the Gulf, conducted at depths where this species is expected, have yielded only a few specimens of this species.

**Bathymetric distribution** *Symphurus billykrietei* is commonly collected on mud substrates on the outer continental shelf (Table 10) at depths ranging from 117 m (one specimen, VIMS 1601) to 650 m (one specimen, VIMS 9190). The bathymetric center of abundance, where over 91% (82/90) of specimens were collected, is in moderate depths between 201–380 m. Only two specimens were trawled at greater depths

(one each at 397 and 650 m), whereas nine others were trawled at shallower depths (48–183 m). Specimens of the shallowest and deepest captures for this species were taken off Virginia. As with most other deepwater tonguefishes, little is known concerning the ecology of this species.

**Remarks** One lot (UMML 27173) containing four specimens, one male (77.2 mm) and three gravid females (68.4, 70.6, and 73.5 mm) collected at 366 m in the Straits of Florida south of the Dry Tortugas (24°18'N, 82°33'W), is tentatively identified as *S. billykrietei*, but not included in the type series or in summaries of counts, morphometrics, and life history information. These specimens agree in some characteristics, such as ID pattern, meristic features, and pigmentation, with other specimens of *S. billykrietei*. However, several differences between these fish and those identified as *S. billykrietei* preclude positive identification. Prominent crossbands on the ocular surface, a dark stripe along basal regions of the dorsal and anal fins, and presence of a pigmented spot at the caudal-fin base are characteristic of both *S. billykrietei* and *S. ginsburgi*. However, eye diameter measurements in these specimens are larger (133–155 HL) than those (ED 102–147 HL) usually encountered in *S. billykrietei* and are more similar to measurements of *S. stigmosus* (described below) or *S. ginsburgi* (see below). Another difference is that the eyeballs of these specimens are more rounded and contiguous along their uppermost borders, quite unlike the condition found in *S. ginsburgi* or *S. billykrietei*, where the more elongate eyeballs are usually separated in the orbital sac by a small, but obvious, space. The rounded shape and close proximation of the eyeballs in these specimens is reminiscent of conditions found in *S. stigmosus*. But here again, significant differences between these specimens and those identified as *S. stigmosus* preclude positive identification. For example, specimens in UMML 27173 lack conspicuous blotches on dorsal and anal fins (characteristic of *S. stigmosus*), all have a spot at the caudal-fin base not found on any *S. stigmosus*, and longitudinal scale counts of all four specimens are lower (85–91) than those for *S. stigmosus*. In fact, these scale counts are more similar to those found in *S. billykrietei* or *S. ginsburgi* (Table 7). Possibly, these specimens are hybrids between *S. billykrietei* and *S. stigmosus*. Alternatively, the similarity of many features of these specimens to those of *S. ginsburgi* raises the possibility that they are that species, to date known only from off southeastern Brazil (at 21°S) to Uruguay. It is doubtful, however, that these specimens are *S. ginsburgi*, because the eyeballs differ in shape and arrangement within the orbital sac in relation to those in specimens of *S. ginsburgi* from off South America. These specimens from the Straits of Florida would also represent a northward extension of some 4,500–4,800 km beyond the northernmost location previously recorded for *S. ginsburgi* (see summary of capture locations for that species listed below).

**Comparisons** Among congeners, *S. billykrietei* is most similar to the western South Atlantic *S. ginsburgi*. Meristic features of these species overlap completely (see Tables 1–9), and there are many other similarities between these species in overall body shapes (see Table 15) and pigmentation patterns (compare Figs. 16 and 24). Despite varying degrees of overlap in 20 morphometric features examined, significant differences ($P<0.05$) were found (ANCOVA, Table 15) between these species in the following relations (Figs. 18–19): TKL on SL; HL on SL; SNL on HL; and for SNL, HL, UJL, and ED each regressed on trunk length. In a comparison of the two species, the most distinctive differences are that *S. billykrietei* has a longer trunk length in relation to its standard length, a shorter head with shorter postorbital length, and the snout, upper jaw, and eye are also smaller in comparison with those respective features in *S. ginsburgi*. Although several statistically significant differences in morphometric features

**Table 15**

Shape differences between *Symphurus ginsburgi* ($n$=53) and *S. billykrietei* ($n$=53) revealed by ANCOVA for selected morphometric features. Abbreviations defined in methods section; asterisks indicate significant values ($P<0.05$).

| Species | Relationship | $P$ |
|---|---|---|
| *ginsburgi* | $TKL = 0.801\ SL - 1.29$ | 0.009* |
| *billykrietei* | $TKL = 0.827\ SL - 2.13$ | |
| *ginsburgi* | $HL = 0.199\ SL + 1.30$ | 0.004* |
| *billykrietei* | $HL = 0.182\ SL + 1.43$ | |
| *ginsburgi* | $SNL = 0.218\ HL - 0.148$ | 0.018* |
| *billykrietei* | $SNL = 0.141\ HL + 0.877$ | |
| *ginsburgi* | $SNL = 0.0522\ TKL + 0.293$ | 0.005* |
| *billykrietei* | $SNL = 0.0376\ TKL + 0.751$ | |
| *ginsburgi* | $HL = 0.246\ TKL + 1.72$ | 0.010* |
| *billykrietei* | $HL = 0.218\ TKL + 2.02$ | |
| *ginsburgi* | $UJL = 0.0505\ TKL + 0.515$ | 0.041* |
| *billykrietei* | $UJL = 0.0405\ TKL + 0.713$ | |
| *ginsburgi* | $ED = 0.0348\ TKL + 0.194$ | 0.016* |
| *billykrietei* | $ED = 0.0285\ TKL + 0.117$ | |

were found, the best visualized demarcation of differences between these species is the ratio of ED to TKL plotted against head length (Fig. 20). There is little ontogenetic change evident in this ratio for *S. billykrietei*, and a slight increase in the ratio with increasing head length for *S. ginsburgi*; however, the ratio is usually greater for *S. ginsburgi* than for *S. billykrietei*, especially in larger individuals. For *S. ginsburgi*, 87% of 54 individuals had a ratio exceeding 3.5, whereas 96% of the specimens had a ratio exceeding 3.4. In contrast, estimated ratios in specimens of *S. billykrietei* ($n$=69) were lower, with 91% of the specimens having a ratio of ED to TKL less than 3.5, whereas 94% had a ratio less than 3.6. *Symphurus billykrietei* is also a larger species than *S. ginsburgi* (compare Figs. 7B and 8A), reaching maximum known size of 119 mm, with most adult specimens (72/88) reaching lengths greater than 65 mm, and females not reaching maturity until a minimum of 80 mm. In contrast, *S. ginsburgi* reach only ca. 90 mm, with most specimens much smaller (55/61 specimens were smaller than 65 mm); some female *S. ginsburgi* begin maturing at sizes as small as 44 mm and some gravid females are as small as 51–53 mm.

*Symphurus billykrietei* is similar to *S. stigmosus*, another deepwater, western North Atlantic tonguefish in this species group, but differs most noticeably from this species in lacking the prominent series of pigmented blotches alternating with unpigmented areas of equal or greater size on the posterior two-thirds of the dorsal and anal fins characteristic of *S. stigmosus*. *Symphurus billykrietei* usually

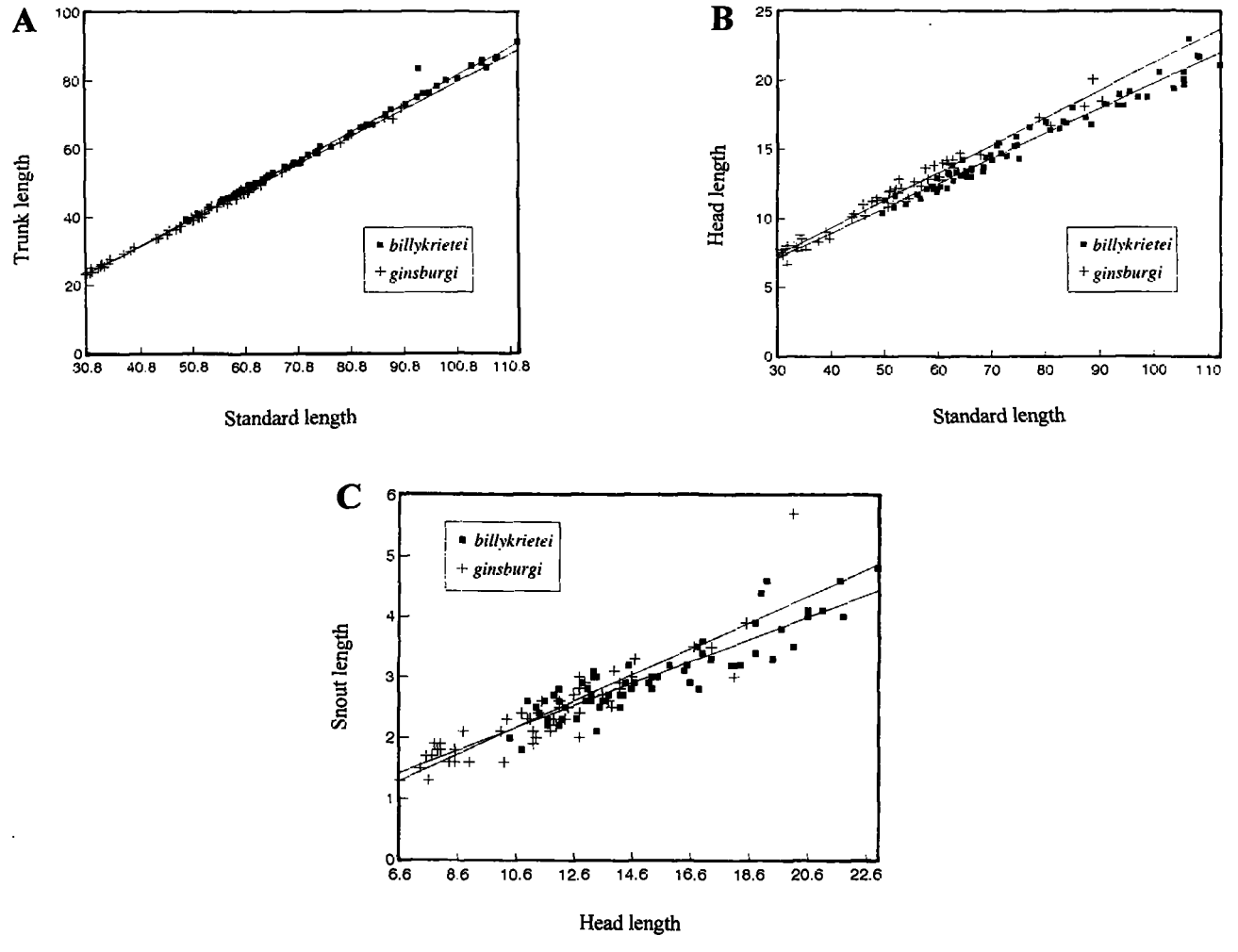


**Figure 18**

Comparisons of selected morphometric features of *Symphurus billykrietei* and *S. ginsburgi* (measurements in mm). (**A**) Trunk length versus standard length. (**B**) Head length versus standard length. (**C**) Snout length versus head length. (Regression equations and $P$-values for differences between lines appear in Table 15.)

has a pattern of bold, ocular-surface crossbanding and a pigmented spot on the scaly basal portion of the caudal fin, features lacking in *S. stigmosus*. The lower eye diameter in *S. billykrietei* is also smaller (98–156 HL, $\bar{x}$=120) than that in *S. stigmosus* (128–171 HL, $\bar{x}$=152). Smaller eye size is also evident in plotting ratios of ED to TKL against head length (Fig. 20); 91% of the *S. billykrietei* ($n$=69) have a ratio less than 3.5, whereas 94% have a ratio less than 3.6. In contrast, 10/12 *S. stigmosus* have a ratio exceeding 3.7, and none have a ratio less than 3.5. The two species differ in eyeball shape (compare Fig. 21A with 21B). In *S. billykrietei*, the eyeball is more elongate, with its length slightly greater than its width, and usually there is a small space between the eyeballs. In contrast, the eyeball of *S. stigmosus* is more rounded, and uppermost aspects of the eyeballs are usually contiguous.

Among other western Atlantic members of this species group, meristic features of *S. billykrietei* partially overlap those of *S. marginatus*, *S. pusillus*, and *S. piger*. From *S. marginatus*, *S. billykrietei* differs in having crossbanding on the ocular surface (lacking in *S. marginatus*) and in lacking the dark brown blotch on the caudal region of the ocular side of the body that characterizes *S. marginatus*. *Symphurus billykrietei* also has lower meristic features (dorsal-fin rays 89–95 vs. 93–104; anal-fin rays 76–84 vs. 80–89, and total vertebrae 50–53, usually 51–52 vs. 52–56, usually 52–54 in *S. marginatus*), and a relatively stockier and deeper body with its greatest

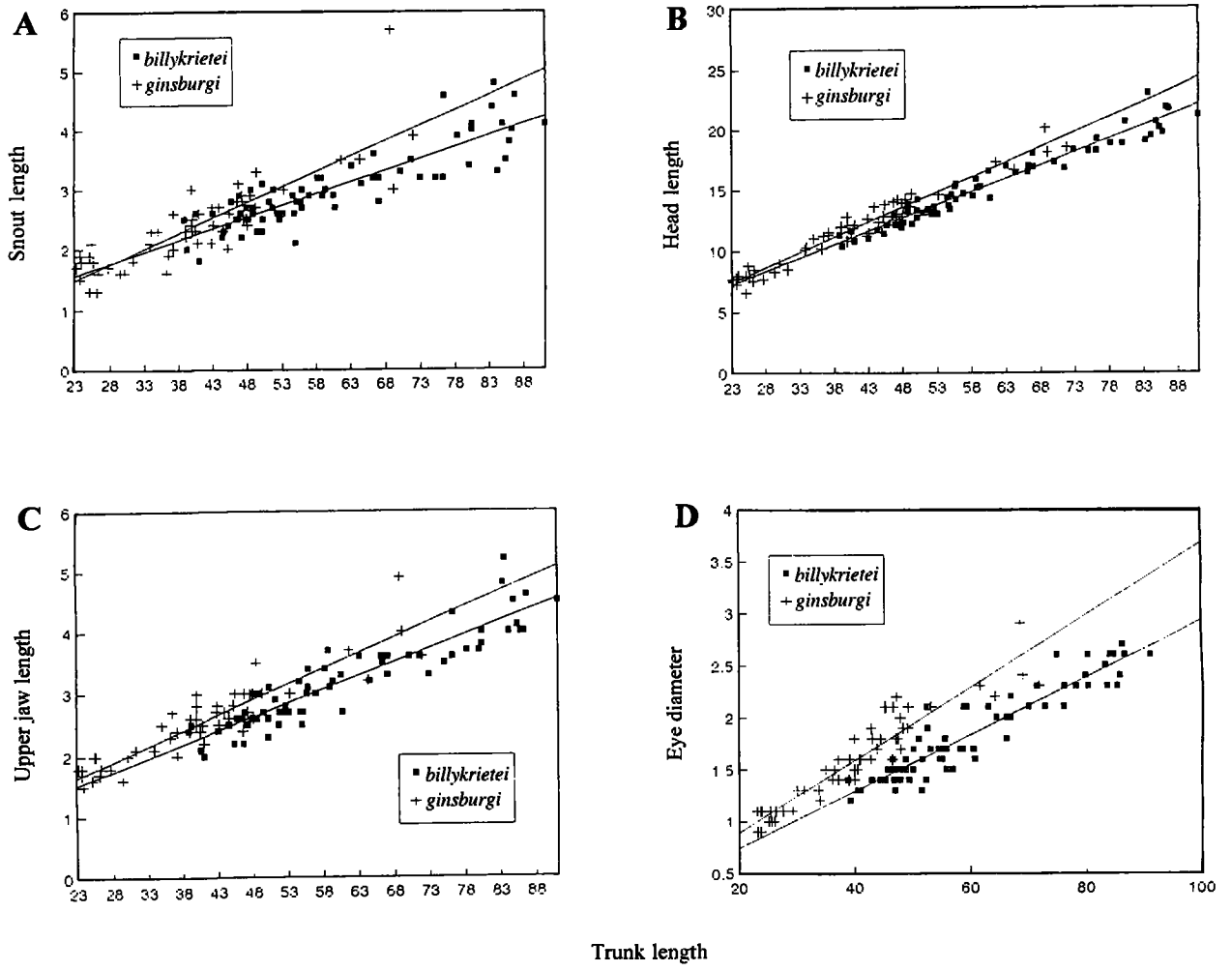


**Figure 19**

Comparison of selected morphometric features of *Symphurus billykrietei* and *S. ginsburgi* (measurements in mm). (**A**) Snout length versus trunk length. (**B**) Head length versus trunk length. (**C**) Upper jaw length versus trunk length. (**D**) Eye diameter versus trunk length. (Regression equations and *P*-values for differences between lines appear in Table 15.)

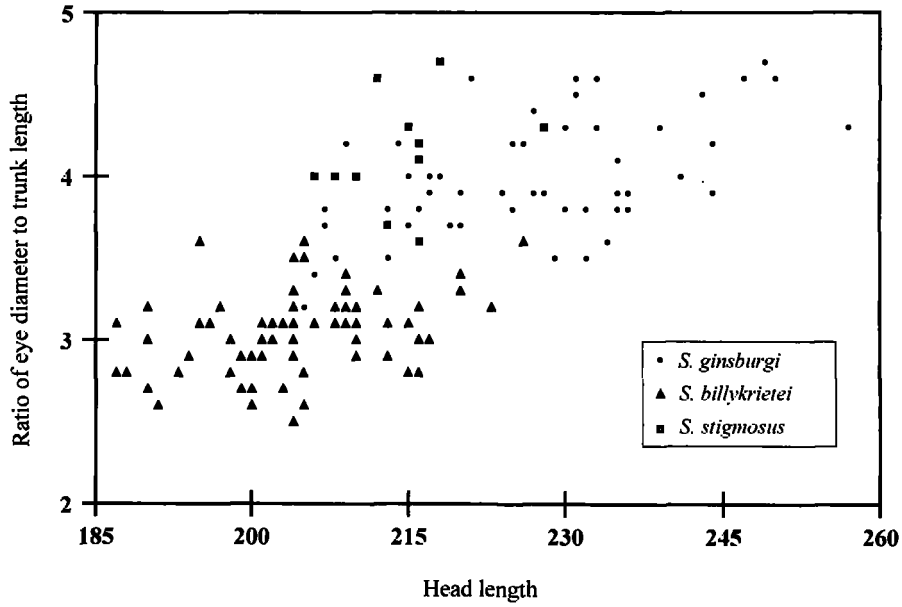


**Figure 20**

Relation of the ratio of eye diameter to trunk length, plotted against head length (in thousandths of SL) for *Symphurus billykrietei*, *S. stigmosus*, and *S. ginsburgi*.

depth in the anterior one-third (vs. a more elongate body with more uniform body depth and greatest depth at body midpoint in *S. marginatus*).

The ocular-side coloration in *S. billykrietei* is very similar to that observed in the sympatric *S. pusillus*, but differs from this species in its higher and mostly nonoverlapping meristic features (dorsal-fin rays 89–95 vs. 83–88 in *S. pusillus*; anal-fin rays 76–84 vs. 71–75; and 50–53 total vertebrae vs. 47–49 in *S. pusillus*). The two species also differ in that *S. billykrietei* has a dark brown stripe along basal margins of the dorsal and anal fins, whereas these fins in *S. pusillus* lack a basal stripe, instead having only a diffuse speckling of brown pigment, and, on their distal margins, often a yellowish color.

Some meristic features and aspects of ocular-side coloration of *S. billykrietei* are similar to those in *S. piger*, a deepwater species widespread in the Gulf of Mexico and Caribbean Sea. *Symphurus billykrietei* differs from *S. piger* in lacking a fifth hypural (present in *S. piger*), in its more elongate body (compare Figs. 16 and 34), in its more numerous fin rays (89–95 dorsal-fin rays and 76–84 anal-fin rays in *S. billykrietei* vs. 88 or fewer dorsal-fin rays and 74 or fewer anal-fin rays in *S. piger*), total vertebral counts (50–53 in *S. billykrietei* vs. 49 or fewer in *S. piger*), and in its longitudinal scale count (80–100 in *S. billykrietei* vs. 62–75 in *S. piger*).

*Symphurus billykrietei* can be distinguished from the eastern Atlantic *S. nigrescens* (which also possesses a 1-3-2 ID pattern, 12 caudal-fin rays, and black peritoneum) by modal differences in meristic features (dorsal-fin rays 89–95 vs. 82–92, usually 84–91 in *S. nigrescens*; anal-fin rays 76–84 vs. 69–79 in *S. nigrescens*; and 50–53, usually 51–52, total vertebrae vs. 47–51, usually 48–50, vertebrae in *S. nigrescens*). This species also has a longer caudal fin (100–147 SL, $\bar{x}$=121) than that of *S. nigrescens* (76–122 SL, $\bar{x}$=105).

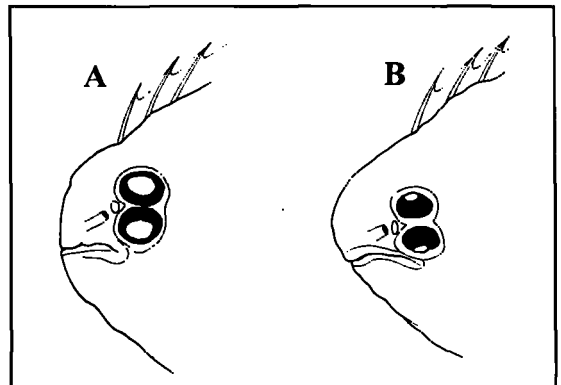


**Figure 21**

Schematic illustration indicating relative shapes and positions of eyeballs within the orbital sac for three species of western Atlantic *Symphurus*. (**A**) Round, nearly contiguous eyes of *S. stigmosus*. (**B**) Elongate, noncontiguous eyes of *S. billykrietei* and *S. ginsburgi*.

**Figure 22**
*Symphurus stigmosus* new species, Holotype, USNM 326635, 126.2 mm SL, Caribbean Sea 21°04'N, 86°19'W.

## *Symphurus stigmosus*, new species (Figs. 8B, 20–23; Tables 1–10, 16) Blotchfin tonguefish

*Aphoristia diomedeana* (not of Goode and Bean, 1885). Goode and Bean, 1895:461 (in part) (specimen from Blake station off Dominica (probably MCZ 27968) is *S. stigmosus*).

*Symphurus diomedianus* (not of Goode and Bean, 1885). Ginsburg, 1951:194 (in synonymy; based on specimen from off Dominica originally listed in Goode and Bean, 1896).

*Symphurus species* C. Munroe, 1992:368, 377 (ID pattern; geographic, bathymetric distributions; data for *S. stigmosus* included in account of *Symphurus* species C).

**Holotype** USNM 326635; (126.2 mm); off Yucatan Peninsula, 21°04'N, 86°19'W; 352 m; 10 Sep 1967. Collection information for six paratypes listed in Appendix.

**Diagnosis** *Symphurus stigmosus* is a deepwater species, distinguished from all congeners by the following combination of characters: predominant 1-3-2 ID pattern; 12 caudal-fin rays; 4 hypurals; 92–95 dorsal-fin rays; 78–81 anal-fin rays; 51–52 total vertebrae; 98–100 scales in longitudinal series; black peritoneum; relatively large eye without pupillary operculum; eyeballs rounded with their uppermost aspects usually contiguous (Fig. 21A); teeth along entire margin of ocular-side jaws; ocular-side lower jaw without fleshy ridge; no scales on blind sides of dorsal- and anal-fin rays; ocular surface usually uniformly light brown or yellowish, without prominent crossbands or darkly pigmented blotch on caudal region of body; blind side uniformly yellowish, without pepper-dots; dark brown longitudinal stripe on basal one-third of dorsal and anal fins covering both fin rays and intervening membranes; usually with series of distinct, darkly pigmented blotches alternating with unpigmented areas of somewhat larger size on posterior two-thirds of dorsal and anal fins; and with caudal fin uniformly hyaline, without spots or blotches.

**Description** A medium-size species attaining maximum lengths of ca. 127 mm SL. ID pattern 1-3-2 (Table 2). Caudal-fin rays 12 (11/12 specimens), rarely 11 (Table 3). Dorsal-fin rays 92–95 (Table 4). Anal-fin rays 78–81 (Table 5). Total vertebrae 51–52 (Table 6). Hypurals 4 (12/12). Longitudinal scales 98–100 (Table 7). Scale rows on head posterior to lower orbit 19–22 (Table 8). Transverse scales 40–49 in five individuals that could be counted (Table 9).

Proportions of morphometric features presented in Table 16. Body relatively deep, maximum depth in anterior one-third of body; body depth tapering rapidly posterior to midpoint. Trunk relatively long. Preanal length slightly shorter than body depth. Head moderately short and relatively wide, somewhat narrower than body depth. Head length shorter than head width (HW:HL 1.1–1.3, $\bar{x}$=1.2). Postorbital length considerably shorter than body depth. Lower head lobe width slightly less than postorbital length; somewhat narrower than upper head lobe. Lower opercular lobe of ocular side considerably

**Table 16**

Morphometrics for holotype (USNM 326635) and 11 additional specimens of *Symphurus stigmosus*. (Abbreviations defined in methods section; SL is expressed in mm; characters 2 to 15 are expressed in thousandths of SL; 16 to 22 in thousandths of HL; *n* = no. of specimens measured.)

| Character | Holotype | *n* | Range | Mean | SD |
|---|---|---|---|---|---|
| 1. SL | 126.2 | 12 | 54.4–126.2 | 82.7 | 19.49 |
| 2. BD | 310 | 12 | 252–310 | 281.0 | 21.27 |
| 3. TKL | 784 | 12 | 772–792 | 786.0 | 5.74 |
| 4. PDL | 54 | 12 | 22–57 | 46.3 | 9.73 |
| 5. PAL | 250 | 12 | 225–270 | 244.9 | 13.42 |
| 6. DBL | 950 | 12 | 943–974 | 954.8 | 9.00 |
| 7. ABL | 742 | 12 | 724–794 | 755.4 | 19.06 |
| 8. PL | 78 | 9 | 57–78 | 70.6 | 7.58 |
| 9. PA | 65 | 11 | 42–65 | 51.8 | 7.48 |
| 10. CFL | 119 | 11 | 109–138 | 127.3 | 10.54 |
| 11. HL | 216 | 12 | 206–228 | 214.0 | 5.74 |
| 12. HW | 265 | 12 | 230–270 | 252.2 | 13.66 |
| 13. POL | 138 | 12 | 124–142 | 135.1 | 5.42 |
| 14. UHL | 162 | 12 | 129–192 | 156.7 | 19.74 |
| 15. LHL | 128 | 12 | 105–130 | 119.3 | 7.83 |
| 16. POL | 637 | 12 | 599–658 | 631.1 | 19.52 |
| 17. SNL | 212 | 12 | 160–226 | 198.8 | 20.62 |
| 18. UJL | 202 | 12 | 173–250 | 209.8 | 18.65 |
| 19. ED | 128 | 12 | 128–171 | 151.5 | 11.88 |
| 20. CD | 220 | 12 | 180–282 | 220.8 | 29.63 |
| 21. OPLL | 348 | 12 | 234–361 | 319.2 | 34.60 |
| 22. OPUL | 311 | 12 | 184–311 | 232.5 | 34.59 |

wider than upper opercular lobe. Snout short and rounded; covered with small ctenoid scales. Dermal papillae well developed on blind-side snout; occasionally also present on ocular-side snout. Anterior nostril on ocular side usually just reaching anterior margin of lower eye when depressed posteriorly. Jaws short; maxilla usually extending posteriorly to point between verticals through anterior margin of pupil of lower eye and anterior margin of eye. Ocular-side lower jaw without pronounced fleshy ridge. Teeth well developed on blind-side jaws. Ocular-side dentary with row of teeth along complete margin of jaw. Ocular-side premaxilla with single row of slender teeth along margin, or occasionally only with teeth on anterior three-fourths of bone. Chin depth usually slightly larger than snout length. Lower eye moderately large and rounded (Fig. 21A); eyes usually equal in position; eyeballs usually contiguous at least at midpoint, sometimes nearly contiguous, usually without measurable space between eyeballs. Anterior and medial surfaces of eyes partially covered with 3–5 rows of small ctenoid scales. Pupillary operculum absent (but iris often with minute marginal projection at upper midpoint projecting nto pupil). Dorsal-fin origin usually reaching vertical through anterior margin of upper eye, occasionally only reaching anteriorly to point equal with vertical through anterior margin of pupil of upper eye; predorsal length long. Scales absent on blind sides of dorsal- and anal-fin rays. Pelvic fin moderately long; longest pelvic-fin ray when depressed posteriorly reaching base of first anal-fin ray. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anus, or occasionally extending posteriorly almost to anal-fin origin (membrane torn in most specimens). Caudal fin moderately long. Scales moderately small, ctenoid on both sides of body.

**Pigmentation (Fig. 22)** Coloration similar for both sexes. Ocular surface usually uniformly yellowish to yellowish-brown, without prominent crossbands or pigmented blotches on head and body, occasionally with diffuse mottling of small brown melanophores scattered over body surface or with scales on head and anterior body edged in white. Older specimens completely faded, uniformly grayish-purplish brown. Ocular-side outer opercle usually with same background coloration as body; no pigmented spot at upper angle of ocular-side opercle. Inner linings of both opercles and isthmus on both sides of body usually unpigmented; some specimens with scattering of small, white spots on inner opercular linings and both sides of isthmus. Ocular-side lips usually unpigmented, some specimens with light speckling of pigment spots, but without pronounced pigmented band. Blind side uniformly yellowish. Faded specimens without scales with median series of conspicuous dark black dermal melanophores along axis of vertebral column on both sides of body (Fig. 5B, number 9); especially prominent in anterior two-thirds of body. Peritoneum usually dark black (spotted in older, faded specimens), showing through abdominal wall on both sides.

Dorsal and anal fins lightly pigmented anteriorly; with darkly pigmented, basal longitudinal stripe and 4–6 conspicuous dark brown or black blotches on posterior two-thirds of fins. Basal portions of dorsal and anal fins with continuous, dark brown stripe equally developed on proximal half of fin rays and connecting membranes on postabdominal region of body; stripe not intensifying in caudal region or continuing onto caudal fin. Series (usually 4, sometimes 5) of darkly pigmented, nearly rectangular blotches, beginning on posterior two-thirds of dorsal fin and at about midpoint of anal fin. Blotches beginning from about middle and extending nearly to distal tips of fin rays. Blotches on dorsal fin not always parallel with those on anal fin. Pigmented blotches in each fin spaced unevenly; first and second blotches of nearly same size (about 4–5 fin rays wide) alternat-

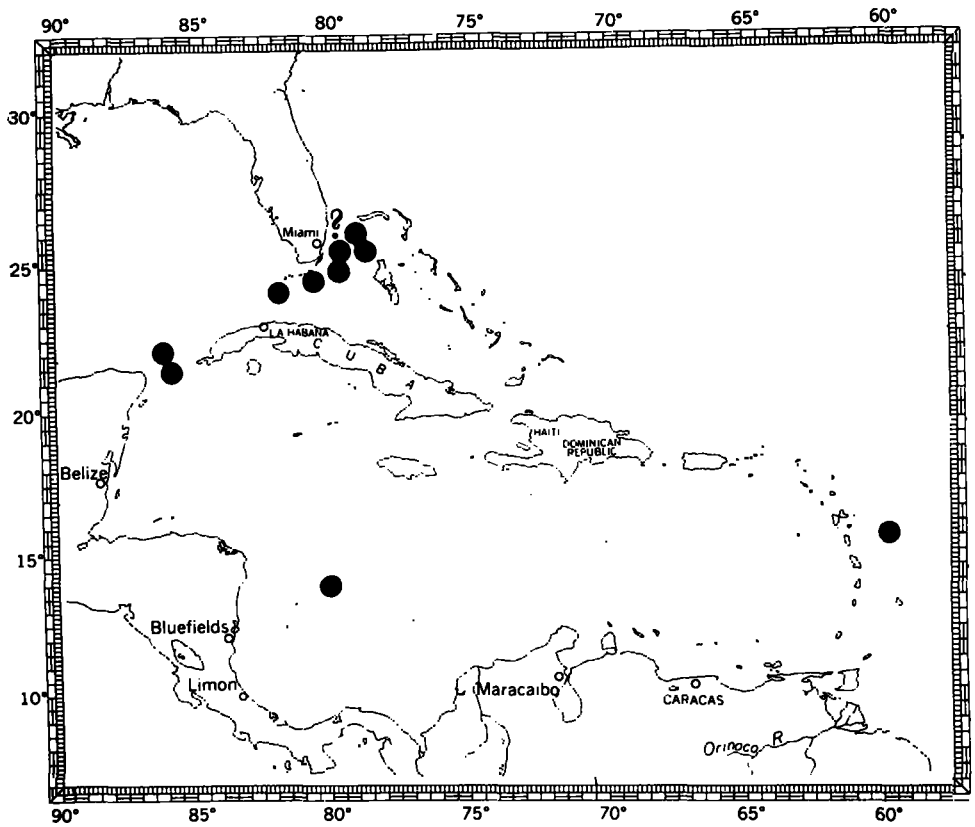


**Figure 23**

Geographic distribution of *Symphurus stigmosus* based on material examined (discussion of geographic distribution appears in species account).

ing with similar number of unblotched fin rays; two posteriormost blotches larger (6–8 fin rays wide) than blotches on anterior regions of fins and separated by more unblotched fin rays. Caudal fin uniformly hyaline, without pigmented spot on scaly, basal portion.

**Size and sexual maturity (Fig. 8B)** *Symphurus stigmosus* reaches ca. 127 mm. Size-related life history information was available only for 11 specimens, six males (59.6–98.8 mm) and five females (54.4–126.2 mm). Of females, three (85.4, 91.6, and 126.2 mm) were mature, the latter two were gravid. Two others (65.5 and 73.1 mm) had elongate ovaries without evidence of developing ova, and the smallest immature female had ovaries just undergoing elongation.

**Etymology** From the Latin *stigmosus*, meaning full of marks, in reference to the distinctive blotches on dorsal and anal fins of this species.

**Geographic distribution (Fig. 23)** In deep waters of the tropical Atlantic in the Gulf Stream and Straits of Florida between southern Florida and the Bahamas; the Straits of Florida off the Tortugas region; in the Caribbean Sea off the Yucatan Peninsula, Mexico; near Serrana Bank, Colombia (14°14'N, 80°28.5'W); and in the Lesser Antilles off Dominica. Six of 12 specimens were taken off southern Florida, four were collected off Yucatan Peninsula, and a single specimen was taken in collections off Serrana Bank and Dominica, respectively. A collection containing five specimens (UMML 15642) from the Straits of Florida (24°40–42'N, 80°23–20'W at 258 m) may be this species (see "Remarks" section below). Most specimens of *S. stigmosus* were collected in deep waters underlying strong surface currents, such as the Yucatan Channel and beneath the Florida Current. None of these had accompanying information regarding substrate composition at the collection site, so it is uncertain if this species occurs on unique substrates underlying strong surface currents. Of interest though is a comment in the *Silver Bay* cruise 26 report (prepared by H.R. Bullis Jr., 25 Nov 1960) noting that off the western edge of the Great Bahama Bank, in the area where several *S. stigmosus* specimens were captured, there were heavy deposits of decaying vegetation, apparently washed down off the Bahama Bank, which blanketed the

bottom out to depths of 250 fathoms and greatly hampered gear efficiency in this area. If bottom conditions such as those predominate at locations inhabited by this species, it may account for the relatively small numbers of *S. stigmosus* captured thus far.

**Bathymetric distribution** Twelve specimens of *S. stigmosus* were collected between 192 and 373 m (Table 10). Three were taken at depths of 192–202 m, whereas the remaining nine specimens were collected between 281 and 373 m.

**Remarks** The specimen from off Dominica (MCZ 27968) may be that identified by Goode and Bean (1896:461) as *Aphoristia* (=*Symphurus*) *diomedea,* and later cited, but stated as not having been examined by Ginsburg (1951:194), despite a label in the jar that was signed and dated November, 1950, by Ginsburg identifying this specimen as *S. plagusia*. The specimen is in poor condition and completely faded. It is definitely not *S. diomedeanus* or *S. plagusia* because it has a 1-3-2 ID pattern, 12 caudal-fin rays, no pupillary operculum, and some black pigment remaining on the peritoneum (*S. diomedeanus* and *S. plagusia* have a 1-4-3 ID pattern and an unpigmented peritoneum; *S. diomedeanus* also has 10 caudal-fin rays and a pupillary operculum). The fact that Goode and Bean mistakenly identified this fish as *Aphoristia* (=*Symphurus*) *diomedea* (a species they described that features prominent spots on the dorsal and anal fins) indicates that it probably had prominent blotches on the fins, characteristic of *S. stigmosus*, when first examined by Goode and Bean in the late 1800's.

Five specimens in UMML 15642 (53.7–89.5 mm) have counts and some measurements matching those for specimens of *S. stigmosus* and are tentatively identified as this species, but data for those specimens are not included in summaries. Although these fish have a relatively large eye, as in *S. stigmosus*, estimated ratios of eye diameter to trunk length for these specimens are somewhat lower (3.4–3.9) than that calculated for other specimens (3.5–4.8, but usually greater than 4.0) of this species. Also, the eyeballs are not contiguous, as they are in other *S. stigmosus* specimens. Other features that would help in identifying these specimens, such as scale counts or fin pigmentation patterns, are unavailable because the specimens lack scales and large patches of skin, and are completely faded.

**Comparisons** Within *Symphurus*, *S. stigmosus* is most similar to two other deepwater species in this species group, the western South Atlantic *S. ginsburgi* and western North Atlantic *S. billykrietei*. The new species is distinguished from *S. billykrietei* in the "Comparisons" section of the species account for that species (see also Figs. 20–21).

*Symphurus stigmosus* differs from *S. ginsburgi* in having the series of prominent, pigmented blotches alternating with unpigmented areas of equal or greater size on the posterior two-thirds of the dorsal and anal fins, a feature that is lacking in *S. ginsburgi*. *Symphurus ginsburgi* has a bold pattern of crossbanding on the ocular surface and has a pigmented spot on the scaly basal portion of the caudal fin, features lacking in *S. stigmosus*. In addition, the eyeballs of the two species differ in shape and appearance (compare Fig. 21, A–B). In *S. stigmosus,* the eyeball is more rounded, with upper aspects of the eyeballs contiguous, or nearly contiguous, within the orbital sac. In contrast, the eyeball of *S. ginsburgi* is more elongate with its length slightly greater than its width, and usually there is a small space between eyeballs within the fleshy orbital sac. *Symphurus stigmosus* differs further from *S. ginsburgi* in being a larger species, reaching lengths of ca. 127 mm (see Fig. 8B), with mature females being larger than 85 mm (only three such females known), whereas *S. stigmosus* is much smaller, reaching maximum sizes of ca. 90 mm, with most (55/61, 90%) being smaller than 65 mm, and females maturing at sizes as small as 44 mm (gravid females as small as 51–53 mm).

Among other western Atlantic *Symphurus* species with a 1-3-2 ID pattern and black peritoneum, meristic features of *S. stigmosus* overlap partially with those of *S. marginatus, S. pusillus*, and *S. piger*. *Symphurus marginatus* lacks the alternating series of darkly pigmented blotches and unpigmented areas of greater size on the dorsal and anal fins present on the fins of *S. stigmosus,* and *S. stigmosus* lacks the dark brown blotch on the caudal region of the ocular side of the body featured in *S. marginatus*. *Symphurus stigmosus* also has lower meristic features (dorsal-fin rays 92–95 vs. 93–104 in *S. marginatus*; anal-fin rays 76–84 vs. 80–89, total vertebrae 51–52 vs. 51–56, usually 52–54 in *S. marginatus*), and a relatively stockier and deeper body (greatest depth in anterior one-third of body vs. more elongate body with more uniform body depth and greatest depth at body midpoint in *S. marginatus*).

*Symphurus stigmosus* has some features reminiscent of those observed in the sympatric *S. pusillus* but differs from this species in its higher, nonoverlapping, meristic features (dorsal-fin rays 92–95 vs. 83–88 in *S. pusillus*; anal-fin rays 78–81 vs. 71–75; and 51–52 total vertebrae vs. 47–49 in *S. pusillus*), and dorsal and anal fin pigmentation. *Symphurus stigmosus* has a dark brown stripe along the basal margins of the dorsal and anal fins in combination

with a series of pigmented blotches on these fins, whereas the dorsal and anal fins of *S. pusillus* have only a diffuse speckling of brown pigment basally with the distal margins of these fins yellowish, but the fins definitely lack a stripe or heavily pigmented blotches. The new species also lacks the pigmented spot on the caudal-fin base present in *S. pusillus*.

Some meristic features and aspects of the ocular-side coloration of *S. stigmosus* are reminiscent of those found in *S. piger*, a deepwater species with widespread distribution in the Gulf of Mexico and Caribbean Sea. In addition to the pigmented blotches on the dorsal and anal fins, the new species also differs from *S. piger* in lacking the fifth hypural present in *S. piger*, in its higher fin-ray and total vertebral counts (88 or fewer dorsal-fin rays, 74 or fewer anal-fin rays, and 49 or fewer total vertebrae in *S. piger*), and in its much smaller and more numerous scales (98–100 scales in a longitudinal series in *S. stigmosus* vs. 62–75 in *S. piger*).

*Symphurus stigmosus* can be distinguished from the deepwater, eastern Atlantic species *S. nigrescens* (which also possesses a 1-3-2 ID pattern, 12 caudal-fin rays, and black peritoneum) by modal differences in meristic features (dorsal-fin rays 92–95 vs. 82–92, usually 84–91 in *S. nigrescens*; anal-fin rays 78–81 vs. 69–79; and 51–52 total vertebrae vs. 47–51, usually 48–50, vertebrae in *S. nigrescens*). This species also has a longer caudal fin (109–138 SL, $\bar{x}$=127) and larger eye (128–171 HL, $\bar{x}$=152) than does *S. nigrescens* (caudal fin 76–122 SL, $\bar{x}$=105; eye diameter 91–153 HL, $\bar{x}$=120).

In fin pigmentation, *S. stigmosus* is also similar to the western Atlantic *S. diomedeanus*, but differs from this species in peritoneum color (black vs. unpigmented in *S. diomedeanus*), and ID pattern (1-3-2 vs. 1-4-3 in *S. diomedeanus*). The new species also has a different number of caudal-fin rays (12 in *S. stigmosus* vs. 10 in *S. diomedeanus*) and lacks the pupillary operculum characteristic of *S. diomedeanus*. Also, the pigmented blotches on the fins of the new species are nearly rectangular in shape, whereas fin pigmentation of *S. diomedeanus* usually consists of a series of nearly spherical spots.

**Figure 24**
*Symphurus ginsburgi* Menezes and Benvegnú, Holotype, MZUSP 12339, 61.5 mm SL, Brazil 31°31'S, 49°52'W.

### *Symphurus ginsburgi* Menezes and Benvegnú, 1976 (Figs. 7B, 18–21, 24–25; Tables 1–10, 15, 17) Ginsburg's tonguefish

*Symphurus pterospilotus* (not of Ginsburg, 1951). Roux, 1973:175 (continental shelf, Brazil).

*Symphurus ginsburgi* Menezes and Benvegnú, 1976:146 (original description; counts, measurements, photograph, depth distribution, maturity data; southern Brazil). Menni et al., 1984:201 (southern Brazil and Uruguay; based on Menezes and Benvegnú, 1976). Séret and Andreata, 1992:94 (three specimens; southern Brazil; 248–262 m). Munroe, 1992:368, 376 (ID pattern; geographic, bathymetric distributions). Andreata and Séret, 1995:590 (continental shelf, Brazil).

*?Symphurus civitatum* (not of Ginsburg, 1951). Lazzaro, 1977:69 (continental shelf, Uruguay; 184 m; specimen not examined in present study). Menni et al., 1984:201 (listed, Uruguay; based on Lazzaro, 1977).

*Symphurus plagiusa* (not of Linnaeus, 1766). Séret and Andreata, 1992:94 (continental shelf, Brazil; three specimens; 200–217 m).

**Diagnosis** *Symphurus ginsburgi* can be distinguished from all congeners, except the western North Atlantic *S. billykrietei* and *S. stigmosus*, by the combination of predominant 1-3-2 ID pattern; 12 caudal-fin rays; 4 hypurals; 50–52 total vertebrae; 87–95 dorsal-fin rays; 74–81 anal-fin rays (73–81 reported by Menezes and Benvegnú, 1976); 87–94 scales in longitudinal series; relatively large eye without pupillary operculum; narrow space between eyeballs within fleshy orbital sac; black peritoneum; teeth along entire margin of ocular-side jaws; absence of fleshy ridge on ocular-side lower jaw; absence of scales on blind sides of dorsal- and anal-fin rays; ocular surface pigmentation yellowish to light brown usually with bold pattern of dark brown crossbands, but without darkly pigmented blotch on caudal region of body; blind side uniformly whitish or yellowish, without pattern of pepper-dots; dorsal and anal fins with dark brown stripe along basal margin of fins, some specimens with series of several more darkly pigmented fin rays alternating with series of lightly pigmented fin rays of approximately similar size; and with small darkly pigmented spot on scaly portion (proximal one-third) of caudal fin, but without distinct blotches or spots on distal two-thirds of caudal fin. *Symphurus ginsburgi* differs from *S. billykrietei* in its relatively larger eye, shorter trunk, longer head, longer postorbital length, longer snout, and longer upper jaw. *Symphurus ginsburgi* is readily distinguished from *S. stigmosus* by its pattern of crossbanding on the ocular surface (absent in *S. stigmosus*), in lacking darkly pigmented blotches alternating with unpigmented or only lightly pigmented areas of somewhat greater size on the dorsal and anal fins (present in *S. stigmosus*), and *S. ginsburgi* has a pigmented spot on the caudal-fin base that is lacking in *S. stigmosus*.

**Description** A diminutive species attaining maximum sizes of ca. 90 mm SL. ID pattern usually 1-3-2

(56/60 specimens), less frequently 1-2-3, 1-3-3, or 1-4-2 (Table 2). Caudal-fin rays normally 12 (49/55), less frequently 10 or 11 (Table 3). Dorsal-fin rays 87–95 (Table 4). Anal-fin rays 74–81 (Table 5). Total vertebrae 50–52 (58/58), usually 51–52 (Table 6). Hypurals 4 (58/58). Longitudinal scale rows 87–94 (Table 7). Scale rows on head posterior to lower orbit 15–20, usually 18–21 (Table 8). Transverse scales 32–44, usually 37–42 (Table 9).

Proportions of morphometric features presented in Table 17. Body moderately deep; maximum depth in anterior one-third of body; body tapering rapidly posterior to midpoint. Trunk relatively short. Preanal length shorter than body depth. Head long and narrow, head width slightly narrower than body depth. Head length usually shorter than head width (HW:HL 0.96–1.25, $\bar{x}$=1.1). Postorbital length considerably shorter than body depth. Lower head lobe width less than postorbital length; narrower than upper head lobe. Lower opercular lobe of ocular side considerably wider than upper opercular lobe. Snout moderately long and somewhat pointed; covered with small ctenoid scales. Dermal papillae present, but not well developed on blind-side snout. Anterior nostril on ocular side, when depressed posteriorly, just reaching anterior margin of lower eye in about one-half specimens examined; just short of reaching anterior margin of lower eye in remainder of specimens. Jaws short; maxilla usually extending posteriorly to vertical through anterior margin of lower eye, less frequently reaching vertical through anterior margin of pupil of lower eye. Ocular-side lower jaw without fleshy ridge. Teeth well developed on blind-side jaws. Lower jaw on ocular side with row of teeth along complete margin of jaw. Usually only anterior three-fourths of margin of ocular-side premaxilla with row of slender teeth. Chin depth usually equal to or slightly larger than snout length. Lower eye moderately large and somewhat elongate; eyes usually equal in position or with upper eye slightly in advance of lower eye and usually with small space between eyeballs within orbital sac. Anterior and medial surfaces of eyes covered with 3–5 rows of small scales; 4–8 small ctenoid scales in narrow interorbital region. Pupillary operculum absent. Dorsal-fin origin usually at vertical through anterior margin of pupil of upper eye; occasionally anterior to vertical through anterior margin of upper eye, or rarely more posterior and at vertical through midpoint of pupil of upper eye; predorsal length moderate. Scales absent on blind sides of dorsal- and anal-fin rays. Pelvic fin long; longest pelvic-fin ray, when extended posteriorly, usually reaching base of first anal-fin ray. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anus, or occasionally extending more posteriorly almost to anal-fin origin (membrane torn in many specimens). Caudal fin moderately long. Scales small, strongly ctenoid on ocular side, less strongly ctenoid on blind side.

**Table 17**

Morphometrics for holotype (MZUSP 12339) and 54 additional specimens of *Symphurus ginsburgi*. (Abbreviations defined in methods section; SL is expressed in mm; characters 2 to 15 are expressed in thousandths of SL; 16 to 22 in thousandths of HL; *n* = no. of specimens measured.)

| Character | Holotype | *n* | Range | Mean | SD |
|---|---|---|---|---|---|
| 1. SL | 61.5 | 54 | 30.8–90.4 | 51.9 | 15.14 |
| 2. BD | 293 | 30 | 205–324 | 285.8 | 25.67 |
| 3. TKL | 769 | 54 | 743–795 | 773.6 | 12.93 |
| 4. PDL | 58 | 30 | 33–79 | 59.9 | 9.97 |
| 5. PAL | 249 | 30 | 201–271 | 240.2 | 17.18 |
| 6. DBL | 942 | 30 | 921–971 | 939.4 | 10.17 |
| 7. ABL | 728 | 30 | 693–795 | 742.3 | 22.86 |
| 8. PL | 58 | 27 | 54–89 | 67.8 | 8.22 |
| 9. PA | 57 | 30 | 46–94 | 62.5 | 8.69 |
| 10. CFL | 122 | 26 | 104–148 | 123.3 | 8.76 |
| 11. HL | 231 | 54 | 205–257 | 226.6 | 12.66 |
| 12. HW | 263 | 30 | 220–272 | 244.0 | 14.28 |
| 13. POL | 143 | 54 | 133–159 | 145.3 | 6.73 |
| 14. UHL | 163 | 28 | 116–181 | 150.2 | 16.36 |
| 15. LHL | 122 | 30 | 96–138 | 113.1 | 9.80 |
| 16. POL | 620 | 54 | 587–746 | 642.2 | 29.38 |
| 17. SNL | 197 | 54 | 156–284 | 204.9 | 23.56 |
| 18. UJL | 183 | 54 | 177–253 | 217.5 | 18.99 |
| 19. ED | 155 | 54 | 116–164 | 136.6 | 10.92 |
| 20. CD | 254 | 30 | 152–271 | 226.5 | 27.73 |
| 21. OPLL | 324 | 30 | 214–364 | 287.0 | 36.28 |
| 22. OPUL | 211 | 30 | 160–312 | 220.1 | 39.03 |

**Pigmentation (Fig. 24)** Coloration similar for both sexes. Ocular surface usually light brown to yellowish with small dark melanophores scattered over body surface, and usually with 2–5 (usually 4) irregular, dark brown crossbands on head and body. Crossbands on body 4–10 scale rows wide, not continued onto dorsal and anal fins. Anteriormost crossband on opercular region of head, faintly pigmented. Body crossbands, except second anteriormost, more intensely shaded dorsally and ventrally, somewhat diffuse along body midsection. Second crossband, located immediately posterior to operculum, almost always continuous across body and most intensely pigmented. Ocular-side outer opercle usually with same general background coloration as body; occasionally with small pigmented spot at angle of operculum. Inner linings of opercles and isthmus on both sides of body unpigmented. Ocular-side lips usually with small speckling of pigment spots, but

without pronounced band of pigment. Blind side uniformly off-white to yellowish, except faded specimens that have lost scales with median series (Fig. 5B, number 9) of conspicuous dermal melanophores along axis of vertebral column (visible on both sides of body); melanophores especially prominent along vertebrae in anterior two-thirds of body. Peritoneum black, showing through abdominal wall on both sides.

Dorsal and anal fins lightly pigmented anteriorly. Basal portions of dorsal and anal fins darken posterior to region of anteriormost crossband on body, forming continuous or nearly continuous narrow stripe along length of fins but not extending onto caudal fin. Basal stripe in some specimens prominent, especially on proximal portions of fin rays; others with basal stripe rather inconspicuous, with darker pigment concentrated only on anterior surfaces of basal part of fin rays with little or no pigment on connecting membranes, and darkest in regions corresponding to crossbands on body. Caudal fin usually with small, nonocellated, dark brown pigment spot on scale-covered base (proximal one-third) of fin. Distal two-thirds of caudal fin unpigmented.

**Size and sexual maturity (Fig. 7B)** *Symphurus ginsburgi* is a diminutive species attaining maximum lengths of only 90 mm (Menezes and Benvegnú, 1976), but of 62 fish examined in the present study, only six were larger than 65 mm. The largest, a male (81.0 mm), was only slightly larger than the largest female (78.9 mm). Among 54 specimens for which sexual maturity was determined, 25 (30.8–81.0 mm) were males, 23 were females (31.6–78.9 mm), and six were immature fish (30.9–36.3 mm) for which sex was indeterminate.

Based on reproductive stages of females (Fig. 7B), *S. ginsburgi* matures around 50 mm. Of 23 females, 16 (44.3–78.9 mm) were mature, of which eight (51.6–78.9 mm), including five smaller than 60 mm (51.6–57.5 mm), were gravid. Two others (44.3–46.4 mm) with elongate ovaries were not gravid. Seven immature females, with gonads just undergoing posterior elongation, were 31.6–39.8 mm. Menezes and Benvegnú (1976) also noted the small size at maturity for this species, with gravid females in their study ranging from 58–79 mm.

**Geographic distribution (Fig. 25)** On the continental shelf in the western South Atlantic from southeastern Brazil (21°31'S) to ca. Maldonado, Uruguay (35°18'S) (Menezes and Benvegnú, 1976; Séret and Andreata, 1992).

**Bathymetric distribution** *Symphurus ginsburgi* occurs on mud substrates at moderate depths (103–300 m) on the continental shelf (Table 10). Of the specimens reported by Menezes and Benvegnú (1976), 94% (86/91) were collected between 135 and 200 m, whereas an additional five specimens were taken between 103 and 111 m. Séret and Andreata (1992) captured three specimens between 200 and 300 m on the continental shelf off southeastern Brazil. Other than depth of capture information and brief observations on sexual maturation, little else is known concerning the ecology of this species.

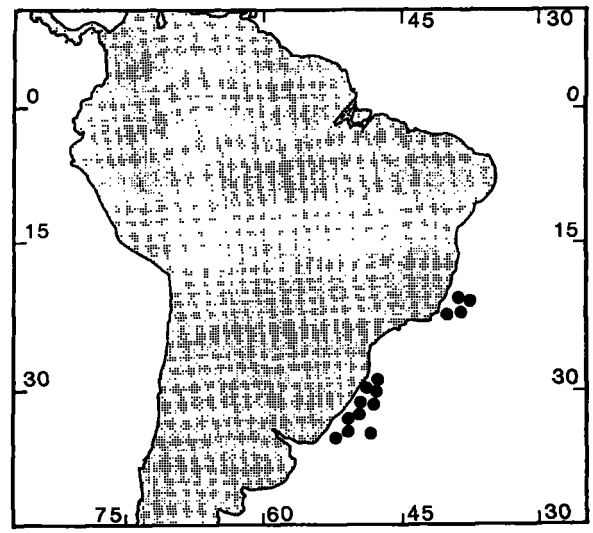


**Figure 25**
Geographic distribution of *Symphurus ginsburgi* based on material examined (discussion of geographic distribution appears in species account).

**Comparisons** Of species of *Symphurus*, *S. ginsburgi* is most similar to the deepwater, western North Atlantic *S. billykrietei* and *S. stigmosus*. Differences between these species are highlighted in Figs. 18–21 and Table 15, and discussed in the "Comparisons" sections for *S. billykrietei* and *S. stigmosus*.

Among other Atlantic species characterized by a 1-3-2 ID pattern and black peritoneum, some meristic features of *S. ginsburgi* overlap partially with those of the western Atlantic *S. marginatus*, *S. pusillus*, and *S. piger*, and the eastern Atlantic *S. nigrescens*. From *S. marginatus*, *S. ginsburgi* can be distinguished by its pattern of crossbanding on the ocular surface (vs. lacking in *S. marginatus*) and its lack of the dark brown blotch on the caudal region of the ocular side of the body that characterizes *S. marginatus*. *Symphurus ginsburgi* differs further from *S. marginatus* in its lower, and mostly nonoverlapping, meristic features (dorsal-fin rays 87–95 vs. 93–104 in *S. marginatus*, anal-fin rays 74–81 vs. 80–89, and 50–52 total vertebrae vs. 51–56,

usually 52–54 in *S. marginatus*), and in its stockier body with its greatest depth in the anterior one-third of the body (vs. a more elongate body with relatively uniform depth throughout its length and greatest depth near the body midpoint in *S. marginatus*). *Symphurus ginsburgi* can easily be distinguished from *S. nigrescens* by modal differences in dorsal-fin rays (87–95 vs. 82–92, usually 84–91), anal-fin rays (74–81 vs. 69–79 in *S. nigrescens*), and total vertebrae (50–52, usually 51–52 vs. 47–51, usually 48–50 in *S. nigrescens*). Also, the caudal fin of *S. ginsburgi* is longer (104–148 SL, $\bar{x}$ = 123) than that of *S. nigrescens* (76–122 SL, $\bar{x}$ =105).

*Symphurus ginsburgi* is similar to the western North Atlantic *S. pusillus* in body coloration, ID pattern, caudal-fin rays, peritoneum color, eye diameter, and relatively small size. However, *S. ginsburgi* differs from *S. pusillus* in its higher, and mostly nonoverlapping, meristic features (anal-fin rays 74–81 vs. 71–75 in *S. pusillus*; dorsal-fin rays 89–95 vs. 83–88; total vertebrae 50–52 vs. 47–49 in *S. pusillus*). Furthermore, many *S. ginsburgi* usually have a dark brown stripe basally along the dorsal and anal fins, whereas *S. pusillus* usually lacks such stripes, instead having its fins usually yellowish with only a diffuse speckling of pigment along the fin rays.

Some meristic features and ocular-side coloration of *S. ginsburgi* are also reminiscent of those found in *S. piger*, which occurs throughout the Gulf of Mexico and Caribbean Sea but thus far is unknown from waters off southern Brazil. *Symphurus ginsburgi* differs from *S. piger* in its higher, and mostly nonoverlapping, fin-ray and total vertebral counts (88 or fewer dorsal-fin rays, 74 or fewer anal-fin rays, and 49 or fewer total vertebrae in *S. piger*), in its much higher longitudinal scale count (87–94 scales in *S. ginsburgi* vs. 62–75 in *S. piger*), in lacking a fifth hypural (present in *S. piger*), in having the isthmus and inner opercular linings unpigmented, and in having a stripe along basal margins of dorsal and anal fins (lightly pigmented isthmus and inner opercular linings and uniformly pigmented fins without basal stripe in *S. piger*).

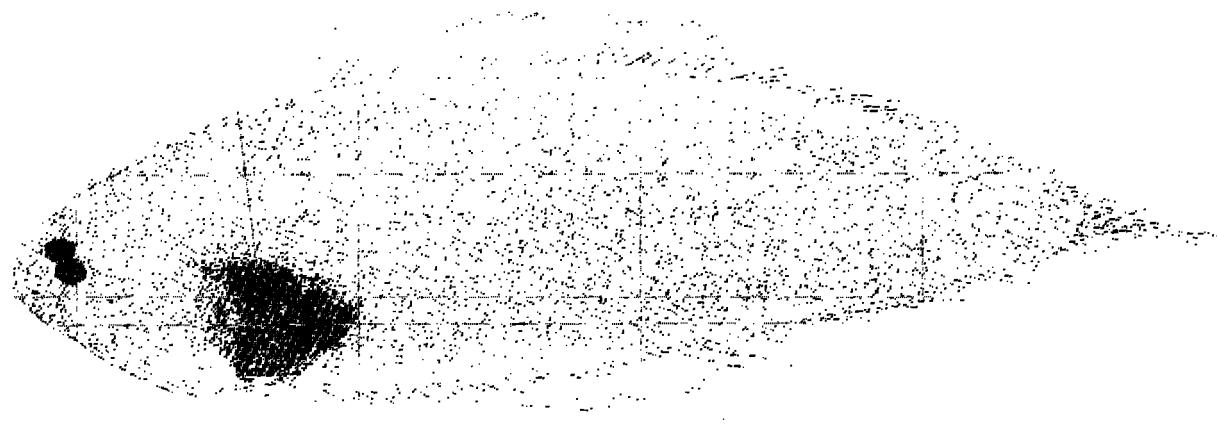

**Figure 26**
*Symphurus pelicanus* Ginsburg, TCWC 6248.2, 58.3 mm SL, Mexico 25°09'N, 97°03'W.

## *Symphurus pelicanus* Ginsburg, 1951 (Figs. 6D, 26–27; Tables 1–10, 18) Longtail tonguefish

*Aphoristia diomedeana* (not of Goode and Bean, 1885) (in part). Goode and Bean, 1896:460 (specimen of *S. pelicanus* included in account of *A. diomedeana*).
*Symphurus pelicanus* Ginsburg, 1951:193 (original description with photograph). Hildebrand, 1954:297 (western Gulf of Mexico). Topp and Hoff, 1972:108 (geographical distribution). Munroe, 1992:368, 377 (ID pattern; geographic, bathymetric distributions). Cervigón et al., 1993:306 (Venezuela).

**Diagnosis** *Symphurus pelicanus* is distinguished from all congeners by the combination of predominant 1-3-2 ID pattern; 12 caudal-fin rays; 4 hypurals; 77–85 dorsal-fin rays; 64–70 anal-fin rays; 43–46 total vertebrae; 9 abdominal vertebrae; 62–70 scales in longitudinal series; absence of pupillary operculum; black peritoneum; teeth along entire margin of ocular-side jaws; absence of fleshy ridge on ocular-side lower jaw; absence of membrane ostia; ocular surface pigmentation uniformly light to medium brown, sometimes with faint crossbands, but without caudal blotch; blind side with pattern of pepper-dots (Fig. 5B, number 9); dorsal, anal, and caudal fins without spots or blotches.

**Description** A dwarf species attaining maximum length of ca. 70 mm SL. ID pattern usually 1-3-2 (56/60 specimens), rarely 1-2-3 or 1-3-3 (Table 2). Caudal-fin rays 12 (50/56), less frequently 11, rarely 10 or 13 (Table 3). Dorsal-fin rays 77–85, usually 78–83 (Table 4). Anal-fin rays 64–70 (Table 5). Total vertebrae 43–46, usually 45–46 (52/60) (Table 6). Hypurals 4 (60/60). Scales somewhat deciduous, most specimens usually missing most or all scales. Longitudinal scale rows 62–70 (Table 7). Scale rows on head posterior to lower orbit 14–17 (Table 8). Transverse scales 24–29 (Table 9).

Proportions of morphometric features presented in Table 18. Body moderately slender, maximum depth almost at midpoint of standard length, or occasionally slightly anterior to midpoint of body; body with gradual taper posterior to midpoint. Preanal length shorter than body depth. Head long and moderately wide, shorter than body depth. Head length usually equal with, or less frequently slightly smaller than, head width (HW:HL 0.84–1.15, $\bar{x}$=1.01). Lower head lobe width less than postorbital length; slightly narrower than upper head lobe. Lower opercular lobe of ocular side usually slightly wider than upper lobe. Snout moderately long and pointed; covered with small ctenoid scales. Dermal papillae well developed on both sides of snout, but less dense on snout on blind side. Anterior nostril on ocular side short, when extended posteriorly, usually not reaching anterior margin of lower eye. Jaws moderately long; maxilla extending posteriorly to vertical through midpoint of lower eye. Ocular-side lower jaw without fleshy ridge. Teeth well developed on blind-side jaws. Teeth

**Table 18**

Morphometrics for holotype (USNM 155234) and 18 additional specimens of *Symphurus pelicanus*. (Abbreviations defined in methods section; SL is expressed in mm; characters 2 to 14 are expressed in thousandths of SL; 15 to 21 in thousandths of HL; *n* = no. of specimens measured.)

| Character | Holotype | *n* | Range | Mean | SD |
|---|---|---|---|---|---|
| 1. SL | 50.2 | 19 | 27.2–69.2 | 53.4 | 10.62 |
| 2. BD | 285 | 19 | 235–315 | 290.6 | 19.56 |
| 3. PDL | 62 | 19 | 55–83 | 67.7 | 7.59 |
| 4. PAL | 241 | 19 | 219–267 | 246.0 | 11.95 |
| 5. DBL | 938 | 19 | 917–945 | 932.3 | 7.59 |
| 6. ABL | 759 | 19 | 518–812 | 742.7 | 58.52 |
| 7. PL | 64 | 17 | 45–78 | 65.6 | 8.60 |
| 8. PA | 40 | 19 | 40–72 | 51.1 | 9.29 |
| 9. CFL | 167 | 17 | 128–185 | 151.4 | 17.03 |
| 10. HL | 215 | 19 | 211–254 | 230.6 | 10.99 |
| 11. HW | 225 | 19 | 210–259 | 233.7 | 13.16 |
| 12. POL | 147 | 19 | 144–170 | 155.7 | 7.24 |
| 13. UHL | 145 | 19 | 109–156 | 134.3 | 15.17 |
| 14. LHL | 100 | 19 | 100–136 | 119.6 | 9.16 |
| 15. POL | 685 | 19 | 632–714 | 675.2 | 18.00 |
| 16. SNL | 139 | 19 | 136–226 | 177.1 | 21.35 |
| 17. UJL | 213 | 19 | 193–250 | 219.6 | 16.67 |
| 18. ED | 93 | 19 | 93–158 | 125.2 | 13.70 |
| 19. CD | 167 | 19 | 167–244 | 196.0 | 21.81 |
| 20. OPLL | 232 | 19 | 214–299 | 250.6 | 22.84 |
| 21. OPUL | 222 | 19 | 191–344 | 269.6 | 33.95 |

on ocular-side jaws very small. Lower jaw with teeth along nearly entire marginal length of dentary; ocular-side premaxilla with teeth usually along margin of anterior three-fourths of jaw, occasionally with row of slender teeth along complete margin of premaxilla. Chin depth slightly larger than snout length. Lower eye relatively large; eyes usually equal in position. Anterior and medial surfaces of eyes partially covered with 3–4 rows of small ctenoid scales; 1–3 small ctenoid scales in narrow interorbital region. Pupillary operculum absent. Dorsal-fin origin posterior to vertical through midpoint of upper eye; usually only reaching vertical through posterior margin of upper eye, occasionally not reaching as far anteriorly; predorsal length long. Scales absent on blind sides of dorsal- and anal-fin rays. Pelvic fin long; longest pelvic-fin ray, when extended posteriorly, usually reaching base of first, occasionally second, anal-fin ray. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anus, or occasionally extending posteriorly nearly to anal-fin origin (membrane torn in most specimens). Caudal fin long. Scales large, strongly ctenoid on both sides of body.

**Pigmentation (Fig. 26)** Coloration similar for both sexes. Ocular surface usually uniformly light brown to yellowish and without prominent crossbands. Some specimens with irregular, very lightly shaded areas on ocular surface. Older specimens mostly faded, almost whitish in color, with fins light yellowish. Crossbands, when present, faintly pigmented and barely perceptible. Ocular-side outer opercle usually with similar pigmentation as background color on body; occasional specimens with dark pigment spot at dorsal margin of opercular opening, or with diffuse pattern of dark pigment on ventral region of ocular-side operculum. Inner linings of both opercles and isthmus on both sides of body speckled with melanophores in some specimens; other usually older, faded specimens lacking such pigment. Ocular-side lips usually speckled, but without well-developed pigment band. Blind side off-white and thickly sprinkled with very small pepper-dots over entire surface from about angle of jaws to caudal region in heavily pigmented individuals (Fig. 5B, number 9); some older specimens with pepper-dots finer, more sparsely distributed, and often difficult to discern without magnification. Speckling of pepper-dots usually heaviest on regions of blind side overlying dorsal- and anal-fin pterygiophores. Peritoneum black, visible through abdominal wall on both sides.

Dorsal, anal, and caudal fins with basal one-third of fin rays light brown or yellowish, not pigmented differently from general body coloration; distal two-thirds of dorsal- and anal-fin rays hyaline or light yellow. Specimens without scales with series of internal, dark black, spots at bases of anterior 10–20 dorsal-fin rays. Some specimens with dense concentration of melanophores forming irregular, poorly defined spot at scaly portion of caudal-fin base. Caudal fin usually yellowish or hyaline over entire length.

**Size and sexual maturity (Fig. 6D)** *Symphurus pelicanus* is a dwarf species attaining maximum lengths of about 70 mm. Most specimens were 31–60 mm. Males and females attain similar sizes. The largest specimen examined was a male 69.2 mm; the largest female measured 65.4 mm. Only five fish larger than 60 mm were found. Of 63 specimens for which size-related life history information was available, there were 29 males (34.6–69.2 mm), 33 females (36.7–65.4 mm), and one juvenile (27.2 mm) of indeterminate sex. Based on reproductive stages of females, sexual maturity occurs at sizes of 37–40 mm. There were 28 mature females 37.2–65.4 mm. The smallest females with elongate ovaries were 37.2–40.9 mm, and all but three females larger than 40.0 mm were mature with either elongate or gravid ovaries. Five immature females, all with ovaries undergoing posterior elongation, but without developing ova evident, were 36.7–51.6 mm.

**Geographic distribution (Fig. 27)** On the continental shelf from the Straits of Florida in the eastern Gulf of Mexico (based on a single capture) but most common west and south of the Mississippi Delta region on the inner continental shelf to Guyana (the easternmost capture at 58°53'W). There was also an unusual capture (UMML 1328), perhaps an expatriated individual, of an adult taken on the surface in the Sargasso Sea (29°55'N, 70°20'W).

Throughout its range, *S. pelicanus* occurs primarily on silt and soft mud substrates in neritic waters, including the continental shelf off the Mississippi Delta, west through the Gulf of Mexico to northern Mexico, exclusive of live-bottom areas off the Yucatan Peninsula (Hildebrand, 1954), and south through Caribbean regions of Central and South America to Guyana. Thus far, *S. pelicanus* is unknown from areas in the eastern and far southwestern Gulf of Mexico, the Antilles, or from Caribbean locations with narrow continental shelves, or extensive reef development and live-bottom habitats.

**Bathymetric distribution** *Symphurus pelicanus* inhabits moderate depths (24–133 m) on the inner continental shelf (Table 10). Of 64 specimens with depth information, the majority (49/64, 75%) were collected between 31 and 70 m. The shallowest recorded bottom capture was a solitary specimen (54.3 mm; UMML 34371) at 24 m. An unusual capture of a 44.1-mm individual (UMML 1328) was at the surface in the Sargasso Sea (29°55'N, 70°20'W). Only 13 specimens were collected deeper than 80 m, with the deepest of three specimens (UMML 30181) taken at 133 m. The depth range of *S. pelicanus* encompasses those of *S. parvus, S. diomedeanus,* and *S. tessellatus* and some collections made off Panama and Colombia included all four species.

**Ecology** Little is known of the ecology of this diminutive flatfish.

**Comparisons** Among Atlantic species of tonguefishes, *S. pelicanus* is most similar in meristic features to the western Atlantic *S. piger* and eastern Atlantic *S. nigrescens*. *Symphurus pelicanus* differs substantially from these in having black pepper-dots (Fig. 5B) on the blind side of the body (absent in the others), and it also has lower meristic features (dorsal-fin rays 77–85 vs. 80–88, usually 83–88 in *S. piger*, and 82–92 in *S. nigrescens*; anal-fin rays 64–70 vs. 68–74 in *S. piger*, and 69–79 in *S. nigrescens*; total vertebrae 43–46 vs. 45–49, usually 47–49 in *S. piger,* and 47–51 in *S. nigrescens*). *Symphurus pelicanus* can be distinguished further from *S. piger*

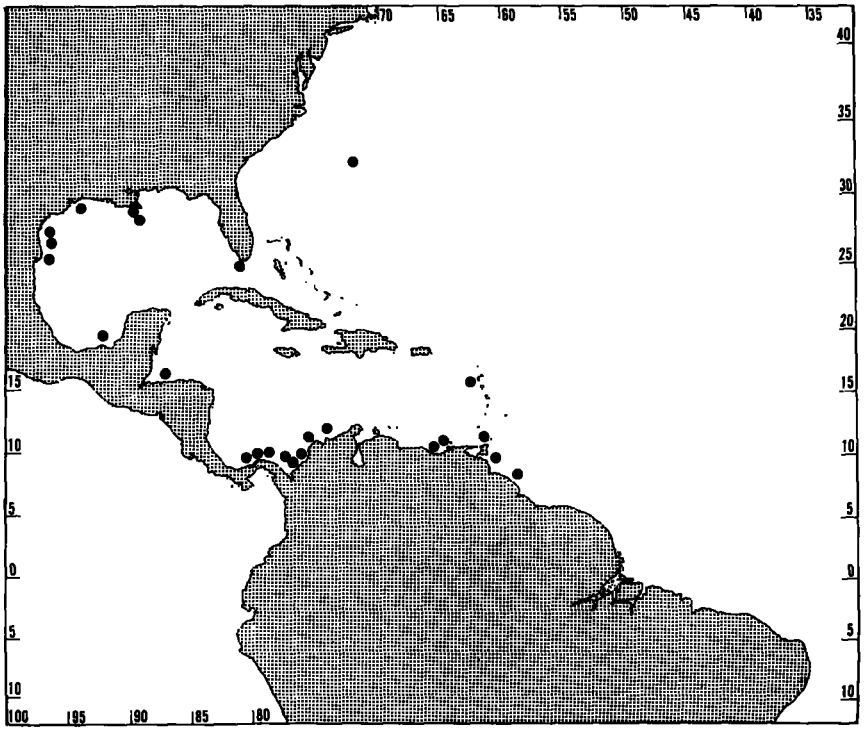


**Figure 27**

Geographic distribution of *Symphurus pelicanus* based on material examined (discussion of geographic distribution appears in species account).

by having one less hypural (4 vs. 5 in *S. piger*) and by its much smaller size (70 vs. 140 mm for *S. piger*). From *S. nigrescens, S. pelicanus* is further differentiated in having uniformly pigmented dorsal and anal fins without darkly pigmented blotches (vs. dorsal and anal fins with pigmented blotches in many *S. nigrescens*).

Among other Atlantic species with a 1-3-2 ID pattern, 12 caudal-fin rays, and a black peritoneum, *S. pelicanus*, in its relatively small size, is somewhat similar to *S. pusillus*. Although dorsal-fin ray counts for *S. pusillus* partially overlap with those observed for *S. pelicanus,* these species differ in their nonoverlapping counts of anal-fin rays (64–70 vs. 71–75 in *S. pusillus*), *S. pusillus* also lacks the pepper-dot pattern on the blind side of the body characteristic of *S. pelicanus*, which has fewer longitudinal scales (62–70 vs. 77–87 in *S. pusillus*) and fewer total vertebrae (43–46 vs. 47–49 in *S. pusillus*). The isthmus and inner opercular linings in *S. pusillus* are unpigmented (vs. speckled with melanophores in *S. pelicanus*).

The pattern of pepper-dots on the blind side of the body in *S. pelicanus* is reminiscent of that found in some specimens of *S. arawak*. However, *S. pelicanus* is easily recognized from *S. arawak* by its black peritoneum (vs. unpigmented in *S. arawak*), relatively uniform ocular-side coloration (some *S. arawak* have darkened caudal blotch), and differences in meristic features (see Tables 4–9). Salient differences between these species are discussed in more detail in the "Comparisons" section of the account for *S. arawak*.

Meristic features, adult sizes, and depth of occurrence of *S. pelicanus* overlap completely with those of *S. parvus* and there are also partial overlaps with some meristic features for *S. ommaspilus*. The most obvious distinctions between *S. pelicanus* and these other species occur in their pigmentation patterns, namely peritoneum color (black in *S. pelicanus* vs. unpigmented in these others), absence of a pepper-dot pattern of pigment spots on the blind surface of *S. parvus* and *S. ommaspilus* (present in *S. pelicanus*), and the absence in *S. pelicanus* of a blotch on the ocular-side caudal region of the body (well-developed in *S. parvus*) or absence of spots on the dorsal and anal fins (present in *S. ommaspilus*). *Symphurus pelicanus* is also distinguished from both species by its caudal-fin ray count (12 vs. 10 in *S. parvus* and *S. ommaspilus*), in lacking a pupillary operculum and membrane ostia (both well developed in *S. parvus* and *S. ommaspilus*), and by differences in ID pattern (1-3-2 vs. 1-4-2 in *S. ommaspilus*, and 1-4-2 or 1-5-2 in *S. parvus*). *Symphurus pelicanus* also has a longer caudal fin and more slender body than these other species.

Of all species in the genus, *S. pelicanus* is most similar to the eastern Pacific *S. gorgonae*. Both have 12 caudal-fin rays, a black peritoneum, and pepper-dots on the blind side of the body. However, *S. pelicanus* differs from *S. gorgonae* primarily in its modally lower counts (dorsal-fin rays 77–85, usually 78–83 vs. 80–89, usually 82–88; anal-fin rays 64–70 vs. 63–74, usually 68–74 in *S. gorgonae*; and total vertebrae 43–46, usually 45–46 vs. 46–49, usually 46–48 in *S. gorgonae*). All other eastern Pacific *Symphurus* have fin-ray and vertebral counts exceeding those of *S. pelicanus*.

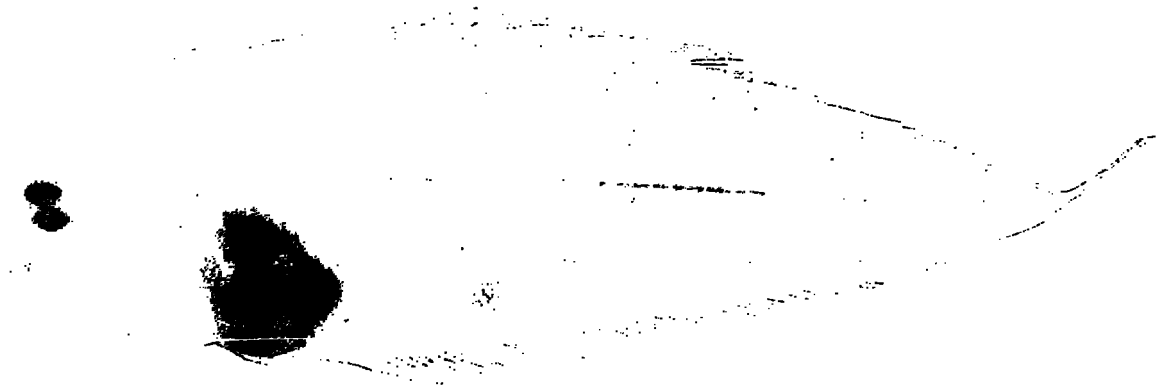

**Figure 28**
*Symphurus pusillus* (Goode and Bean), USA 4822, 38.5 mm SL, Gulf of Mexico 26°25'N, 84°15'W.

### *Symphurus pusillus* (Goode and Bean, 1885) (Figs. 6C, 28–31; Tables 1–10, 19) Northern tonguefish

*Aphoristia pusilla* Goode and Bean, 1885:590 (original description; off Long Island, New York). Goode and Bean, 1896:461 (based on preceding specimens; redescription, figure).

*Symphurus pusillus*. Jordan and Goss, 1889:325 (suggested synonymy with *S. plagiusa*). Jordan and Evermann, 1898:2710 (after Goode and Bean) (redescription, counts). Evermann and Marsh, 1900:332 (in key). Chabanaud, 1939:26 (western Atlantic, Gulf Stream). Ginsburg, 1951:197 (redescription, comparison of type series). Fowler, 1952:143 (New Jersey, offshore records). Topp and Hoff, 1972:108 (geographical distribution). Munroe, 1992:368, 377 (ID pattern; geographic, bathymetric distributions).

**Misidentifications** Baughman, 1950:138 (near Corpus Christi, Texas; specimen actually *S. plagiusa*). Longley and Hildebrand, 1941:50 (Tortugas, Florida; specimen actually *S. piger*). Kyle, 1913:145 (figure, brief description of symmetrical larval form; more probably *S. ommaspilus*, *S. minor*, or *S. parvus*).

**Diagnosis** *Symphurus pusillus* differs from all congeners by the combination of predominant 1-3-2 ID pattern; 12 caudal-fin rays; 4 hypurals; 83–88 dorsal-fin rays; 71–75 anal-fin rays; 47–49 total vertebrae; 9 abdominal vertebrae; 77–87 scales in longitudinal series; black peritoneum; absence of pupillary operculum; teeth along entire margin of ocular-side jaws; ocular-side lower jaw without fleshy ridge; absence of scales on blind sides of dorsal- and anal-fin rays; absence of membrane ostia; relatively long (11.5–15.4% SL) caudal fin; ocular-surface pigmentation of crossbanding without caudal blotch; no pepper-dot pigmentation on blind side of body; dorsal, anal, and caudal fins without spots.

**Description** A dwarf species attaining maximum lengths of only about 77 mm SL. ID pattern usually 1-3-2 (22/25 specimens), less frequently 1-2-3 or 1-3-3 (Table 2). Caudal-fin rays 12 (Table 3). Dorsal-fin rays 83–88 (Table 4). Anal-fin rays 71–75 (Table 5). Total vertebrae 47–49, usually 48–49 (22/26) (Table 6). Hypurals 4 (26/26). (Most specimens lacking scales with scale pockets often damaged. Therefore, scale counts, with exception of head scale rows, can only be estimated.) Longitudinal scale rows 77–87 (Table 7). Scale rows on head posterior to lower orbit 17–19 (Table 8). Transverse scales 33–34 (based only on 2/19 specimens).

Proportions of morphometric features presented in Table 19. Body moderately deep, maximum depth in anterior one-third of body; body tapering moderately posterior to midpoint. Preanal length smaller than body depth. Head relatively long and wide; narrower than body depth. Head nearly as long as wide (HW:HL 0.98–1.19, $\bar{x}$=1.0). Lower head lobe width less than postorbital length; narrower than upper head lobe. Lower opercular lobe on ocular side con-

**Table 19**

Morphometrics for lectotype (USNM 28778) and 19 additional specimens of *Symphurus pusillus*. (Abbreviations defined in methods section; SL is expressed in mm; characters 2 to 14 are expressed in thousandths of SL; 15 to 21 in thousandths of HL; *n* = no. of specimens measured.)

| Character | Lectotype | *n* | Range | Mean | SD |
|---|---|---|---|---|---|
| 1. SL | 54.5 | 20 | 35.2–68.9 | 51.8 | 9.86 |
| 2. BD | 279 | 17 | 257–317 | 280.0 | 15.12 |
| 3. PDL | 55 | 17 | 47–86 | 58.6 | 10.56 |
| 4. PAL | 220 | 17 | 212–278 | 240.1 | 16.90 |
| 5. DBL | 945 | 17 | 914–953 | 941.4 | 10.56 |
| 6. ABL | 756 | 17 | 707–778 | 741.8 | 19.29 |
| 7. PL | — | 11 | 55–79 | 70.2 | 6.68 |
| 8. PA | 46 | 17 | 44–93 | 65.9 | 14.58 |
| 9. CFL | — | 11 | 115–154 | 129.4 | 11.31 |
| 10. HL | 209 | 20 | 206–254 | 225.9 | 15.86 |
| 11. HW | 218 | 17 | 213–262 | 232.6 | 15.71 |
| 12. POL | 141 | 17 | 128–158 | 143.4 | 7.89 |
| 13. UHL | 138 | 17 | 110–171 | 144.6 | 17.29 |
| 14. LHL | 94 | 17 | 77–144 | 104.8 | 17.11 |
| 15. POL | 670 | 17 | 604–696 | 648.2 | 25.24 |
| 16. SNL | 191 | 17 | 156–238 | 202.3 | 22.37 |
| 17. UJL | 226 | 17 | 189–244 | 222.1 | 14.11 |
| 18. ED | 134 | 20 | 103–156 | 131.2 | 16.22 |
| 19. CD | 270 | 17 | 168–273 | 212.8 | 31.55 |
| 20. OPLL | 261 | 17 | 234–375 | 275.3 | 36.68 |
| 21. OPUL | 200 | 17 | 153–268 | 201.5 | 34.65 |

siderably wider than upper opercular lobe. Snout short and somewhat pointed; covered with small ctenoid scales. Dermal papillae well developed on blind-side snout. Anterior nostril on ocular side short, usually not reaching anterior margin of lower eye when extended posteriorly. Jaws moderately long; maxilla extending posteriorly to vertical through anterior margin of pupil of lower eye, or less frequently nearly reaching vertical through midpoint of lower eye. Ocular-side lower jaw without fleshy ridge. Dentition well developed on blind-side jaws. Teeth on ocular-side lower jaw in single row over full length of margin of dentary. Teeth usually present only on anterior three-fourths of margin of ocular-side premaxilla; occasionally teeth along full length of premaxilla. Chin depth slightly larger than snout length. Lower eye moderately large; eyes usually equal in position. Anterior and medial surfaces of eyes partially covered with 3-4 rows of small scales; 1–3 small scales in narrow interorbital region. Pupillary operculum absent. Dorsal-fin origin usually equal with point between verticals through midpoint and anterior margin of upper eye. Scales absent on blind sides of dorsal- and anal-fin rays. Pelvic-fin long; longest pelvic-fin ray, when extended posteriorly, reaching base of first anal-fin ray in approximately one-half of specimens examined. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anus, or occasionally extending posteriorly nearly to anal-fin origin (membrane torn in most specimens). Caudal fin long. Scales small, ctenoid on both sides of body.

**Pigmentation (Fig. 28)** Most specimens examined were faded and had little evidence of any pigmentation. Ginsburg (1951) described coloration of three syntypes as: "The three specimens examined mostly faded, rather light brownish, with traces of crossbands in two specimens, fins yellowish." The following color description is based primarily on three specimens collected most recently, augmented whenever possible with observations from other specimens.

Body coloration similar for both sexes. Ocular surface yellowish, with 2–6 (usually only 3–4 obvious), light brown crossbands more or less continuous across body. Crossbands relatively narrow, usually only 3–6 scale rows wide, beginning at opercular opening and continuing to base of caudal fin. Anteriormost band crossing opercular opening; second crossband on posterior margin of body cavity. Third crossband at body midpoint usually the most prominent, nearly always complete and continued onto dorsal and anal fins. Fourth, fifth, and sixth crossbands posterior to body midpoint, not as well developed across midregion of body as others. Head region dorsad and anteriad to eyes with obvious melanophores in dermis arranged in V-shape pattern extending from body margin to about level of upper eye. Specimens lacking scales with single series of dark black melanophores deep within dermis showing through skin at bases of anteriormost 10–20 dorsal-fin rays. Ocular-side outer opercle with same background pigmentation as body. Inner linings of both opercles and isthmus on both sides of body unpigmented. Ocular-side upper lip occasionally lightly spotted, but usually without well-developed pigmented band (only one specimen had both ocular-side lips with a faint pigment band). Blind side uniformly off-white or yellowish, except specimens lacking scales with median series of prominent, dark black melanophores in dermis along anterior two-thirds of axis of vertebral column, visible through skin on both sides of body (Fig. 5B, number 9). Peritoneum black, visible through abdominal wall on both sides.

Dorsal and anal fins with somewhat diffuse brown pigment on basal one-half of fin rays, most apparent in caudal region of body. Specimens with well-developed body crossbands usually with small, lightly pigmented blotches on dorsal and anal fins corresponding to crossbands. Distal portions of fin rays without

pigment in older specimens; somewhat yellowish in recently captured specimens. Four specimens (UF 29778, USA 4822, VIMS 5573) with small, darkly pigmented, almost spherical spot on scaly portion at caudal-fin base; distal portion of caudal fin usually unpigmented, or somewhat yellowish in more recently collected specimens.

**Size and sexual maturity (Fig. 6C)** *Symphurus pusillus* is a dwarf species. The largest specimen, a 76.9 mm female, is only slightly larger than the largest male (62.7 mm). Most specimens ranged between 38 and 55 mm. Of 20 specimens examined for size-related life history information, nine were males (35.2–62.7 mm), 11 females (40.0–76.9 mm), and one of indeterminate sex was immature (38.6 mm). Based upon reproductive stages of females, sexual maturity occurs at ca. 40 mm. Nine females were mature. Gravid females ranged in size from 40.0 to 76.9 mm. Other females, 41.6–58.4 mm, although not gravid, were mature with elongate ovaries containing ripening ova. Two females measuring 40.0 and 48.2 mm were immature with ovaries undergoing elongation.

**Geographic distribution (Fig. 29)** In the western North Atlantic on the continental shelf along the east coast of the United States from off Long Island, New York (40°N), southward to Florida, and extending into the eastern Gulf of Mexico westward to the region of DeSoto Submarine Canyon (29°N, 88°50'W). Most specimens were collected on the continental shelf between Cape Hatteras and southern Florida. This species has been irregularly collected and is poorly represented in collections. Most samples consist of solitary individuals, undoubtedly reflecting difficulties in collecting this small species at the relatively great depths it inhabits.

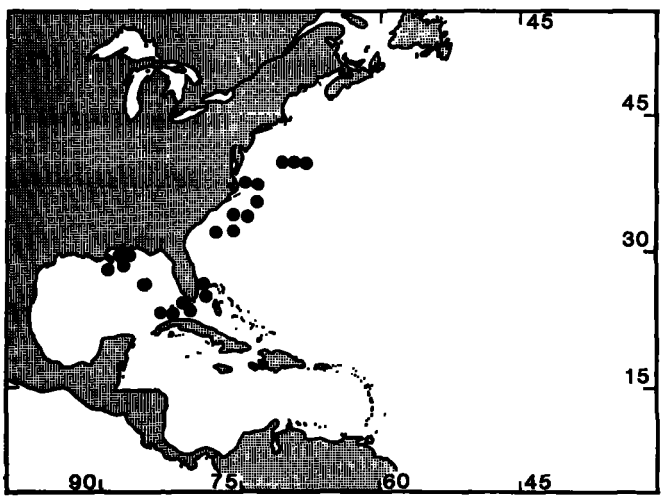


**Figure 29**

Geographic distribution of *Symphurus pusillus* based on material examined (discussion of geographic distribution appears in species account).

Baughman (1950:138) reported two specimens purportedly of this species from the western Gulf of Mexico near Corpus Christi, Texas. However, these specimens (USNM 93584 and not USNM 93854 as listed in Baughman's paper) are actually *S. plagiusa*.

**Bathymetric distribution** *Symphurus pusillus* inhabits mud substrates in moderate depths (102–233 m) on the continental shelf (Table 10). Most of 21 specimens with depth of capture information were collected at 115–233 m. Only two specimens (USNM 153099) occurred shallower than 110 m (at 102 m).

**Remarks** Goode and Bean (1885b:590) based their description of *Aphoristia pusilla* on three specimens collected from off Long Island, New York. Of the three syntypes, one female (USNM 28778) in the best overall condition is designated as the lectotype. The other two syntypes in USNM 28730 and USNM 325958 (formerly 28778, in part) now become paralectotypes. The lectotype (54.5 mm) was collected in 139 m at 40°01'N, 69°56'W on 4 Aug 1881. It has a 1-3-2 ID pattern, 12 caudal-fin rays, 87 dorsal- and 73 anal-fin rays, 48 total vertebrae, and ca. 83 scales in longitudinal series.

**Comparisons** In some meristic and other features, *S. pusillus* resembles two deep-water species, the western Atlantic *S. piger* and the eastern Atlantic *S. nigrescens*. Fin-ray counts of *S. pusillus* overlap almost completely those of *S. piger*. However, this species differs from *S. piger* in having more longitudinal scales (77–87 vs. 62–75 in *S. piger*), an unpigmented isthmus and unpigmented inner opercular linings (both structures lightly pigmented in *S. piger*), in four hypurals (vs. 5 in *S. piger*), in its different morphometrics (Fig. 30, A–B), and *S. pusillus* is a much smaller species (see Figs. 6C and 8D), attaining maximum lengths of only about 77 mm, whereas, *S. piger* reaches lengths nearly double that size (ca. 130 mm).

*Symphurus pusillus* and the eastern Atlantic *S. nigrescens* are possibly a closely related species pair with distributions on the continental shelf on either side of the Atlantic. Although only slight differences in meristic features are noted between *S. pusillus* and *S. nigrescens*, these species are distinct in that *S. pusillus* has a longer caudal fin (11.5–15.4% SL vs. 7.6–12.2% SL in *S. nigrescens*; Fig. 31), and the dorsal and anal fins in *S. pusillus* are pigmented basally, but not distally, and these fins usually lack

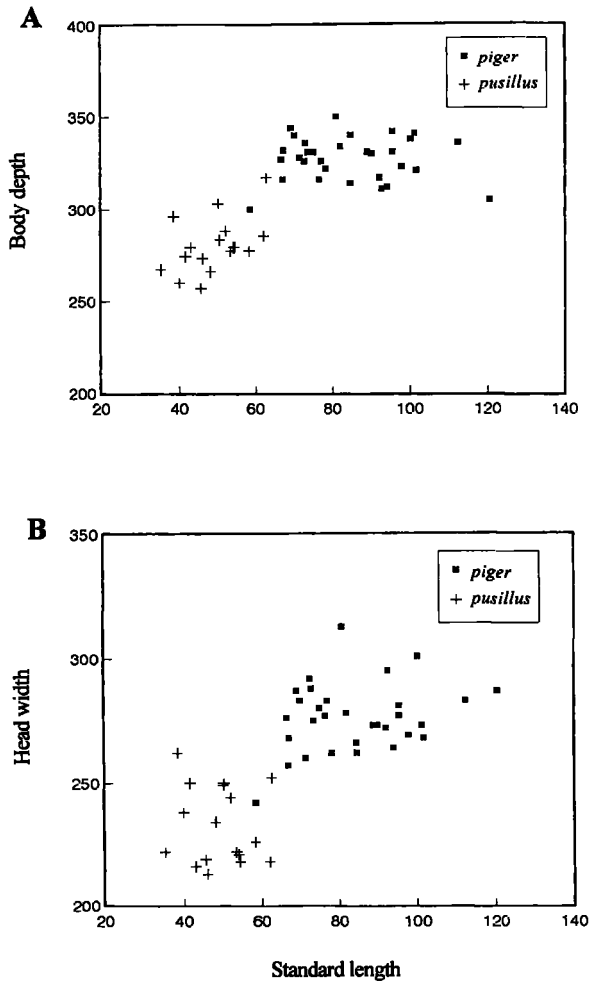


**Figure 30**

Comparisons of selected morphometric features for *Symphurus pusillus* and *S. piger*. (**A**) Body depth (thousandths of standard length) versus standard length (mm). (**B**) Head width (thousandths of standard length) versus standard length (mm).

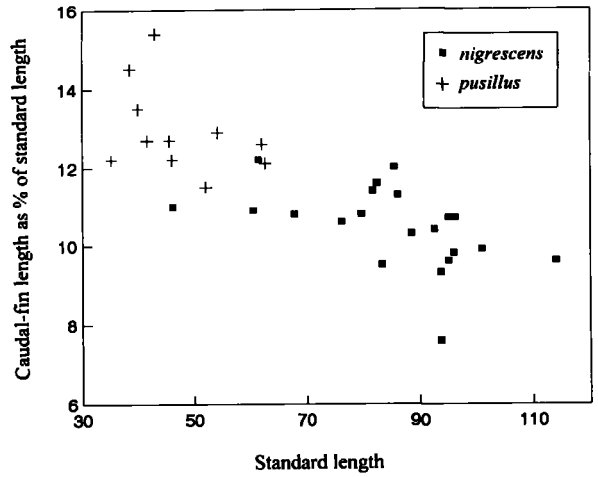


**Figure 31**

Comparison of caudal-fin length (expressed in percent standard length) versus standard length for *Symphurus pusillus* (western Atlantic) and *S. nigrescens* (eastern Atlantic).

darkly pigmented blotches (if blotches are present, they are small and only lightly pigmented) or lack any noticeably dark pigment streaks on the fin rays. In contrast, *S. nigrescens* usually has quite colorful dorsal and anal fins featuring a series of alternating dark blotches and unpigmented areas entirely throughout these fins, or if pigmented blotches are not present, then the individual fin rays throughout the entire dorsal and anal fins are streaked with dark pigment over their entire lengths. *Symphurus pusillus* is also a smaller species reaching maximum sizes of only ca. 77 mm and maturing at sizes as small as 45 mm, whereas, *S. nigrescens* attains larger sizes (to 117 mm and not reaching maturity until 70 mm or larger).

*Symphurus pusillus* has some morphological features similar to those observed in the western Atlantic *S. pelicanus* and *S. rhytisma*. Differences between these species are substantial and discussed in the "Comparisons" sections in accounts for *S. rhytisma* and *S. pusillus*.

Some meristic features and ocular-side coloration of *S. pusillus* are similar to those found in *S. billykrietei*, *S. ginsburgi*, and *S. stigmosus*. In fact, throughout its range *S. pusillus* co-occurs with, but is not usually syntopic with, *S. billykrietei* (only one lot in VIMS collection (1905) taken at 40°N and 233 m, and coincidentally, the deepest known capture for *S. pusillus*, contained both species) and *S. stigmosus*. *Symphurus pusillus* differs from all three species in its generally lower, mostly nonoverlapping, meristic features (dorsal-fin rays 83–88 vs. 87–95, anal-fin rays 71–75 vs. 74–84, and total vertebrae 47–49 vs. 50–53 in the others). Other differences between *S. pusillus* and these species are discussed in the "Comparisons" sections for *S. ginsburgi*, *S. billykrietei*, and *S. stigmosus*, respectively.

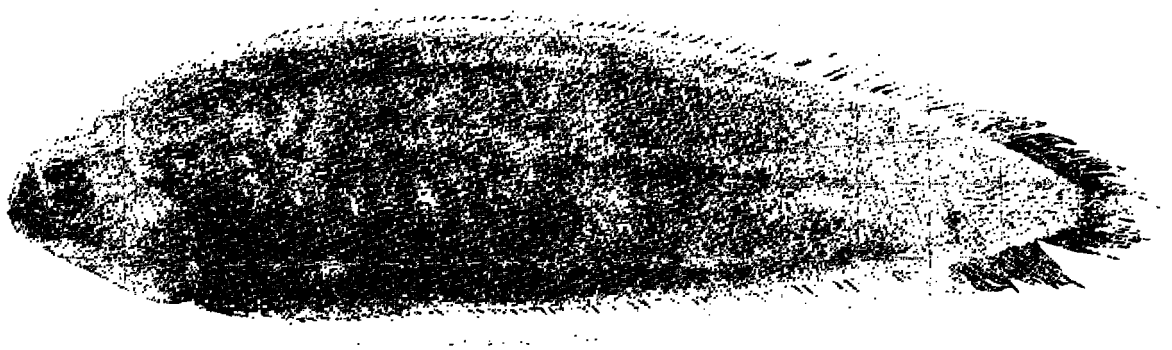

**Figure 32**
*Symphurus marginatus* (Goode and Bean), USNM 236609, 115 mm SL, Florida 29°39'N, 80°11'W.

## *Symphurus marginatus* (Goode and Bean, 1886) (Figs. 8C, 32–33; Tables 1–10, 20) Margined tonguefish

*Aphoristia marginata* Goode and Bean, 1886:154 (in part); (original description; Gulf of Mexico, off Mississippi; nontype specimen from *Fish Hawk* Station 1154 belongs to *S. nebulosus*). Goode and Bean, 1896:459 (in part); (redescription with figure; based on Goode and Bean, 1886).

*Symphurus marginatus*. Jordan and Goss, 1889:323 (after Goode and Bean). Jordan and Evermann, 1898:2706 (after Goode and Bean). Evermann and Marsh, 1900:332 (in key). Chabanaud, 1939:26 (American Atlantic). Ginsburg, 1951:198 (counts, measurements, distribution, in key). Fowler, 1952:143 (New Jersey, offshore record based on Goode and Bean). Bright, 1968:58 (four specimens, central Gulf of Mexico; 585–732 m). Topp and Hoff, 1972:107 (geographical distribution). Potts and Ramsey, 1987:88 (Gulf of Mexico; color description; 333–832 m). Séret and Andreata, 1992:94 (one specimen; southern Brazil; 600 m). Munroe, 1992:368, 377 (ID pattern; geographic, bathymetric distributions).

*Symphurus diomedianus* (not of Goode and Bean, 1885). Longley and Hildebrand, 1941:49 (Tortugas, Florida).

*Symphurus plagusia* (not of Schneider, in Bloch and Schneider, 1801). Séret and Andreata, 1992:94 (southern Brazil; five specimens; 640 m).

**Diagnosis** *Symphurus marginatus* is a deepwater species that can be distinguished from all congeners by the following combination of characters: predominant 1-3-2 ID pattern; 12 caudal-fin rays; 4, or less frequently, 5 hypurals; 93–104 dorsal-fin rays; 80–89 anal-fin rays; 51–56 total vertebrae; 86–99 scales in longitudinal series; absence of pupillary operculum; black peritoneum; teeth along entire margin of ocular-side jaws; absence of fleshy ridge on ocular-side lower jaw; absence of scales on blind sides of dorsal- and anal-fin rays; elongate, somewhat slender body of nearly uniform depth along anterior two-thirds; ocular surface pigmentation featuring dark brown caudal blotch; posterior one-third of dorsal and anal fins with large caudal blotch, but without spots; and caudal fin without spots or blotches.

**Description** A medium-size species attaining a maximum length of ca. 146 mm SL. ID pattern usually 1-3-2 (77/98 specimens), less frequently 1-3-3 (11/98) and 1-2-3, rarely 1-2-2 (Table 2). Caudal-fin rays 12 (97/101), rarely 11 or 13 (Table 3). Dorsal-fin rays 93–104, usually 95–101 (Table 4). Anal-fin rays 80–89 (Table 5). Total vertebrae 51–56, usually 52–54 (92/97) (Table 6). Hypurals 4 (41/57 specimens), less frequently 5 (16/57 specimens). Longitudinal scale rows 86–99, usually 88–96 (Table 7). Scale rows on head posterior to lower orbit 16–19, usually 17–18 (Table 8). Transverse scales 30–37 (Table 9).

Proportions of morphometric features presented in Table 20. Body relatively elongate, of nearly uniform width along anterior two-thirds, with gradual taper

**Table 20**

Morphometrics for holotype (MCZ 27967) and 29 additional specimens of *Symphurus marginatus*. (Abbreviations defined in methods section; SL is expressed in mm; characters 2 to 14 are expressed in thousandths of SL; 15 to 21 in thousandths of HL; *n* = no. of specimens measured.)

| Character | Holotype | *n* | Range | Mean | SD |
|---|---|---|---|---|---|
| 1. SL | 90.1 | 30 | 56.9–146.1 | 106.5 | 18.08 |
| 2. BD | 218 | 30 | 200–315 | 250.3 | 27.14 |
| 3. PDL | 58 | 30 | 44–81 | 56.0 | 7.33 |
| 4. PAL | 203 | 30 | 182–256 | 219.1 | 17.40 |
| 5. DBL | 942 | 30 | 919–956 | 944.0 | 7.34 |
| 6. ABL | 741 | 30 | 616–846 | 768.2 | 34.22 |
| 7. PL | — | 24 | 42–74 | 58.0 | 8.24 |
| 8. PA | 50 | 30 | 27–74 | 52.9 | 11.50 |
| 9. CFL | — | 25 | 80–125 | 105.9 | 11.46 |
| 10. HL | 192 | 30 | 127–221 | 182.1 | 15.56 |
| 11. HW | 196 | 30 | 147–227 | 191.2 | 16.74 |
| 12. POL | 119 | 30 | 99–144 | 112.0 | 8.88 |
| 13. UHL | 90 | 30 | 90–133 | 110.3 | 11.86 |
| 14. LHL | 115 | 30 | 84–129 | 97.1 | 11.08 |
| 15. POL | 618 | 30 | 571–802 | 617.0 | 41.52 |
| 16. SNL | 185 | 30 | 168–331 | 207.2 | 31.91 |
| 17. UJL | 231 | 30 | 180–331 | 213.6 | 25.77 |
| 18. ED | 150 | 30 | 125–248 | 148.6 | 22.98 |
| 19. CD | 144 | 30 | 144–256 | 197.4 | 30.83 |
| 20. OPLL | 300 | 30 | 208–372 | 290.4 | 36.30 |
| 21. OPUL | 156 | 30 | 144–331 | 218.9 | 38.03 |

posteriorly beyond this point. Body depth increasing with size, juveniles with narrower body, usually proportionately less than 280 SL; adults with body depth ranging from 280–315 SL. Preanal length slightly shorter than body depth. Head moderately long and relatively narrow, slightly shorter than body depth. Head usually just slightly wider than long (HW:HL 0.84–1.25, $\bar{x}$=1.05). Lower head lobe narrow, slightly less than postorbital length; slightly narrower than upper head lobe. Lower opercular lobe of ocular side considerably wider than upper lobe. Snout short, somewhat pointed; covered with small ctenoid scales. Poorly developed dermal papillae occasionally present on blind-side snout. Anterior nostril on ocular side long, when depressed posteriorly, usually falling just short of anterior border of lower eye (about two-thirds of specimens), or just reaching to anterior border of lower eye in about one-third of specimens. Jaws moderately long; maxilla extending posteriorly to vertical through anterior margin of lower eye. Ocular-side lower jaw without fleshy ridge. Teeth well developed on blind-side jaws. Ocular-side dentary with row of teeth along complete margin of jaw; ocular-side premaxilla usually with single row of teeth along anterior four-fifths of margin of jaw, occasionally with complete tooth row. Chin depth slightly smaller than snout length. Lower eye large; eyes usually equal in position, with large and obvious lens. Anterior and medial surfaces of eyes partially covered with 4-6 small ctenoid scales; 4–6 small ctenoid scales in narrow interorbital region. Pupillary operculum absent. Dorsal-fin origin usually equal with vertical through midpoint of upper eye, occasionally located more posteriorly, only reaching vertical through posterior margin of upper eye. Scales absent on blind sides of dorsal- and anal-fin rays. Pelvic fin short; longest pelvic-fin ray, when extended posteriorly, usually reaching base of first anal-fin ray. Posteriormost pelvic-fin ray connected to body by short delicate membrane terminating anterior to anus, or occasionally reaching posteriorly to anal-fin origin (membrane torn in most specimens). Caudal fin short. Relatively small ctenoid scales on both sides of body.

**Pigmentation (Fig. 32)** Coloration similar for both sexes. Ocular surface usually uniformly dark brown, sometimes with yellowish tint, without crossbands. The most consistent and obvious pigmentation in preserved specimens are longitudinal black stripes along bases of the dorsal and anal fins, and a dark brown blotch, roughly circular in outline, usually covering the entire ocular-side caudal region. Caudal blotch usually extending over ca. 10 scale rows and 13–14 posteriormost fin rays of dorsal and anal fins; occasionally caudal blotch extended onto caudal-fin base. Ocular-side outer opercle with background coloration of body. Inner linings of opercles and isthmus on both sides of body usually unpigmented. Ocular-side upper lip with variably pigmented band; ocular-side lower lip occasionally spotted, but without prominent pigment band. Small patch of pigment of variable intensity occasionally at base of anterior nostril. Blind side off-white, or yellowish. Peritoneum black, usually visible through abdominal wall on both sides. Anal pore white.

Basal one-half of dorsal- and anal-fin rays in anterior two-thirds of body uniformly pigmented with dark brown or black pigment forming longitudinal stripe along fin-ray bases; distal one-half of those fin rays unpigmented or only lightly pigmented with diffuse melanophores. Caudal region of body, especially proximate to caudal blotch, with fin rays of dorsal and anal fins heavily pigmented. Caudal fin usually heavily pigmented on proximal one-half; distal one-half with diffuse pattern of light melanophores of similar coloration to anterior two-thirds of ocular-side of body, or occasionally unpigmented.

***Size and sexual maturity (Fig. 8C)*** *Symphurus marginatus* is a medium-size tonguefish attaining maximum lengths of about 146 mm. Most specimens were much smaller; nearly one-half of 93 specimens

examined for size-related life history information were 100–120 mm, whereas another 22% were 80–100 mm. Females attain somewhat larger sizes. The largest *S. marginatus* examined in this study was a female of 146.1 mm; the largest male measured 130.5 mm. Specimens <80 mm are generally rare in collections; only 10 in this size range were available for study. Of specimens examined, 43 were males (56.9–130.5 mm) and 51 females (58.7–146.1 mm), with 49 females being mature (79–146 mm). Sexual maturity in females occurs at a relatively large size (ca. 79–90 mm). The smallest female with elongate ovaries was 78.6 mm, and all but one female larger than 80 mm had elongate ovaries. Most females 85–105 mm, although having elongate ovaries, lacked evident mature ova. The smallest gravid female was 87.5 mm, but this size is apparently unusual, because only three of 20 other females smaller than 105 mm were gravid. Two females, 58.7 and 80.1 mm, were immature with ovaries scarcely elongate.

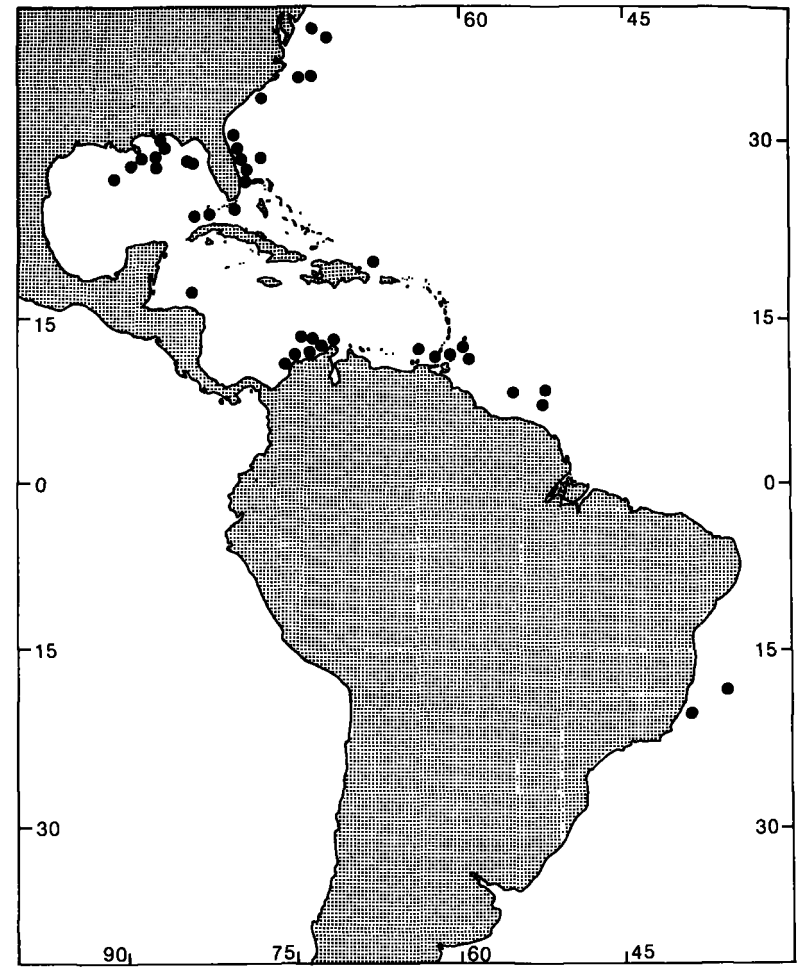


**Figure 33**

Geographic distribution of *Symphurus marginatus* based on material examined (discussion of geographic distribution appears in species account).

**Geographic distribution (Fig. 33)** Primarily in deepwater outer continental shelf habitats from off New Jersey (39°55'N) southward along the eastern United States, in eastern and central regions of the Gulf of Mexico (to Louisiana, 91°18'W), off the Bahamas, the Greater Antilles at Puerto Rico, widespread throughout the southern Caribbean Sea from Honduras to Venezuela, and from Trinidad and Tobago to southeastern Brazil (21°34'S) (Séret and Andreata, 1992). Although *S. marginatus* has occasionally been collected as far north as southern New Jersey (39°N) and Virginia (36°N), the majority of specimens were taken farther south, primarily off southern Florida, in eastern and central regions of the Gulf of Mexico, and throughout the southern Caribbean Sea. Southernmost records for this species (Séret and Andreata, 1992) are for specimens from off southeastern Brazil (ca. 21°S).

**Bathymetric distribution** This species usually inhabits deepwater soft mud substrates on the outer continental shelf and upper continental slope. *Symphurus marginatus* has been collected at depths of 37–750 m (Table 10), but its center of abundance occurs between 320 and 550 m, where the majority of specimens (88/108 or 81%) were collected. Of 108 specimens with available depth information, only nine were collected at depths shallower than 300 m. Single specimens were collected at 37 m (UMML 17440, east coast of Florida), 66 m (UMML 35237, Nicaragua), and 72 m (MCZ 58657, Nicaragua); whereas three specimens (UMML 30106) collected at 10–11°N off Costa Rica were taken at 45 m. Two specimens were collected between 280 and 290 m (UMML 35240; Colombia) and one (UMML 35231; Florida) was taken at 293 m. Only 11 specimens were taken deeper than 550 m. The two deepest captures (three specimens at 713 m, USU 1371; and one specimen at 750 m, FMNH 47908) were taken off Brazil and in the Gulf of Mexico, respectively. Potts and Ramsey (1987) reported a depth range of 333–832 m for this species in the Gulf of Mexico. Little is known concerning life history of this species.

**Remarks** In the original description, Goode and Bean (1886:154) mistakenly identified a specimen of *S. nebulosus* as their new species, *Aphoristia marginata*. This specimen, however, was not designated

as part of the type series and therefore does not compromise the original concept of *Aphoristia marginata*.

Metzelaar's reference (1919:134) to *S. marginatus* from Saint Eustatius is based on a misidentified specimen (ZMA 119.422) of *S. ommaspilus*.

**Comparisons** *Symphurus marginatus* has somewhat similar geographic and bathymetric distributions throughout the Caribbean Sea and Gulf of Mexico as those reported for *S. piger* (see below), and these are the only western Atlantic species with a combination of a 1-3-2 ID pattern, black peritoneum, and five hypurals (although five hypurals occur much less frequently in *S. marginatus*—only 28% of 57 specimens of this species had this count vs. 99% of 136 specimens of *S. piger*). However, these distinctive species are not usually collected syntopically and the two species can be readily identified (compare Figs. 32 and 34). *Symphurus marginatus* lacks crossbands on the ocular surface and has a prominent blotch on the ocular-side caudal region, whereas *S. piger* usually has prominent crossbands and lacks any blotch on the ocular-side caudal region. The isthmus and inner opercular linings of *S. marginatus* are unpigmented, whereas those of *S. piger* are lightly sprinkled with melanophores, and basal margins of the dorsal and anal fins in *S. marginatus* have a dark brown stripe that is absent in *S. piger*. *Symphurus marginatus* also differs from *S. piger* by its much higher and nonoverlapping meristic features (93–104 dorsal-fin rays vs. 80–88 in *S. piger;* 80–89 anal-fin rays vs. 68–74; 86–99 scales in a longitudinal series vs. 62–75; and 51–56 total vertebrae vs. 45–49 in *S. piger*). In addition, *S. marginatus* has a more elongate body (BD 200–315, $\bar{x}$=250) with a relatively narrow head (147–227 SL, $\bar{x}$=191) compared with that of *S. piger* (wide body 244–350 SL, $\bar{x}$=322 and wide head 242–313 SL, $\bar{x}$=277).

The relatively elongate body of *S. marginatus* is reminiscent of other Atlantic slender-bodied, deepwater species, namely the western Atlantic *S. nebulosus*, and *S. ligulatus* and *S. vanmelleae* from the eastern Atlantic. *Symphurus marginatus* is readily distinguished from *S. nebulosus* and *S. ligulatus* by its fewer caudal-fin rays (12 vs. 14 in these others), from all three species by differences in ID pattern (1-3-2-2-2 in *S. marginatus* vs. 1-2-2-2-2 in *S. nebulosus* and *S. ligulatus* and 1-2-2-1-2 in *S. vanmelleae*), and its generally lower meristic features (93–104 dorsal-fin rays in *S. marginatus* vs. 105–113 in *S. nebulosus*, 101–108 in *S. vanmelleae*, and 102–113 in *S. ligulatus*; 80–89 anal-fin rays in *S. marginatus* vs. 91–98 in *S. nebulosus*, 86–93 in *S. vanmelleae*, and 90–102 in *S. ligulatus*; 51–56 total vertebrae in *S. marginatus* vs. 57–60 in *S. nebulosus*, 55–59 in *S. vanmelleae*, and 56–61 in *S. ligulatus*; 86–99 scales in a longitudinal series in *S. marginatus* vs. 120–135 in *S. nebulosus*, 107–124 in *S. vanmelleae*, and 115–135 in *S. ligulatus*). In addition, all three species lack the dark brown ocular-side caudal blotch present in *S. marginatus*. From *S. vanmelleae*, *S. marginatus* differs further in having only nine abdominal vertebrae (vs. 10 or 11).

Differences between *S. marginatus* and *S. billykrietei*, *S. ginsburgi*, and *S. stigmosus*, three other western Atlantic members of this species group, are discussed in the "Comparisons" section of each species account, respectively.

*Symphurus marginatus* is similar in some meristic features to the western Atlantic, shallow-water species, *S. tessellatus*, *S. oculellus*, and *S. caribbeanus*, but is easily recognized from all three by its black peritoneum (unpigmented in these other species), well-developed dentition on ocular-side jaws (vs. absent or reduced dentition on ocular-side jaws), and differences in pigmentation patterns. The ocular surface in *S. marginatus* is uniformly pigmented with a single dark brown blotch in the caudal region, the isthmus and inner opercular linings are unpigmented, and spots or blotches are lacking on the ocular-side opercle. In contrast, the ocular surface of these other species usually has well-developed crossbands, the ocular-side isthmus and inner opercular linings are heavily pigmented, and all lack the dark brown caudal blotch characteristic of *S. marginatus*. Both *S. tessellatus* and *S. oculellus* also differ in having a dark blotch on the outer surface of the ocular-side opercle. *Symphurus marginatus* has a different ID pattern (1-3-2) than that in these others (1-4-3 ID pattern).

Approximately 28% (16/57) of the *S. marginatus* examined had five hypurals (the remainder had four). Four other species in the genus, the western Atlantic *S. piger* and eastern Pacific *S. microlepis*, *S. diabolicus*, and *S. oligomerus*, also have the combination of a 1-3-2 ID pattern, 12 caudal-fin rays, black peritoneum, and five hypurals. Differences between *S. marginatus* and *S. piger* were discussed above. *Symphurus marginatus* is easily distinguished from the eastern Pacific species because they lack the large dark brown blotch on the ocular-side caudal region. From *S. oligomerus*, *S. marginatus* differs further in having dorsal and anal fins with a dark brown stripe along the basal margins (vs. an alternating series of rectilinear pigmented blotches and unpigmented regions on the dorsal and anal fins and no basal stripe in *S. oligomerus*). Meristic features of *S. marginatus* are distinctly lower than those of *S. microlepis* and *S. diabolicus* (less than 105 dorsal-fin rays, 90 or fewer anal-fin rays, and 56 or fewer vertebrae in *S. marginatus* vs. more than 105 dorsal-fin rays and 91 anal-fin rays, and more than 56 total vertebrae in these other species).

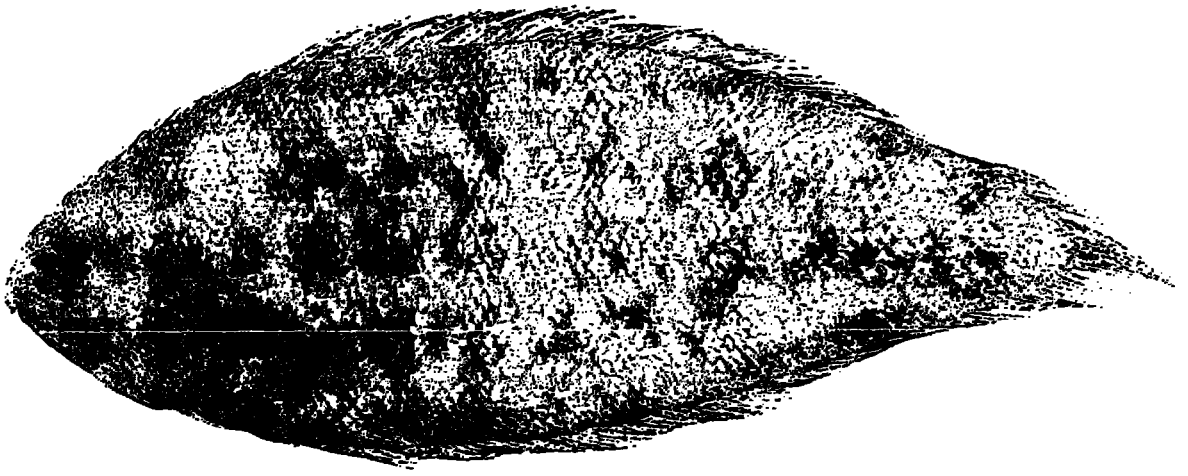

**Figure 34**
*Symphurus piger* (Goode and Bean), USNM 159211, 106 mm SL, French Guiana 7°18'N, 53°32'W.

## *Symphurus piger* (Goode and Bean, 1886) (Figs. 8D, 30, 34–35; Tables 1–10, 21) Deepwater tonguefish

*Aphoristia pigra* Goode and Bean, 1886:154 (in part) (original description; more than one species in account). Goode and Bean, 1896:460 (in part) (redescription, figure; based on specimens in previous citation). Cockerell, 1912:172 (brief discussion and figure of scales).

*Symphurus piger*. Jordan and Goss, 1889:326 (after Goode and Bean, 1886). Jordan and Evermann, 1898:2705 (after Goode and Bean, 1886). Evermann and Marsh, 1900:332 (in key). Chabanaud, 1939:26 (Caribbean Sea, 457 m). Ginsburg, 1951:197 (in part; more than one species in redescription; designation of lectotype). Topp and Hoff, 1972:108 (distribution). Guitart, 1978:727 (Cuba; figure, counts, in key). Potts and Ramsey, 1987:89 (Gulf of Mexico; color description; 92–194 m). Munroe, 1992:368, 377 (ID pattern; geographic, bathymetric distributions).

*Symphurus pusillus* (not of Goode and Bean, 1885). Longley and Hildebrand, 1941:50 (Tortugas, Florida).

**Diagnosis** *Symphurus piger* is a deepwater species distinguished from all congeners by the combination of predominant 1-3-2 ID pattern; 12 caudal-fin rays; 5 hypurals; 80–88 dorsal-fin rays; 68–74 anal-fin rays; 45–49 total vertebrae; 62–75 scales in longitudinal series; black peritoneum; absence of pupillary operculum; teeth along entire margin of ocular-side jaws; absence of fleshy ridge on ocular-side lower jaw; absence of scales on blind side of dorsal- and anal-fin rays; wide body; wide head; ocular surface pigmentation with strong crossbanding pattern without caudal blotch; and dorsal, anal, and caudal fins without spots or blotches.

**Description** A medium-size *Symphurus* attaining maximum lengths of ca. 130 mm SL. ID pattern usually 1-3-2 (137/141 specimens), rarely 1-2-2 or 1-3-3 (Table 2). Caudal-fin rays usually 12 (134/139), rarely 10, 11, or 13 (Table 3). Dorsal-fin rays 80–90, usually 83–88 (Table 4). Anal-fin rays 68–74 (Table 5). Total vertebrae 45–49, usually 47–49 (137/142) (Table 6). Hypurals 5 (138/139 specimens; 1/139 with 4 hypurals). Longitudinal scale rows 62–75, usually 66–73 (Table 7). Scale rows on head posterior to lower orbit 16–21, usually 17–19 (Table 8). Transverse scales 32–38 (Table 9).

Proportions of morphometric features presented in Table 21. Body relatively deep, maximum depth in anterior one-third of body; body tapering relatively rapidly posterior to midpoint. Preanal length shorter

**Table 21**

Morphometrics for holotype (MCZ 27965) and 32 additional specimens of *Symphurus piger*. (Abbreviations defined in methods section; SL is expressed in mm; characters 2 to 14 are expressed in thousandths of SL; 15 to 21 in thousandths of HL; *n* = no. of specimens measured.)

| Character | Holotype | *n* | Range | Mean | SD |
|---|---|---|---|---|---|
| 1. SL | 84.6 | 33 | 58.6–120.5 | 85.0 | 14.71 |
| 2. BD | 314 | 33 | 244–350 | 322.5 | 23.09 |
| 3. PDL | 53 | 33 | 46–90 | 58.4 | 7.98 |
| 4. PAL | 260 | 33 | 176–327 | 255.4 | 26.40 |
| 5. DBL | 947 | 33 | 910–954 | 941.6 | 7.98 |
| 6. ABL | 742 | 33 | 730–778 | 748.5 | 12.65 |
| 7. PL | 58 | 33 | 58–86 | 73.3 | 7.13 |
| 8. PA | 32 | 33 | 28–67 | 46.1 | 9.09 |
| 9. CFL | 142 | 33 | 103–168 | 147.9 | 13.92 |
| 10. HL | 234 | 33 | 182–256 | 236.8 | 12.58 |
| 11. HW | 266 | 33 | 242–313 | 276.8 | 13.63 |
| 12. POL | 155 | 33 | 149–226 | 160.6 | 13.22 |
| 13. UHL | 147 | 33 | 124–198 | 171.3 | 13.08 |
| 14. LHL | 136 | 33 | 103–142 | 126.5 | 9.76 |
| 15. POL | 662 | 33 | 633–910 | 680.0 | 61.58 |
| 16. SNL | 182 | 33 | 172–282 | 203.7 | 19.10 |
| 17. UJL | 202 | 33 | 188–338 | 228.2 | 29.60 |
| 18. ED | 146 | 32 | 101–167 | 118.1 | 13.84 |
| 19. CD | 222 | 33 | 190–317 | 232.5 | 26.91 |
| 20. OPLL | 328 | 33 | 269–401 | 321.8 | 29.94 |
| 21. OPUL | 242 | 33 | 170–375 | 226.9 | 37.52 |

than body depth. Head long and wide; head length shorter than body depth. Head much shorter than wide (HW:HL 1.03–1.44, $\bar{x}$=1.21). Lower head lobe width considerably less than postorbital length; narrower than upper head lobe. Lower opercular lobe of ocular side considerably wider than upper opercular lobe. Snout short, somewhat rounded; covered with small ctenoid scales. Dermal papillae usually well developed on blind side of snout. Anterior nostril on ocular side long, when depressed posteriorly, reaching anterior border of lower eye in about one-half of specimens, falling just short of anterior margin of lower eye in remaining specimens. Jaws long; maxilla usually extending posteriorly to vertical through mid-point of lower eye; less frequently reaching vertical through posterior margin of pupil of lower eye. Ocular-side lower jaw without fleshy ridge. Teeth well developed on blind-side jaws. Teeth along entire margin of ocular-side dentary. Anterior three-fourths of margin of ocular-side premaxilla usually with teeth; occasionally teeth over entire marginal surface of premaxilla. Chin depth slightly larger than snout length. Lower eye relatively small; eyes usually equal in position. Anterior and medial surfaces of eyes usually covered with 4–5 short rows of small ctenoid scales; 3–7 small ctenoid scales in narrow interorbital region. Pupillary operculum absent. Dorsal-fin origin usually equal with vertical through posterior margin of pupil of upper eye, occasionally reaching vertical through anterior margin of upper eye. Scales absent on blind sides of dorsal- and anal-fin rays. Pelvic fin moderately long; longest pelvic-fin ray, when extended posteriorly, usually reaching base of first anal-fin ray. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anus, or occasionally extending posteriorly almost to anal-fin origin (membrane torn in most specimens). Caudal fin long. Scales large, ctenoid; with cteni about equally developed on both sides of body.

**Pigmentation (Fig. 34)** Coloration generally similar in both sexes. Ocular surface usually dark brown with 3–10 (usually 5–8) well-developed, darker brown, sharply-contrasting, rather narrow crossbands on head and body. Crossbands continued onto dorsal and anal fins as small, elongate or irregularly shaped, somewhat diffuse, blotches. Occasionally, crossbands scarcely evident against exceptionally dark background coloration. Individuals from several locations presumably collected on light-colored sandy substrates yellowish, with faint, almost imperceptible crossbands. Older specimens mostly faded with little evidence of crossbanding. First crossband on body immediately posterior to operculum. Second and third crossbands, usually darkest; crossing body immediately posterior to operculum and almost at midpoint, respectively. Number and degree of completeness of crossbands variable in posterior one-half of body. Posteriormost crossband just anterior to caudal-fin base. Ocular-side outer opercle with background coloration as body. Inner linings of both opercles and isthmus on both sides of body lightly pigmented. Ocular-side lips usually with dark band of pigment, occasional specimens with only light spotting on lips. Blind side uniformly yellowish-white. Peritoneum black, visible through abdominal wall on both sides.

Dorsal and anal fins generally lightly pigmented anteriorly, usually becoming increasingly darker brown, but not black, on posterior one-third to one-half of body; dorsal and anal fins without definite spots. Fin rays usually evenly pigmented along their lengths. Dorsal and anal fins more heavily sprinkled with melanophores, or with melanophores coalesced into irregular elongate blotches, in regions proximate to body crossbands. Caudal-fin rays and membranes uniformly darkly pigmented throughout length of fin; without pigmented spot at caudal-fin base.

**Size and sexual maturity (Fig. 8D)** *Symphurus piger* is a medium-size species attaining a maximum

size of ca. 130 mm; however, most specimens were much smaller (80–105 mm). Only 15/161 (10.7%) fish examined for size-related life history information were larger than 110 mm. Males and females attain similar sizes. The largest *S. piger* was a female measuring 127 mm; the largest male was 118 mm. Among 161 specimens examined for life history information, were 88 males (51.6–118.3 mm), 70 females (57.9–127.1 mm), and three immature fish (27.3–51.2 mm) of indeterminate sex. Sexual maturity of females occurs at ca. 69 mm. Mature females ($n$=66) were 69.1–127.1 mm, and all females larger than 73 mm were mature with fully elongate ovaries. The smallest gravid female was 69.1 mm. Four females, 57.9–66.6 mm, were immature with ovaries just undergoing elongation.

**Geographic distribution (Fig. 35)** On outer continental shelf and upper continental slope from off southern Florida (off St. Augustine, ca. 30°N), Florida Straits, and Bahamas, infrequently in the Gulf of Mexico, and south through the Caribbean Sea, including waters off the Greater and Lesser Antilles, as well as off Mexico (Yucatan Peninsula), Central America, and northern South America to about French Guiana (7°N, 53°W). According to material available, *S. piger* is primarily a tropical species widespread in relatively deepwater areas through the Caribbean Sea and tropical Atlantic Ocean.

Only a few lots containing this species were taken in the Gulf of Mexico. Of these, one (UF 44356, containing one large adult of 127 mm) was from the eastern Gulf, off the Mississippi Delta of Louisiana (29°12'N, 88°25'W), whereas three others are from southern Florida (FDNR 12566) and the Tortugas region (USNM 117176; USNM 117287). Three lots (TCWC 4468.11; 6097.14; and 6207.17), totalling 21 specimens, were collected on the continental shelf in the western Gulf off Yucatan (18.5–20.3°N). Baughman's (1950) report of *S. piger* from Freeport, Texas, is based on a specimen (CAS-SU 40556) of *S. civitatium*. Relative scarcity of specimens from the Gulf of Mexico indicates that *S. piger* is probably not a regular component of the resident deep-sea fauna of this region, particularly in northcentral and northwestern areas of the Gulf.

**Bathymetric distribution** *Symphurus piger* occurs on relatively deep soft mud bottoms on the outer continental shelf and upper continental slope. Depth-of-capture information for 175/178 specimens (Table 10) reveals that this species has been collected over a wide depth range (92–549 m). However, the center of abundance occurs between 141 and 300 m where

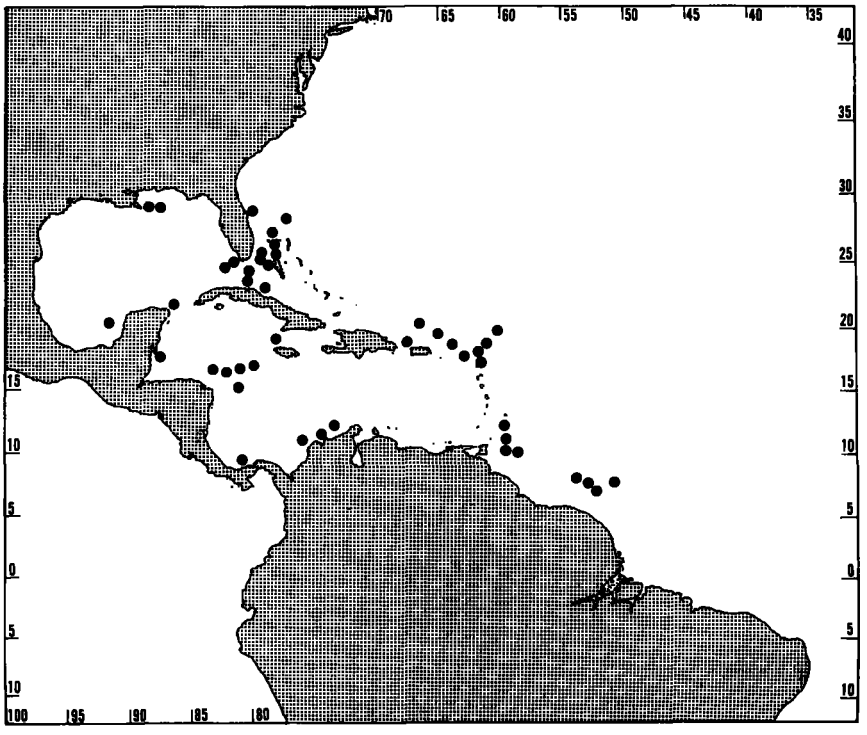


**Figure 35**

Geographic distribution of *Symphurus piger* based on material examined (discussion of geographic distribution appears in species account).

143/175 (82%) of the individuals were captured. Of interest is the capture of a 27.3 mm specimen at 329 m, and a 38.5 mm specimen at 238 m, indicating that small juveniles also occur at depths inhabited by adults. Only 5/175 (3%) *S. piger* have been collected at depths shallower than 110 m, the shallowest capture (92 m) being that of three specimens (UMML 35255) taken off the Netherlands Antilles. Only 21/175 (12%) fish were taken deeper than 300 m, with the deepest record (UMML 7124) being that of four specimens taken at 549 m off Puerto Rico.

**Remarks** In his revision of western Atlantic tonguefishes, Ginsburg (1951) stated that he was unsure which, if any, of specimens on which the original description was based, was the holotype of *A. pigra*. He selected (1951:197) the specimen from *Blake* Station XXIII (now MCZ 27965) as the lectotype. This action was invalid, because in the original description Goode and Bean (1886:154) designated the specimen from Station XXIII as "the type" of *A. pigra* and listed specimens from *Albatross* Stations 2318 and 2405 as collateral types (=paratypes in current terminology), not cotypes as stated in Ginsburg (1951). This distinction is important because of all presently available specimens believed to form the basis for the description of *A. pigra*, the only specimen that is actually this species is the holotype collected at *Blake* Station XXIII (see below).

Among seven type specimens included in the original description of *A. pigra* (Goode and Bean, 1886), all still extant, with the exception of the holotype, are *S. parvus* Ginsburg, 1951. In addition, among other, nontype material listed in the original description, Goode and Bean included specimens of a third species, *S. minor* Ginsburg, 1951. The status or existence of this material, other than the holotype, is presently somewhat confusing. Ginsburg (1951) and I have tried unsuccessfully to locate all specimens included in the original description of *A. pigra*. Difficulty with tracing this material results from the fact that specimens in the original description were listed only by *Albatross* or *Blake* station numbers. Goode and Bean, furthermore, did not always provide the number of specimens examined from each station.

Although some tonguefishes from these stations were located, it is uncertain whether these are the specimens used by Goode and Bean. For example, Ginsburg (1951) was unsure that specimens he examined from *Albatross* Station 2318 were the ones used by Goode and Bean in the original treatment of *A. pigra*. Ginsburg was also unable to locate two specimens from *Albatross* Station 2405 and an unknown number of specimens from Station 2425 listed in the original description of this species. It is noteworthy that Ginsburg discussed not four specimens from *Albatross* Station 2318, as in Goode and Bean's original description, but rather six specimens. Apparently, Ginsburg was unaware of the discrepancy.

During the course of the present study, attempts were made to locate the six paratypes of *A. pigra* and to discover the reason for the discrepancy in specimen number. Field data now included with these six USNM specimens reveal that all jar labels and museum registers list data only for *Albatross* Station 2318. If station data for all six specimens are correct, Goode and Bean either erred in listing only four specimens from this station (not likely), or two additional specimens collected at this station were not included in the original description (possible). If, however, the four specimens from *Albatross* Station 2318, as reported in Goode and Bean's account, are the correct number, and these authors used all available material, then station information for two of the six specimens now listed from *Albatross* Station 2318 have been lost or transposed prior to examination by Ginsburg. Efforts to retrace the history of these specimens prior to their inclusion in USNM holdings, including a check of museum registers and catalogue of the Bureau of Fisheries Collection at the USNM, uncovered no additional information. A search through accession files at the USNM regarding transfer of these specimens from the Bureau of Fisheries also was unsuccessful because no accession number(s) were listed for the specimens. Therefore, I cannot unequivocally demonstrate that the discussion below regarding the history of paratype material for *A. pigra* is fully correct.

The six specimens listed in Ginsburg (1951) supposedly collected from *Albatross* Station 2318 are now assigned the following museum numbers: four are USNM 74330 (three were designated as *S. parvus* paratypes by Ginsburg; the fourth, not listed in Ginsburg, was on loan at the time to P. Chabanaud (MNHN) is also *S. parvus* but was not designated as a paratype); the two other specimens from *Albatross* Station 2318 also are part of the type series of *S. parvus*. One specimen is now USNM 84491, the holotype of *S. parvus* and the other (USNM 152733) is a paratype of *S. parvus*. Both specimens originally were contained in the same jar (indicated both in museum catalogue records and on jar labels). These (USNM 84491 and 152733) may be the two specimens from *Albatross* Station 2405 listed in Goode and Bean's account of *A. pigra*. If this assumption is correct, then these specimens together with the four in USNM 74330 would account for the six paratypes of *A. pigra*.

The fate and status of the remaining material listed in the original description of *A. pigra* is as follows. Specimens from *Albatross* Station 2374 (nontype sta-

tus for *A. pigra*) are now paratypes (USNM 131590, 131591) of *S. minor* Ginsburg. The whereabouts of specimens (unknown number) from *Albatross* Station 2425 (nontype status for *A. pigra*) are unknown. Both Ginsburg and I were unsuccessful in locating these specimens.

**Comparisons** *Symphurus piger* is only one of five species in the genus (the western Atlantic *S. marginatus* and eastern Pacific *S. microlepis*, *S. diabolicus*, and *S. oligomerus* are the others) with the combination of a 1-3-2 ID pattern, 12 caudal-fin rays, black peritoneum, and five hypurals. *Symphurus piger* is readily distinguished from *S. marginatus* by differences in pigmentation and by its lower and nonoverlapping meristic features. Further comparisons between *S. piger* and *S. marginatus* are listed in the "Comparisons" section of the species account for *S. marginatus*. A discussion of characteristics distinguishing *S. piger* from *S. oligomerus*, *S. microlepis*, and *S. diabolicus* follows after the comparisons with other western Atlantic species.

Among Atlantic species with a 1-3-2 ID pattern, *S. piger* is most similar in some meristic features to the western Atlantic *S. pusillus*, the eastern Atlantic *S. nigrescens*, and the shallow-water western Atlantic *S. rhytisma*. *Symphurus piger* is readily distinguished from all three by its much larger scales (62–75 longitudinal scales vs. 72–97 in these other species) and by its hypural count (5 vs. 4 in the others). *Symphurus piger* differs further from *S. rhytisma* in its black peritoneum (unpigmented in *S. rhytisma*) and by its much larger size (to at least 130 mm vs. 45 mm in *S. rhytisma*). Features further distinguishing *S. piger* from *S. pusillus* (see Fig. 30) and *S. rhytisma* are discussed in the "Comparisons" sections in the accounts for each of those species.

Differences between *S. piger* and other western Atlantic species (*S. ginsburgi*, *S. billykrietei*, *S. stigmosus*, and *S. pelicanus*) possessing a 1-3-2 ID pattern, 12 caudal-fin rays, and a black peritoneum are discussed in the "Comparisons" sections of each species account.

*Symphurus piger* is quite distinctive from *S. microlepis* and *S. diabolicus*, having a much stockier and deeper body with the greatest depth occurring in the anterior one-third, compared with *S. microlepis* or *S. diabolicus* which have a more elongate shape (BD 244–350 in *S. piger* vs. 203 and 279, respectively, for *S. microlepis* and *S. diabolicus*) with body depth nearly equal over the anterior two-thirds. *Symphurus piger* has much lower meristic features in comparison with those of the other species (dorsal-fin rays 80–88 in *S. piger* vs. 106–109 in the others; anal-fin rays 68–74 vs. 92–94; 62–75 longitudinal scales vs. 126–135; and 45–49 total vertebrae vs. 57–58 in *S. microlepis* and *S. diabolicus*).

*Symphurus piger* is distinguished from *S. oligomerus* by its relatively uniformly pigmented dorsal and anal fins (vs. dorsal and anal fins of *S. oligomerus* with alternating series of boldly pigmented blotches and unpigmented areas), and differences in many meristic features (those of *S. piger* listed first): 80–88 dorsal-fin rays vs. 87–97; 68–74 anal-fin rays vs. 72–83; 62–75 longitudinal scales vs. 86–96; and 45–49 vs. 48–52 total vertebrae).

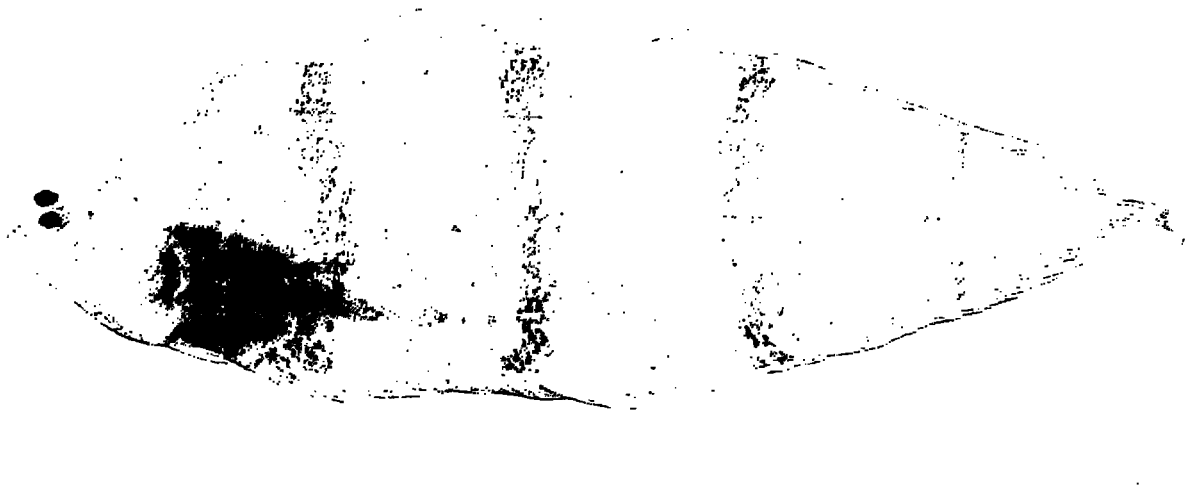

**Figure 36**
*Symphurus trewavasae* Chabanaud, USNM 290668, 113.1 mm SL, Uruguay 33°50'S, 51°51'W.

## *Symphurus trewavasae* Chabanaud, 1948 (Figs. 8E, 36–37; Tables 1–10, 22) Trewavas's tonguefish

*Symphurus plagiusa* (not of Linnaeus, 1766). Regan, 1914:23 (Cabo Frio, Brazil). Lazzaro, 1973:245 (Puerto Quequén, Argentina; in key). Roux, 1973:176 (southern Brazil). Menni et al., 1984:202 (reidentifications; previous citations by Roux (1973) for Brazil, and Lazzaro (1973) for Argentina correspond to *S. trewavasae*).

*Symphurus trewavasae* Chabanaud, 1948:508 (original description; Cabo Frio, Brazil). Ginsburg, 1951:185 (brief comparison with *S. plagiusa*). Menezes and Benvegnú, 1976:144 (redescription, photograph; diagnosed from *S. plagiusa*; ecological notes). Menni et al., 1984:202 (southern Brazil to Argentina). Munroe, 1992:369, 377 (ID pattern; geographic, bathymetric distributions). Andreata and Séret, 1995:590 (continental shelf, Brazil).

*Symphurus plagusia* (not of Schneider, in Bloch and Schneider, 1801). Andreata and Séret, 1995:590 (in part; specimen from 23°07'S, 42°03'W is *S. trewavasae*).

**Diagnosis** *Symphurus trewavasae* is readily distinguished from all congeners by the combination of predominant 1-3-3 ID pattern; 10 caudal-fin rays; 4 hypurals; 88–94 dorsal-fin rays; 73–79 anal-fin rays; 47–51, usually 48–49, total vertebrae; 67–77 scales in longitudinal series; unpigmented peritoneum; absence of pupillary operculum; absence of scales on blind sides of dorsal- and anal-fin rays; teeth along entire margin of ocular-side dentary; anterior one-half or less of margin of ocular-side premaxilla with teeth; lack of fleshy ridge on ocular-side lower jaw and membrane ostia; ocular surface with bold pattern of crossbands without caudal blotch; lack of pepper-dot pigment on blind side of body; and dorsal, anal, and caudal fins without spots or blotches.

**Description** A medium-size tonguefish attaining maximum size of ca. 139 mm SL. ID pattern usually 1-3-3 (49/73 specimens), less frequently 1-4-2 (11/73) or 1-3-2 (4/73) (Table 2). Caudal-fin rays 10 (Table 3). Dorsal-fin rays 88–94 (Table 4). Anal-fin rays 73–79 (Table 5). Total vertebrae 47–51, usually 48–49 (56/70) (Table 6). Hypurals 4 (70/70). Longitudinal scale rows 67–77, usually 71–77 (Table 7). Scale rows on head posterior to lower orbit 15–20, usually 16–17 (Table 8). Transverse scales 31–37, usually 32–35 (Table 9).

Proportions of morphometric features presented in Table 22. Body moderately deep; greatest depth from approximately region of tenth anal-fin ray to midpoint of body; body tapering fairly rapidly posterior to midpoint. Head moderately short and moderately wide, narrower than body depth. Head shorter than wide (HW:HL 1.04–1.49, $\bar{x}$=1.2). Lower head lobe width less than postorbital length; narrower than

**Table 22**

Morphometrics for holotype (BMNH 1913.12.4:264) and 19 additional specimens of *Symphurus trewavasae*. (Abbreviations defined in methods section; SL is expressed in mm; characters 2 to 14 are expressed in thousandths of SL; 15 to 21 in thousandths of HL; *n* = no. of specimens measured.)

| Character | Holotype | *n* | Range | Mean | SD |
|---|---|---|---|---|---|
| 1. SL | 117.0 | 20 | 69.1–131.0 | 107.3 | 17.17 |
| 2. BD | 310 | 19 | 267–419 | 307.9 | 31.01 |
| 3. PDL | 41 | 20 | 36–50 | 41.4 | 4.25 |
| 4. PAL | 197 | 20 | 184–243 | 217.1 | 15.05 |
| 5. DBL | 959 | 20 | 952–969 | 959.6 | 4.35 |
| 6. ABL | 791 | 20 | 757–812 | 783.1 | 15.56 |
| 7. PL | 70 | 18 | 57–80 | 68.8 | 6.29 |
| 8. PA | 64 | 20 | 37–83 | 60.8 | 12.76 |
| 9. CFL | 116 | 19 | 83–129 | 114.2 | 13.70 |
| 10. HL | 193 | 20 | 154–197 | 182.0 | 10.62 |
| 11. HW | 260 | 20 | 206–260 | 227.2 | 15.92 |
| 12. POL | 128 | 20 | 106–132 | 118.7 | 8.41 |
| 13. UHL | 170 | 19 | 122–199 | 151.3 | 20.28 |
| 14. LHL | 103 | 19 | 73–123 | 100.8 | 13.89 |
| 15. POL | 664 | 20 | 613–696 | 651.7 | 25.95 |
| 16. SNL | 181 | 20 | 181–263 | 206.0 | 22.84 |
| 17. UJL | 186 | 20 | 186–250 | 218.8 | 17.72 |
| 18. ED | 124 | 20 | 114–162 | 130.6 | 12.67 |
| 19. CD | 159 | 20 | 159–264 | 227.2 | 26.08 |
| 20. OPLL | 283 | 19 | 216–419 | 293.6 | 46.52 |
| 21. OPUL | 186 | 19 | 159–297 | 227.3 | 38.54 |

upper lobe. Lower opercular lobe on ocular side usually considerably wider than upper lobe. Snout short and rounded; covered with small ctenoid scales. Dermal papillae evident, but not highly developed, on blind-side snout. Anterior nostril on ocular side short, not reaching anterior border of lower eye when depressed posteriorly. Jaws moderately long; maxilla usually extending posteriorly to vertical through anterior margin of pupil of lower eye. Ocular-side lower jaw without fleshy ridge. Teeth well developed on blind-side jaws. Dentary on ocular side with slender teeth along entire margin; a small number of slender teeth on anterior one-half to one-third of margin of ocular-side premaxilla. Chin depth usually slightly larger than snout length. Lower eye relatively large; eyes usually equal in position, occasionally eyes slightly subequal with upper in advance of lower eye. Anterior and medial surfaces of eyes and narrow interorbital space partially covered with 4–6 small ctenoid scales. Pupillary operculum absent. Dorsal-fin origin usually equal with, or occasionally slightly anterior to, vertical through anterior margin of upper eye; predorsal length long. Scales absent from blind sides of dorsal- and anal-fin rays. Pelvic fin moderately long; longest pelvic-fin ray, when extended posteriorly, usually reaching base of first anal-fin ray. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anus, or occasionally extending posteriorly nearly to anal-fin origin (membrane torn in most specimens examined). Caudal fin moderately long. Scales large, ctenoid; with cteni about equally developed on both sides of body.

**Pigmentation (Fig. 36)** Body coloration similar for both sexes. Ocular surface usually medium to light brown or straw-colored, with 3–7 (usually 3–5) complete, sharply contrasting dark brown crossbands on head and body. Crossbands not continued on dorsal and anal fins. Crossbands on head and posteriormost body usually faint and sometimes incomplete, but otherwise usually visible without magnification. Usually three conspicuous crossbands on body between posterior margin of head and base of caudal fin. Anteriormost crossband on body at, or slightly posterior to, opercular opening. Ocular-side outer opercle with small cluster of brown speckles near ventral margin (remnants of incomplete band?). Inner linings of opercles on both sides of body occasionally lightly pigmented. Isthmus unpigmented on both sides of body. Ocular-side upper lip with slight band of pigment; lower lip usually only lightly spotted, without definite pigment band. Blind side uniformly creamy white. Peritoneum unpigmented.

Dorsal- and anal-fin rays, along entire fins, with faint light brown pigment, heaviest on proximal one-half of fin rays; fins without blotches or spots. Caudal fin usually pale throughout entire length, occasionally scale-covered base of caudal fin darker brown than distal, scaleless portion of caudal-fin rays, but without well-developed spot.

**Size and sexual maturity (Fig. 8E)** *Symphurus trewavasae* is a medium-size species reported to attain a maximum size of ca. 139 mm (Menezes and Benvegnú, 1976). The largest specimens examined in this study were males measuring 124, 125, and 131 mm, with the largest female (123 mm) only slightly smaller. Of 48 specimens for which size-related life history information was available, 19 were males (52.5–131.0 mm) and 29 females (63.7–123.8 mm). Based on reproductive stages of females, sexual maturity in the species occurs at ca. 70–80 mm. All but three females larger than 80 mm had fully elongate ovaries and were either gravid or spent. The smallest gravid female was 74 mm. Seven immature females ranged from 69.1–122.9 mm. The smallest of these (69 and 78 mm, respectively) had ovaries just undergoing elongation, whereas ovaries of other immature females were partially elongate without indications of developing ova.

**Geographic distribution (Fig. 37)** Western South Atlantic inner continental shelf from southeastern Brazil to central Argentina. The northernmost record for this species (22°53'S) roughly corresponds to the region off Cabo Frio, Brazil (Menezes and Benvegnú, 1976). The specimen (INIDEP 476) from 45°S represents the southernmost point of capture for this species. The specimen identified as *S. plagiusa* by Lazzaro (1973) from Puerto Quequén, Argentina (ca. 38°S), is also this species.

**Bathymetric distribution** *Symphurus trewavasae* has been collected over a depth range from 7 (this study) to 179 m (Menezes and Benvegnú, 1976), with the majority (60/80, 75%) of captures at moderate depths (40–80 m) on the continental shelf (Table 10). Depth-of-capture information summarized from Menezes and Benvegnú (1976) revealed that ca. 85% of examined specimens were taken between 50 and 100 m, and only three at depths shallower than 40 m. Menezes and Benvegnú noted that all size classes were found at these depths, indicating it is unlikely that this species uses shallow inshore habitats as nursery grounds. The deepest capture reported for the species was for one specimen collected at 179 m (Menezes and Benvegnú, 1976). Shallow-water captures of *S. trewavasae* listed in this study include a specimen (MNHN 1992-1411) taken at 7 m and three others collected between 14–19 m.

**Ecology** Nothing else is known of the biology of this species.

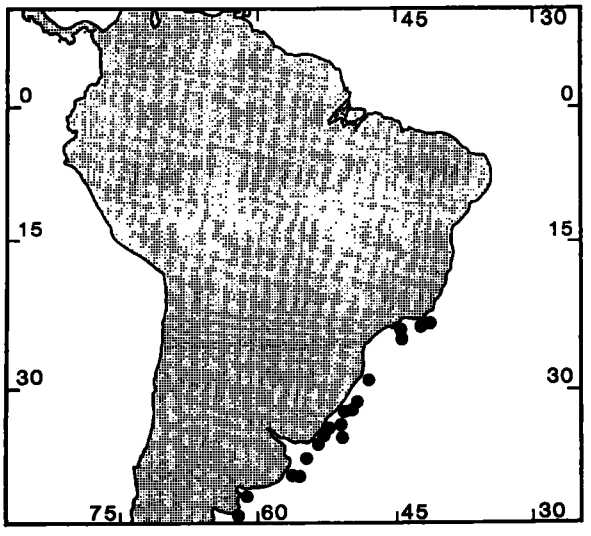


**Figure 37**

Geographic distribution of *Symphurus trewavasae* based on material examined (discussion of geographic distribution appears in species account).

**Remarks** *Symphurus trewavasae* was described by Chabanaud (1948a:508) from specimens taken in coastal waters off Cabo Frio, Brazil. In his revision of western Atlantic *Symphurus,* Ginsburg (1951:185) compared briefly the account of *S. trewavasae* from the literature with data for the North Atlantic *S. plagiusa* and suggested that *S. trewavasae* was possibly not distinct from *S. plagiusa*. He noted that purported eye-size differences between the species, considered diagnostic by Chabanaud (1948a), did not always successfully separate them. Furthermore, Ginsburg pointed out that although there were modal differences in fin-ray counts between the two species, there was sufficient overlap in most features examined to necessitate direct comparison of the two nominal species, an analysis that he did not perform in his study.

Menezes and Benvegnú (1976:145) studied both nominal species in detail and concluded that indeed they were distinct. They noted among several distinct differences that *S. trewavasae* had more dorsal- and anal-fin rays, more scales in a longitudinal series, a shorter gape, and a larger eye. Furthermore, they noted that *S. plagiusa* characteristically has a large, black spot on the upper part of the ocular-side opercle that is absent in *S. trewavasae.* Results of the present study demonstrate that *S. trewavasae* differs from *S. plagiusa* in lacking scales on blind sides of the dorsal- and anal-fin rays and a fleshy ridge on the ocular-side dentary (both present in *S. plagiusa*). *Symphurus trewavasae* has a 1-3-3 predominant ID pattern (1-4-3 or 1-4-2 in *S. plagiusa*). Furthermore, the pigmentation pattern of *S. trewavasae* consists of darkly pigmented crossbanding, without a spot on the outer surface of the ocular-side opercle, and with the isthmus unpigmented, whereas in *S. plagiusa* the ocular surface is usually more uniformly pigmented, or crossbands, when present, are rather subdued, usually with a well-developed black pigment spot on the outer surface of the ocular-side opercle, and with the isthmus is heavily pigmented. *Symphurus trewavasae* also has higher meristic features than *S. plagiusa* (dorsal-fin rays 88–94 vs. 81–91 in *S. plagiusa*; anal-fin rays 73–79 vs. 66–75; total vertebrae 47–51, usually 48–49 vs. 44–49, usually 45–48 in *S. plagiusa*; and 67–77 scales in longitudinal series vs. 76–86 in *S. plagiusa*).

Menezes and Benvegnú (1976) also noted that the relative sizes of the two species differ (*S. plagiusa* reaches sizes of 109–174 mm, vs. *S. trewavasae*, which has a maximum reported size of only 139 mm) and their ecologies differ. *Symphurus trewavasae* usually occurs on the inner continental shelf at depths of 12–190 m, with a center of abundance concentrated mostly between 40 and 110 m (Menezes

and Benvegnú, 1976). Even the smallest specimens of *S. trewavasae* are found in relatively deep waters (12–38 m). In comparison, *S. plagiusa* is a shallow-water species commonly found in estuarine areas and shallow coastal waters at depths usually less than 40 m, with the smallest individuals commonly taken in tidal creeks and coastal embayments rather than open waters on the inner continental shelf (see below).

Menezes and Benvegnú were convinced, on the basis of material they had studied (and I agree), that *S. plagiusa* is absent along the Brazilian coast and that the many references to this species from this area and farther south are probably based on specimens of *S. trewavasae*. Reports of *S. plagiusa* from southern Brazil (Roux, 1973:176) and Argentina (Lazzaro, 1973) are, in all probability, those of *S. trewavasae*.

**Comparisons** Among Atlantic tonguefishes, meristic features of *S. trewavasae* overlap those of several western Atlantic species including *S. piger*, *S. pusillus*, *S. ginsburgi*, *S. billykrietei*, *S. stigmosus*, and the eastern Atlantic *S. nigrescens*. *Symphurus trewavasae* is readily distinguished from these species by its unpigmented peritoneum (vs. black in the others), by having 10 caudal-fin rays (vs. 12), and by its 1-3-3 ID pattern (vs. 1-3-2 in the others).

Counts of caudal-fin rays and total vertebrae for *S. trewavasae* partially overlap those of the western South Atlantic *S. kyaropterygium*, but these sympatric species are easily distinguished because *S. trewavasae* lacks a pupillary operculum and membrane ostia (both well developed in *S. kyaropterygium*); the ocular surface of *S. trewavasae* has strong crossbanding without a dark brown caudal blotch, whereas that of *S. kyaropterygium* usually lacks crossbands and has a well-developed, dark brown blotch on the ocular-side caudal region. *Symphurus trewavasae* differs further in having more dorsal- and anal-fin rays (80–87 and 67–72, respectively, in *S. kyaropterygium*), and a different predominant ID pattern (1-4-2 in *S. kyaropterygium*).

Meristic features of *S. trewavasae* also overlap those of *S. diomedeanus*, *S. plagiusa*, *S. caribbeanus*, *S. civitatium*, and *S. plagusia*, but the ID pattern in *S. trewavasae* differs from these species (usually 1-4-3 in the others), and *S. trewavasae* has fewer caudal-fin rays (10 vs. 12) than do *S. civitatium*, *S. plagusia*, and *S. caribbeanus*. *Symphurus trewavasae* is further distinguished from *S. diomedeanus* in lacking both a pupillary operculum and pigmented spots on the dorsal and anal fins (both features present in *S. diomedeanus*), and in having fewer longitudinal scales (67–77 vs. 79–96 in *S. diomedeanus*). *Symphurus trewavasae*, historically, has often been confused with the western North Atlantic *S. plagiusa*. Differences between these species are listed above in the "Remarks" section. *Symphurus trewavasae* differs further from *S. plagusia*, *S. civitatium*, and *S. caribbeanus* in its much larger eye (114–162 HL vs. 110 HL or smaller in these other species) and in having an unpigmented isthmus and a lightly pigmented inner opercular lining on the ocular side (vs. heavily pigmented ocular-side isthmus and inner opercular lining in these other species). From *S. plagusia* and *S. civitatium*, *S. trewavasae* is further distinguished in lacking the fleshy ridge on the ocular-side dentary, characteristic of the others, and the dorsal-fin origin in *S. trewavasae* is usually positioned at a vertical equal with the midregion of the upper eye, whereas in these others the dorsal-fin origin is situated more anteriorly, usually at a point anterior to the vertical through the anterior margin of the upper eye. *Symphurus trewavasae* has fewer longitudinal scales than does *S. caribbeanus* (67–77 vs. 78–89).

From other species with a 1-3-3 ID pattern (*S. varius*, *S. atramentatus*, and *S. normani*), *S. trewavasae* is readily distinguished in having only 10 caudal-fin rays (vs. 12 in these others). *Symphurus trewavasae* can be further distinguished from the eastern Pacific *S. varius* in having fewer longitudinal scales (67–77 vs. 120–124) and in having four hypurals (vs. five). Some meristic features of *S. trewavasae* are similar to those of the tropical eastern Atlantic *S. normani*, and *S. atramentatus*, which occurs in temperate and tropical regions of the eastern Pacific. However, *S. trewavasae* has sharply contrasting crossbands on the ocular surface, a uniformly pigmented blind side, and lacks an alternating series of boldly pigmented blotches and unpigmented areas on the dorsal and anal fins, whereas *S. normani* has few, if any, faint crossbands on the ocular surface and a pattern of pepper-dots on the blind side of the body, and *S. atramentatus* has a bold pattern of pigmented blotches alternating with unpigmented areas on the dorsal and anal fins. *Symphurus trewavasae* lacks the small ctenoid scales on blind sides of dorsal- and anal-fin rays characteristic of *S. normani*. From *S. atramentatus*, *S. trewavasae* is further distinguished in lacking a pupillary operculum (vs. present), and by its lower meristic features (dorsal-fin rays 92–96, anal-fin rays 77–81, and 50–52 total vertebrae in *S. atramentatus*).

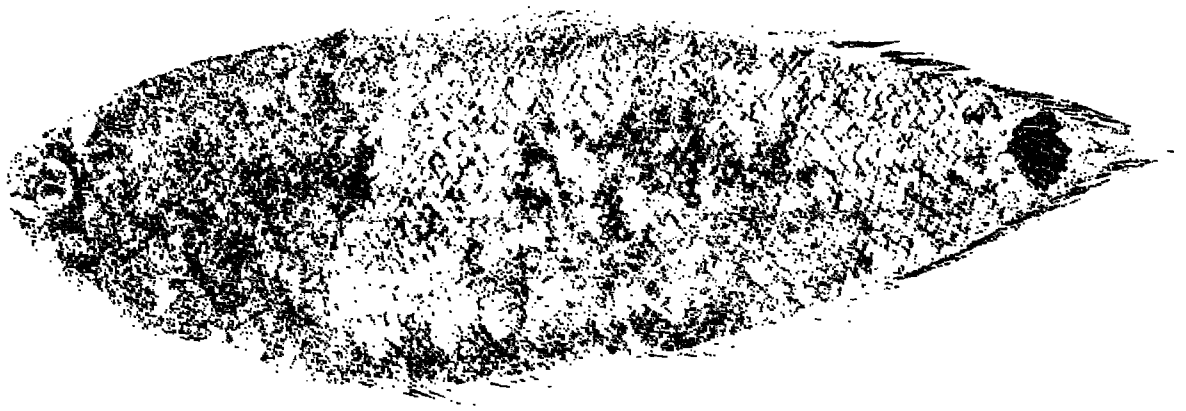

**Figure 38**
*Symphurus kyaropterygium* Menezes and Benvegnú, holotype, MZUSP 12425, 119 mm SL, Brazil 26°34'S, 48°10'W.

## *Symphurus kyaropterygium* Menezes and Benvegnú, 1976 (Figs. 8F, 38–39; Tables 1–10, 23)

*Symphurus parvus* (not of Ginsburg, 1951). Roux, 1973:175 (southern Brazil).

*Symphurus kyaropterygium* Menezes and Benvegnú, 1976:140 (original description with photograph; southern Brazil). Munroe, 1992:370, 381 (ID pattern; geographic, bathymetric distributions).

**Diagnosis** *Symphurus kyaropterygium* is distinguished from all congeners by the combination of 1-4-2 ID pattern; membrane ostia in dorsal and anal fins; 10 caudal-fin rays; 4 hypurals; 80–87 dorsal-fin rays; 67–72 anal-fin rays; 46–49 total vertebrae; 73–81 scales in longitudinal series; presence of well-developed pupillary operculum; unpigmented peritoneum; absence of scales on blind sides of dorsal- and anal-fin rays; with teeth along anterior three-fourths, or occasionally entire margin of ocular-side dentary; with teeth usually extending to midpoint, or slightly posterior to midpoint, of margin of ocular-side premaxilla; ocular surface pigmentation featuring dark brown blotch on caudal region of body; without pepper-dot pigmentation on blind side of body; and dorsal, anal, and caudal fins without spots or blotches.

**Description** A medium-size species attaining a maximum length of ca. 120 mm SL. ID pattern usually 1-4-2 (13/14 specimens), rarely 1-3-3 (Table 2). Caudal-fin rays usually 10 (13/14), rarely 11 (Table 3). Dorsal-fin rays 80–87 (Table 4). Anal-fin rays 67–72 (Table 5). Total vertebrae 46–49, usually 47–48 (12/14) (Table 6). Hypurals 4 (14/14). Longitudinal scale rows 73–81 (Table 7). Scale rows on head posterior to lower orbit 16–18, usually 16–17 (Table 8). Transverse scales 36–39 (Table 9).

Proportions of morphometric features presented in Table 23. Body relatively deep; maximum depth in anterior one-third of body; body tapering fairly rapidly posterior to midpoint. Preanal length considerably shorter than body depth. Head moderately long and wide, head width narrower than body depth. Head length smaller than head width (HW:HL 1.04–1.35, $\bar{x}$=1.2). Lower head lobe width slightly less than postorbital length; slightly narrower than upper head lobe. Lower opercular lobe of ocular side wider than upper opercular lobe. Snout short, rounded, covered with small ctenoid scales. Dermal papillae present on blind-side snout, chin, and dorsal region of head preceding dorsal fin (better developed in larger specimens); ocular side with less extensive development of dermal papillae on snout extending posteriorly almost to level of eyes. Anterior nostril on ocular side short, when depressed posteriorly, usually falling just short of anterior margin of lower eye. Jaws short; maxilla usually extending posteriorly between, but not beyond, verticals through anterior border of lower eye and anterior margin of lower eye pupil. Ocular-side lower jaw without fleshy ridge. Teeth well developed on blind-side jaws. Margin of ocular-side dentary usually with single row of small teeth extending over anterior three-fourths, occasionally

**Table 23**

Morphometrics for holotype (MZUSP 12425) and 11 additional specimens of *Symphurus kyaropterygium*. (Abbreviations defined in methods section; SL is expressed in mm; characters 2 to 14 are expressed in thousandths of SL; 15 to 21 in thousandths of HL; *n* = number of specimens measured.)

| Character | Holotype | *n* | Range | Mean | SD |
|---|---|---|---|---|---|
| 1. SL | 119.6 | 12 | 31.9–119.6 | 93.4 | 23.46 |
| 2. BD | 294 | 12 | 244–319 | 298.7 | 18.87 |
| 3. PDL | 28 | 12 | 28–46 | 35.5 | 5.49 |
| 4. PAL | 174 | 12 | 174–232 | 209.8 | 14.50 |
| 5. DBL | 972 | 12 | 954–978 | 964.2 | 6.77 |
| 6. ABL | 751 | 12 | 751–809 | 783.4 | 19.05 |
| 7. PL | 71 | 10 | 59–85 | 70.8 | 7.05 |
| 8. PA | 50 | 11 | 45–78 | 58.4 | 12.22 |
| 9. CFL | 100 | 11 | 92–119 | 107.3 | 7.63 |
| 10. HL | 156 | 12 | 156–210 | 192.3 | 15.23 |
| 11. HW | 208 | 12 | 208–253 | 235.2 | 12.86 |
| 12. POL | 105 | 12 | 105–142 | 127.4 | 10.54 |
| 13. UHL | 130 | 12 | 130–175 | 151.8 | 14.30 |
| 14. LHL | 100 | 12 | 82–115 | 100.8 | 9.81 |
| 15. POL | 674 | 12 | 624–706 | 663.2 | 24.24 |
| 16. SNL | 166 | 12 | 149–195 | 170.5 | 17.28 |
| 17. UJL | 192 | 12 | 151–227 | 192.1 | 17.55 |
| 18. ED | 139 | 12 | 117–164 | 139.8 | 14.29 |
| 19. CD | 235 | 12 | 165–260 | 211.7 | 29.66 |
| 20. OPLL | 294 | 12 | 179–370 | 298.4 | 46.78 |
| 21. OPUL | 294 | 12 | 166–294 | 213.0 | 35.71 |

along entire margin of dentary. Margin of ocular-side premaxilla with single row of teeth usually extending to midpoint, occasionally teeth extending along margin of premaxilla to slightly posterior to midpoint and almost to vertical through anterior base of anterior nostril. Chin depth somewhat greater than snout length. Lower eye relatively large; slightly smaller than snout length; eyes usually equal in position, occasionally upper eye slightly in advance of lower. Anterior and medial surfaces of eyes partially covered with 4–8 small ctenoid scales; 1–3 scales in narrow interorbital region. Pupillary operculum well developed. Dorsal-fin origin usually equal with vertical through anterior margin of upper eye; occasionally slightly anterior to vertical through anterior margin of upper eye; predorsal length short. Basal part of dorsal-fin membrane from about seventh dorsal-fin ray and backwards, and anal-fin membrane throughout entire length of fin, with series of openings (membrane ostia) between fin rays. Scales absent on blind sides of dorsal- and anal-fin rays. Pelvic-fin long; longest pelvic-fin ray, when extended posteriorly, usually reaching base of first anal-fin ray. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anus, or occasionally extending posteriorly almost to anal-fin origin (membrane torn in most specimens). Caudal fin short. Scales moderate, ctenoid; with cteni about equally developed on both sides of body.

**Pigmentation (Fig. 38)** Body coloration generally similar for both sexes. Ocular surface generally light brown, often mottled with diffuse areas of darker brown pigment, with large, conspicuous, vertically elongate dark brown blotch, approximately 5–7 scale rows in length and 7–9 scale rows wide, situated 3–5 scale rows anterior to caudal-fin base. Scale margins on ocular side of body highlighted with pigment darker than general body coloration. Ocular-side outer opercle with same background coloration as body. Inner linings of opercles and isthmus on both sides of body unpigmented. Slight band of pigment on ocular-side upper lip; ocular-side lower lip infrequently spotted, but without definite band of pigment. Blind side uniformly white or yellowish. Peritoneum unpigmented.

Dorsal- and anal-fin rays variously pigmented, becoming darker in posterior one-third of body, but without defined pattern of spots or blotches. Membrane between fin rays usually lighter than membrane covering fin rays, thereby clearly outlining each fin ray. Caudal fin generally pale; scaly basal portion of caudal fin more darkly pigmented than distal, scaleless half of fin, but without definite spot.

**Size and sexual maturity (Fig. 8F)** *Symphurus kyaropterygium* is a medium-size species attaining lengths of ca. 120 mm. Of 12 specimens examined for size-related life history information, the three largest (120, 110, and 106 mm) were males, and the largest female (106 mm) appeared to be gravid. Two smaller females (74.1, 85.9 mm) were mature with elongate ovaries containing developing ova. These brief observations indicate that *S. kyaropterygium* matures at sizes of ca. 74–85 mm.

**Geographic distribution (Fig. 39)** (Based on original material in Menezes and Benvegnú, 1976.) Inner continental shelf waters in the western South Atlantic off Brazil from Baia da Ilha Grande, Rio de Janeiro (ca. 23°S, 44°30'W), to Rio Grande do Sul (31°24'S, 50°36'W).

**Bathymetric distribution** On the basis of the limited material available, this species apparently inhabits substrates consisting of mud or calcareous mud on the inner continental shelf between 36 and 69 m (Table 10).

**Remarks** Menezes and Benvegnú (1976) regarded the membrane ostia as a unique character distinguishing *S. kyaropterygium* from all congeners. Since

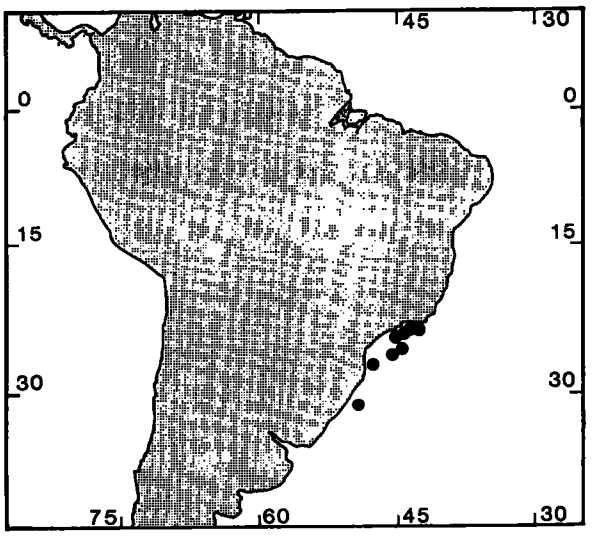


**Figure 39**

Geographic distribution of *Symphurus kyaropterygium* based on material examined (discussion of geographic distribution appears in species account).

that study, Munroe (1987) identified three additional species (*S. minor*, *S. parvus*, and *S. ommaspilus*) that also possess membrane ostia. Munroe pointed out that these four species also have a similar ID pattern (1-4-2), a similar number of caudal-fin rays (10), relatively low meristic features, and all have a well-developed pupillary operculum. Additionally, three of the four (not *S. ommaspilus*) have a similar pigmentation pattern of a prominent, dark brown blotch on the caudal region of the ocular side of the body without pigmented spots on the dorsal and anal fins. In contrast, *S. ommaspilus* lacks the caudal blotch characteristic of these other species but has a single ocellated spot on the dorsal and anal fins. The large number of shared characters may indicate close relation among these four species; it is hypothesized that they comprise a lineage within the genus.

**Comparisons** Of western Atlantic tonguefishes, *S. kyaropterygium* is most similar to the north Atlantic *S. parvus*. *Symphurus kyaropterygium* can be distinguished from *S. parvus* by its more numerous dorsal- (80–87, usually 83–87 vs. 75–86, usually 77–84, in *S. parvus*) and anal-fin rays (67–72 vs. 60–70, usually 62–68), and more longitudinal scales (73–81 vs. 59–78, but usually 59–74 in *S. parvus*) (see Tables 4–7). There may be differences of frequency in ID patterns between these two species (larger sample sizes needed for *S. kyaropterygium*). Of 14 specimens of *S. kyaropterygium*, 13 (94%) had a 1-4-2 ID pattern and none had a 1-5-2 pattern. In contrast, only 33/82 (40%) of *S. parvus* had a 1-4-2 pattern, and 35 (43%) had a 1-5-2 ID pattern. There are differences also in maximum sizes attained by both species. *Symphurus parvus* apparently is a smaller species, reaching a maximum size of only about 88 mm, and individuals as small as 35–50 mm are sexually mature. In contrast, *S. kyaropterygium* attains larger sizes (120 mm), especially before reaching sexual maturity (85 mm or larger).

Meristic and size differences between *S. kyaropterygium* and the Caribbean *S. ommaspilus* and North Atlantic *S. minor* are even more distinct (Tables 4–9), with little or no overlap in most meristic features examined. Also, *S. kyaropterygium* lacks the ocellated spot on dorsal and anal fins characteristic of *S. ommaspilus*. *Symphurus kyaropterygium* is much larger than either of these diminutive flatfishes, reaching maximum lengths of ca. 120 mm, compared with 60 mm in *S. ommaspilus*, and 78 mm in *S. minor*.

Differences between *S. kyaropterygium* and the sympatrically occurring *S. trewavasae* are discussed in the "Comparisons" section in the species account for *S. trewavasae*.

*Symphurus kyaropterygium* is similar to, and cooccurs throughout most of its geographic range with, *S. diomedeanus*. Both possess 10 caudal-fin rays and well-developed pupillary operculum; however, they differ in many characteristics. *Symphurus kyaropterygium* has membrane ostia in the dorsal and anal fins, a well-developed, dark brown blotch on the ocular-side caudal region and lacks spots on dorsal and anal fins (vs. membrane ostia and caudal blotch lacking, and spots usually well developed on posterior anal and dorsal fins in *S. diomedeanus*). *Symphurus kyaropterygium* has fewer dorsal- (80–87 vs. 86–96 in *S. diomedeanus*) and anal-fin rays (67–72 vs. 69–80), fewer longitudinal scales (73–81 vs. 79–96), and a different ID pattern (1-4-2 vs. 1-4-3 in *S. diomedeanus*).

*Symphurus kyaropterygium* differs from the western North Atlantic *S. plagiusa*, which also possesses 10-caudal-fin rays, by having a well-developed pupillary operculum and membrane ostia (both absent in *S. plagiusa*), in its blotch on the ocular-side caudal region, in an unpigmented isthmus and unpigmented inner opercular linings, in lacking a black spot on the outer surface of the ocular-side opercle (vs. no caudal blotch, heavily pigmented isthmus and inner opercular linings, and usually with a conspicuous opercular spot in *S. plagiusa*), and in lacking both a fleshy ridge on the ocular-side lower jaw and scales on blind sides of dorsal- and anal-fin rays (both present in *S. plagiusa*).

Among other species of *Symphurus*, only *S. fasciolaris* from the eastern Pacific has 10 caudal-fin rays. *Symphurus kyaropterygium*, however, has lower fin-ray counts (90–97 dorsal- and 77–81 anal-fin rays in *S. fasciolaris*), and also lacks a caudal-fin spot and the combination of crossbands and rounded spots on the ocular surface, features characterizing *S. fasciolaris*.

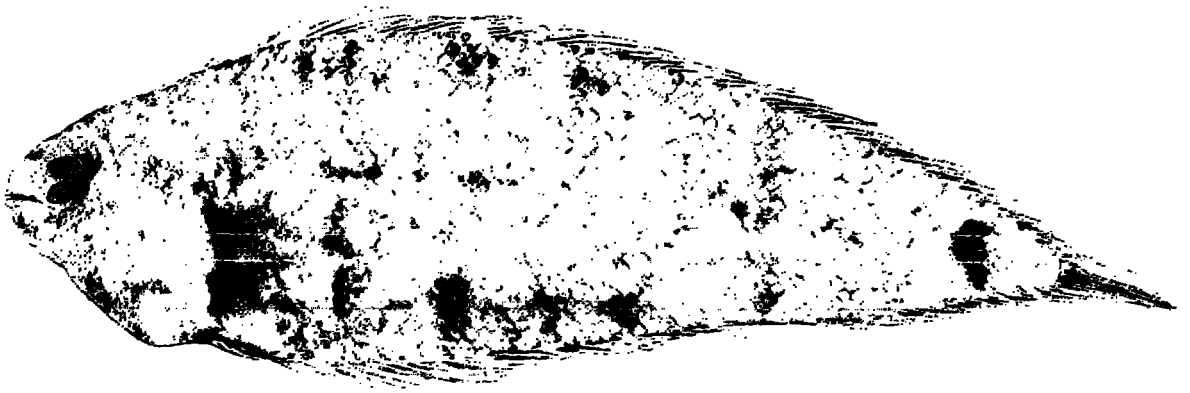

**Figure 40**
*Symphurus minor* Ginsburg, GCRL 76:14893, 51.2 mm SL, Gulf of Mexico, off Perdido Bay, Florida.

## *Symphurus minor* Ginsburg, 1951 (Figs. 6E, 40–41; Tables 1–10, 24) Largescale tonguefish

*Aphoristia pigra* (not of Goode and Bean, 1886). Goode and Bean, 1886:154 (in part) (specimens from *Albatross* Station 2374 may be those included in original description of *A. pigra*).

?*Symphurus pusillus* (not of Goode and Bean, 1885). Kyle, 1913:145 (description and figure of symmetrical larva possibly of this species).

*Symphurus minor* Ginsburg, 1951:192 (original description, photograph). Briggs, 1958:298 (listed, Florida). Topp and Hoff, 1972:83 (distribution, ecological information; west Florida shelf). Markle et al., 1980:59 (single larva, continental shelf off Nova Scotia). Miller and Jorgenson, 1973:305 (meristic features and vertebral counts for two specimens). Scott and Scott, 1988:560 (Canadian Atlantic; after Markle et al., 1980, and Ginsburg, 1951). Munroe, 1992:370, 381 (ID pattern; geographic, bathymetric distributions). Darovec, 1995:88 (distribution on west Florida Shelf).

**Diagnosis** *Symphurus minor* differs from all congeners by the combination of predominant 1-4-2 ID pattern; 10 caudal-fin rays; membrane ostia in dorsal and anal fins; 4 hypurals; 69–81 dorsal-fin rays; 55–64 anal-fin rays; 41–44 total vertebrae; 55–67 scales in longitudinal series; well-developed pupillary operculum; unpigmented peritoneum; absence of scales on blind sides of dorsal- and anal-fin rays; absence of fleshy ridge on ocular-side lower jaw; teeth usually covering entire margin of ocular-side dentary (occasionally only on anterior three-fourths of dentary margin); teeth only on anterior one-half to three-fourths of ocular-side of premaxillary margin; ocular surface with dark brown blotch on caudal region; blind side of body without pattern of pepperdots; dorsal, anal, and caudal fins without spots or blotches; and small adult size (<78 mm).

**Description** A dwarf species attaining maximum lengths of ca. 78 mm SL. ID pattern usually 1-4-2 (74/78 specimens), rarely 1-3-2 or 1-4-3 (Table 2). Caudal-fin rays usually 10 (74/79), less frequently 8, 9, or 11 (Table 3). Dorsal-fin rays 69–81, usually 72–77 (Table 4). Anal-fin rays 55–64 (Table 5). Total vertebrae 41–44, usually 41–43 (74/79) (Table 6). Hypurals 4 (77/77). Longitudinal scale rows 55–67, usually 57–64 (Table 7). Scale rows on head posterior to lower orbit 12–15, usually 13–15 (Table 8). Transverse scales 24–31, usually 28–31 (Table 9).

Proportions of morphometric features presented in Table 24. Body moderately deep, maximum depth in anterior one-third of body; depth tapering rapidly in posterior two-thirds of body. Preanal length less than body depth. Head long and moderately wide, considerably narrower than body depth. Head length usually shorter than head width (HW:HL 0.9–1.2, $\bar{x}$=1.1). Lower head lobe width less than postorbital length; narrower than upper head lobe. Lower opercular lobe of ocular side wider than upper opercular lobe. Snout short and somewhat pointed, covered

**Table 24**

Morphometrics for holotype (USNM 131643) and 30 additional specimens of *Symphurus minor*. (Abbreviations defined in methods section; SL is expressed in mm; characters 2 to 14 are expressed in thousandths of SL; 15 to 21 in thousands of HL; *n* = no. of specimens measured.)

| Character | Holotype | *n* | Range | Mean | SD |
|---|---|---|---|---|---|
| 1. SL | 36.2 | 31 | 22.6–70.6 | 48.1 | 14.79 |
| 2. BD | 279 | 31 | 207–324 | 280.2 | 23.48 |
| 3. PDL | 77 | 31 | 46–80 | 60.2 | 9.70 |
| 4. PAL | 260 | 31 | 209–292 | 250.5 | 17.12 |
| 5. DBL | 975 | 31 | 672–975 | 929.9 | 51.73 |
| 6. ABL | 729 | 31 | 532–775 | 738.8 | 42.01 |
| 7. PL | — | 28 | 51–88 | 74.4 | 7.68 |
| 8. PA | 61 | 31 | 30–77 | 58.7 | 12.06 |
| 9. CFL | — | 28 | 108–152 | 131.9 | 10.65 |
| 10. HL | 224 | 31 | 200–247 | 222.6 | 10.73 |
| 11. HW | 232 | 31 | 198–256 | 240.4 | 12.99 |
| 12. POL | 130 | 31 | 120–154 | 142.6 | 8.61 |
| 13. UHL | 149 | 31 | 136–166 | 152.0 | 9.10 |
| 14. LHL | 116 | 31 | 66–131 | 105.8 | 13.88 |
| 15. POL | 580 | 31 | 580–704 | 641.5 | 29.66 |
| 16. SNL | 222 | 31 | 146–222 | 193.1 | 18.60 |
| 17. UJL | 247 | 31 | 172–247 | 214.9 | 17.46 |
| 18. ED | 160 | 31 | 118–182 | 148.6 | 14.46 |
| 19. CD | 210 | 31 | 145–263 | 194.6 | 30.40 |
| 20. OPLL | 247 | 31 | 200–370 | 277.2 | 44.47 |
| 21. OPUL | 222 | 31 | 132–265 | 206.1 | 29.60 |

with small ctenoid scales. Dermal papillae usually well developed on blind side of snout; occasionally some papillae extending onto anterior region of ocular-side snout. Anterior nostril on ocular side long, when depressed posteriorly, usually reaching anterior margin of lower eye. Jaws moderately long; maxilla usually extending posteriorly to vertical through anterior margin of pupil of lower eye; occasionally reaching vertical through middle of lower eye. Ocular-side lower jaw without fleshy ridge. Teeth well developed on blind-side jaws. Teeth usually covering entire margin of ocular-side dentary, occasionally developed only on anterior three-fourths of dentary margin. Single row of slender teeth on anterior one-half to three-fourths of margin of ocular-side premaxilla (usually extending posteriorly to vertical through anterior base of anterior nostril). Chin depth usually about equal to snout length. Lower eye relatively large; eyes usually equal in position. Anterior and medial surfaces of eyes usually not covered with scales; usually 2–3 small ctenoid scales in narrow interorbital region. Pupillary operculum well developed. Dorsal-fin origin usually at point between verticals through midpoint and anterior margin of upper eye pupil; predorsal length moderately long. Basal region of dorsal-fin membrane from about seventh dorsal-fin ray and backwards, and anal-fin membrane throughout entire length of fin, with series of openings (membrane ostia) between fin rays. Scales absent on blind sides of dorsal- and anal-fin rays. Pelvic fin moderately long; longest pelvic-fin ray, when extended posteriorly, usually reaching base of first anal-fin ray. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anus, or occasionally extending posteriorly to anal-fin origin (membrane torn in most specimens). Caudal fin long. Scales large, ctenoid on both sides of body.

**Pigmentation (Fig. 40)** Body coloration generally similar for both sexes. Ocular surface usually light brown or straw-colored with variable number and arrangement of irregular dusky markings and well-developed dark brown blotch slightly anterior to caudal-fin base; occasional specimens with rather faint, dark brown, crossbands. Caudal blotch usually 4–6 scales in length and 6–9 scales wide (usually reaching across entire body); separated from caudal-fin base by 3–4 lightly pigmented scales. Crossbands, when present, diffuse, irregular, incomplete, often widely interrupted midlaterally. Crossband at midlength of body often somewhat better developed. Ocular-side outer opercle with same background pigmentation as body. Small brown spot of variable intensity usually present on dorsal margin of opercular opening. Inner linings of opercles and isthmus on both sides of body unpigmented. Usually a well-developed, dark brown band of pigment on ocular-side upper lip extending posteriorly to angle of jaws; lower lip infrequently lightly spotted, but without definite pigment band. Blind side uniformly white or yellowish. Peritoneum unpigmented.

Dorsal and anal fins rather lightly pigmented anteriorly, becoming increasingly darker posteriorly, but without distinct spots or blotches. Fin rays uniformly pigmented along their lengths. Membrane between fin rays usually lighter than membrane covering fin rays, thereby clearly outlining each fin ray. Scaly base of caudal fin with small, darkly pigmented area, but without definite spot; distal, scaleless portion of caudal fin lightly pigmented. Blind sides of caudal-fin rays and membrane often with pepper-dot pigmentation, especially conspicuous at fin base.

**Size and sexual maturity (Fig. 6E)** *Symphurus minor* is a dwarf species attaining maximum lengths of ca. 78 mm (Ginsburg, 1951). The largest specimens examined in this study were females (68.1–70.6 mm). The largest males were only slightly smaller, measuring 63.3 and 64.4 mm. Most specimens ranged in size from 40 to 60 mm. For 67 specimens from which

size-related life history information was taken, 16 were males (35.6–64.4 mm), 45 females (29.2–70.6 mm), and 6 (22.6–35.3 mm) were immature and of indeterminate sex. Based on reproductive stages of females, sexual maturity occurs at sizes between 29 and 40 mm. The smallest female with elongate ovaries measured 29.2 mm, whereas the smallest gravid female was 31.6 mm. All females larger than 40 mm had elongate ovaries, and most gravid females were 41.0–70.6 mm. Several of the smallest females (33.8–38.1 mm) were immature with ovaries just undergoing elongation.

**Geographic distribution (Fig. 41)** On live-bottom inner continental shelf substrates of the western North Atlantic (see comments below regarding more northern captures) primarily from North Carolina southward to Florida, in the eastern Gulf of Mexico, including the west coast of Florida, to as far west as the region of DeSoto Canyon. The majority of specimens were collected off southeastern Florida and the inner continental shelf off west Florida. *Symphurus minor* has not been reported from localities in the central and western regions of the Gulf of Mexico, where sand, silt, or mud substrates predominate, and is thus far unknown from live-bottom substrates off the Yucatan Peninsula.

Along the U.S. Atlantic coast, *S. minor* occurs commonly as far north as Cape Hatteras, North Carolina. Two collections, however, taken almost one hundred years apart, record this species from Nova Scotian waters. Ginsburg (1951) designated three specimens trawled off Nova Scotia (44°23'N) as paratypes of *S. minor*. More recently, Markle et al. (1980) captured a single larva during ichthyoplankton collections on the Scotian Shelf (42°21'N, 65°01'W). Isolated captures of *S. minor* in these far northern regions likely represent expatriate individuals transported northward by the Gulf Stream from southern locations.

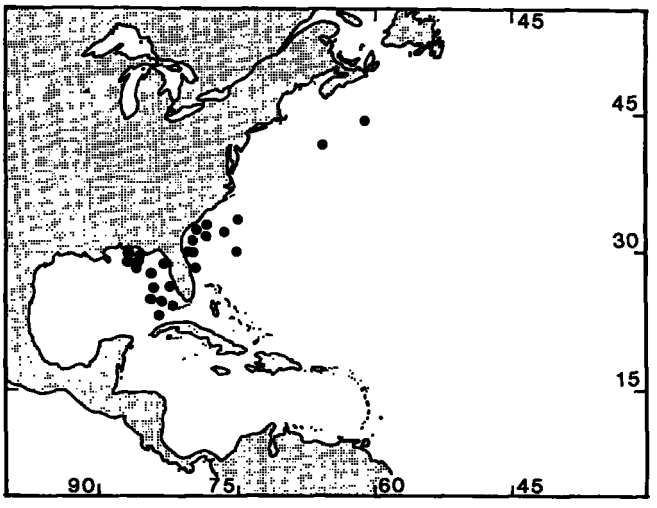


**Figure 41**

Geographic distribution of *Symphurus minor* based on material examined (discussion of geographic distribution appears in species account).

**Bathymetric distribution** *Symphurus minor* has been collected primarily on live-bottom habitats in neritic waters on the inner continental shelf at depths of 18–170 m (Table 10). The center of abundance for this species, based on frequency of occurrence and relative abundance of specimens, occurs between 20 and 60 m, where 65/79 (82%) specimens were captured. Only eight fish were collected at shallower depths (between 18 and 20 m), whereas another six were taken at deeper depths, with the deepest capture reported for the species (Ginsburg, 1951) being that for three specimens (USNM 92614) collected in the same trawl at 170 m on the Scotian Shelf.

**Ecology** Available ecological information is rather limited for this species. Struhsaker (1969) reported *S. minor* as common (present in 10–50% of trawling stations) along the open continental shelf of the southeastern United States. Topp and Hoff (1972) collected 14 specimens (11–70 mm) at water temperatures of 18.5–23.3°C and salinities of 35–36.5‰. Although collected frequently, this species has not been taken in any abundance. In 52 collections examined, 31 contained only a single specimen, 17 had two specimens, and only 6 lots contained three or four specimens. Small size, combined with relative inefficiency of trawls in capturing small pleuronectiform fishes on live-bottom substrates such as those inhabited by *S. minor*, undoubtedly contribute to the relatively small numbers of specimens of this species collected at one time.

Throughout its range off the southeastern coast of the United States, *S. minor* co-occurs with the phenotypically similar *S. parvus*. Although the species are sympatric in this region, they are not syntopic with respect to bathymetric distribution and substrate preference. *Symphurus minor* usually occurs in much shallower waters (20–60 m) than does *S. parvus* (30–110 m, see below), and the two species have not been captured simultaneously. Besides inhabiting deeper waters, *S. parvus* generally occurs on a substrate with a higher concentration of mud or silt, in contrast to the live-bottom substrates usually occupied by *S. minor*.

Based on gonad condition of examined females, spawning appears to take place during summertime with most gravid females collected between June and September. Ripening females appear primarily in collections made from January to March. Nonripe

females (those with long thin gonads showing little evidence of ripening) were collected during November through early March. Topp and Hoff (1972) noted that specimens collected on the west Florida shelf in April had ripening gonads, and the smallest specimens (11–13 mm) in their study were collected in July, August, and November, indicating late spring or summer spawning in this region.

**Remarks** Specimens from *Albatross* Station 2374 (USNM 131590-91) might be those included in the original account of *Aphoristia pigra* (=*S. piger*) as noted in the "Remarks" section in the account for that species. In the original description of *S. minor*, Ginsburg incorrectly reported the catalogue number of the paratype from *Albatross* Station 2372 as USNM 131593. The actual catalog number is USNM 131293 (USNM 131593 is assigned to a lot of *Jenkinsia lamprotaenia*).

The larval specimen described by Kyle (1913) may be that of *S. minor*, but because larval stages of this species are still undescribed, specific identity of the specimen can not be determined at this time.

**Comparisons** Meristic features of *S. minor* overlap widely those of three other western Atlantic dwarf tonguefishes, namely *S. arawak*, *S. ommaspilus*, and *S. parvus*. *Symphurus minor* is easily distinguished from *S. arawak* because it has 10 (vs. 12 in *S. arawak*) caudal-fin rays and a pupillary operculum (lacking in *S. arawak*). Other differences between these species are discussed in the "Comparisons" section of the species account for *S. arawak*.

*Symphurus minor* has many characters similar to those observed in *S. kyaropterygium*, *S. parvus*, and *S. ommaspilus*. All have similar caudal-fin ray counts (10), all possess membrane ostia, and all have a well-developed pupillary operculum. Meristic features of *S. minor* are nonoverlapping with those of *S. kyaropterygium* (see Tables 4–7). However, most meristic features in *S. minor* widely overlap those of *S. parvus* and *S. ommaspilus*. Of all congeners, *S. minor* is most similar to *S. parvus* in meristic features, pigmentation, and overall adult sizes. *Symphurus minor* is distinguished from *S. parvus* by its modally lower counts (dorsal-fin rays 69–81, usually 72–77 vs. 75–86, usually 77–84 in *S. parvus*; anal-fin rays 55–64 vs. 60–70, usually 62–68; and total vertebrae 41–43, usually 42–43 vs. 43–47, usually 44–46, in *S. parvus*). There also are differences between these two species in the frequency of occurrence of predominant ID patterns. Nearly 95% (74/78) of the *S. minor* had a 1-4-2 ID pattern and none had a 1-5-2 pattern, whereas only 40% (33/82) of the *S. parvus* examined had a 1-4-2 pattern and 35/82 (43%) had a 1-5-2 ID pattern.

The most notable differences between *S. minor* and *S. ommaspilus* occur in pigmentation patterns. *Symphurus minor* has a dark brown blotch on the ocular-side caudal region and lacks ocellated spots on dorsal and anal fins, whereas *S. ommaspilus* lacks a blotch on the ocular-side caudal region and possesses a single, conspicuous, ocellated spot on posterior regions of the dorsal and anal fins.

Compared with other *Symphurus* species with 10 caudal-fin rays, *S. minor* has much lower meristic features than those of other western Atlantic species (*S. plagiusa*, *S. jenynsi*, *S. diomedeanus*), and the eastern Pacific *S. fasciolaris*.

**Figure 42**
*Symphurus parvus* Ginsburg, VIMS 8832, 88.2 mm SL, North Carolina 34°23'N, 75°58'W.

## *Symphurus parvus* Ginsburg, 1951 (Figs. 7A, 42–43; Tables 1–10, 25) Pygmy tonguefish

*Aphoristia pigra* (not of Goode and Bean, 1886). Goode and Bean, 1886:154 (in part) (specimens from *Albatross* Station 2318 and Station 2405 may be this species).

*Aphoristia diomedeana* (not of Goode and Bean, 1885). Goode and Bean, 1896:460 (in part) (specimen from *Blake* Station XXV examined).

?*Symphurus pusillus* (not of Goode and Bean, 1885). Kyle, 1913:145 (description and figure of symmetrical larva possibly this species).

*Symphurus parvus* Ginsburg, 1951:192 (original description, photograph). Briggs, 1958:298 (listed, Florida). Topp and Hoff, 1972:85 (occurrence, distribution and ecology on west Florida shelf; limited ecological information). Munroe, 1992:370, 381 (ID pattern; geographic and bathymetric distributions). Darovec, 1995:89 (distribution on west Florida Shelf).

**Misidentification** Gaspar-Dillanes and Espinosa-Pérez, 1989:252 (inner continental shelf, Quintana Roo, Mexico; specimen actually *S. diomedeanus*).

**Diagnosis** *Symphurus parvus* is distinguished from all congeners by the combination of 1-4-2 or 1-5-2 ID pattern; 10 caudal-fin rays; 4 hypurals; membrane ostia in dorsal and anal fins; 75–86 dorsal-fin rays; 60–70 anal-fin rays; 43–47 total vertebrae; 59–78 scales in longitudinal series; well-developed pupillary operculum; unpigmented peritoneum; absence of scales on blind sides of dorsal- and anal-fin rays; absence of fleshy ridge on ocular-side lower jaw; teeth on anterior one-half to three-fourths of margin of ocular-side premaxilla (rarely along entire margin of jaw); teeth extending over entire length, or less frequently, along only anterior three-fourths of margin of ocular-side dentary; ocular surface pigmentation featuring dark brown blotch on caudal region of body; blind side without pattern of pepper-dots; dorsal, anal, and caudal fins without spots or blotches; and relatively small adult size (usually <90 mm).

**Description** A diminutive species attaining maximum lengths of about 88 mm SL. ID pattern 1-5-2 (35/82 specimens) or 1-4-2 (33/82), rarely 1-4-3 or 1-3-2 (Table 2). Caudal-fin rays 10 (70/76), rarely 9 or 11 (Table 3). Dorsal-fin rays 75–86, usually 77–84 (Table 4). Anal-fin rays 60–70, usually 62–68 (Table 5). Total vertebrae 43–47, usually 44–46 (70/78) (Table 6). Hypurals 4 (78/78). Longitudinal scale rows 59–78 (Table 7). Scale rows on head posterior to lower orbit 13–18, usually 14–17 (Table 8). Transverse scales 26–35 (Table 9).

Proportions of morphometric features are presented in Table 25. Body moderately deep, maximum depth in anterior one-third of body; body depth tapering fairly rapidly in posterior two-thirds of body. Preanal length smaller than body depth. Head relatively long and wide, narrower than body depth. Head length slightly less than head width (HW:HL 0.97–

**Table 25**

Morphometrics for holotype (USNM 84491) and 33 additional specimens of *Symphurus parvus*. (Abbreviations defined in methods section; SL is expressed in mm; characters 2 to 14 are expressed in thousandths of SL; 15 to 21 in thousandths of HL; *n* = no. of specimens measured.)

| Character | Holotype | *n* | Range | Mean | SD |
|---|---|---|---|---|---|
| 1. SL | 64.0 | 34 | 33.8–87.3 | 54.4 | 11.68 |
| 2. BD | 300 | 34 | 248–328 | 295.3 | 16.73 |
| 3. PDL | 50 | 34 | 36–69 | 53.8 | 7.22 |
| 4. PAL | 264 | 34 | 211–305 | 249.4 | 21.54 |
| 5. DBL | 950 | 34 | 931–964 | 946.4 | 7.24 |
| 6. ABL | 759 | 34 | 702–795 | 758.2 | 21.19 |
| 7. PL | 78 | 26 | 54–86 | 70.6 | 8.70 |
| 8. PA | 59 | 34 | 38–71 | 55.2 | 8.21 |
| 9. CFL | 122 | 30 | 112–151 | 129.2 | 9.29 |
| 10. HL | 236 | 34 | 180–260 | 230.0 | 16.55 |
| 11. HW | 258 | 34 | 211–279 | 250.5 | 14.16 |
| 12. POL | 156 | 34 | 118–162 | 146.5 | 10.05 |
| 13. UHL | 166 | 33 | 107–181 | 159.2 | 13.60 |
| 14. LHL | 105 | 33 | 88–139 | 110.9 | 11.39 |
| 15. POL | 662 | 34 | 595–688 | 637.7 | 23.82 |
| 16. SNL | 146 | 34 | 146–229 | 191.9 | 19.30 |
| 17. UJL | 185 | 34 | 185–252 | 210.1 | 16.87 |
| 18. ED | 152 | 34 | 105–197 | 153.2 | 20.71 |
| 19. CD | 159 | 34 | 123–263 | 187.0 | 31.45 |
| 20. OPLL | 291 | 33 | 246–371 | 291.6 | 30.69 |
| 21. OPUL | 153 | 33 | 102–246 | 176.9 | 31.70 |

1.39, $\bar{x}$=1.1). Lower head lobe width less than postorbital length; considerably narrower than upper head lobe. Lower opercular lobe of ocular side considerably wider than upper opercular lobe. Snout moderately short, somewhat pointed; covered with small ctenoid scales. Dermal papillae usually well developed on blind side of snout; occasionally extending onto anterior portion of snout on ocular side. Anterior nostril on ocular side long, when depressed posteriorly, usually just reaching anterior margin of lower eye. Jaws short; maxilla usually extending posteriorly to vertical through anterior margin of lower eye, or less frequently, reaching vertical through midpoint of lower eye. Ocular-side lower jaw without fleshy ridge. Teeth well developed on blind-side jaws. Teeth on margin of ocular-side jaws very small. Margin of ocular-side premaxilla with teeth extending over anterior one-half to three-fourths (rarely along entire jaw margin); ocular-side dentary with teeth extending over entire margin of bone; less frequently, teeth along only anterior three-fourths of dentary margin. Chin depth nearly equal with snout length. Lower eye large; eyes usually equal in position. Anterior and medial surfaces of eyes partially covered with 4–8 small ctenoid scales; 1–4 small ctenoid scales in narrow interorbital region. Pupillary operculum well developed. Dorsal-fin origin usually at point equal with verticals through anterior margin of upper eye and anterior margin of pupil of upper eye; predorsal length long. Scales absent on blind sides of dorsal- and anal-fin rays. Basal regions of dorsal-fin membrane from about seventh dorsal-fin ray and backwards, and anal-fin membrane throughout entire length of fin with a series of openings (membrane ostia) between fin rays. Pelvic fin long; longest pelvic-fin ray, when extended posteriorly, usually reaching base of first anal-fin ray. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anus, or occasionally extending posteriorly almost to anal-fin origin (membrane torn in most specimens). Caudal fin long. Scales large, ctenoid on both sides of body.

**Pigmentation (Fig. 42)** Body coloration generally similar for both sexes. Ocular surface usually light brown or yellowish with conspicuous, prominent, dark brown, roughly oblong- or diamond-shaped blotch immediately anterior to caudal-fin base, and variable number and arrangement of irregular dusky markings; occasional specimens with traces of faint, darker brown, incomplete crossbands. Caudal blotch usually covering 4–6 scales in length and 6–9 scales in width (usually crossing entire caudal region of body). Caudal blotch separated from caudal-fin base by 3–4 lightly pigmented scales. Crossbands, when present, diffuse, irregular, incomplete, often widely interrupted midlaterally. Ocular-side outer opercle with same general background pigment as body. Small brown spot of variable intensity usually present at dorsal margin of opercular opening. Inner linings of opercles and isthmus on both sides of body unpigmented. Usually with a well-developed dark brown pigment band on ocular-side upper lip extending posteriorly to angle of maxilla; ocular-side lower lip infrequently lightly spotted, but without definite pigment band. Blind side whitish or yellowish. Peritoneum unpigmented.

Fin rays and membranes of dorsal and anal fins rather lightly pigmented, irregularly flecked and shaded; becoming increasingly darker posteriorly, especially in posterior one-third of fins, but without conspicuous spots or blotches. Fin rays more or less uniformly pigmented along their lengths. Caudal fin usually more darkly pigmented than dorsal or anal fins. Scaly proximal portion of caudal fin with small, more darkly, pigmented area sometimes forming diffuse spot; distal scaleless portion of caudal fin usually completely pigmented to its extremity. Membrane and fin rays of caudal fin on blind side of body with pepper-dot pigmentation, especially well developed at base of fin.

**Size and sexual maturity (Fig. 7A)** *Symphurus parvus* is a diminutive species, attaining maximum sizes of ca. 88 mm. Only nine specimens exceeded 70 mm, and most specimens were much smaller, with 81% of 101 specimens examined for size-related life history information ranging between 40 and 70 mm. Males and females attain similar sizes; the largest specimens examined were males (87.3 and 84.7 mm), whereas the largest female was slightly smaller (80.6 mm). Gaspar-Dillanes and Espinosa-Pérez (1989:252) collected a 176-mm specimen (IBUNAM-P 2493) on the inner continental shelf off Quintana Roo, Mexico, which they identified as *S. parvus*. It is a specimen of *S. diomedeanus*, a species that reaches ca. 207 mm (see below).

Of 101 specimens examined for life history information, 48 were males (33.5–87.3 mm), 48 females (21.8–80.6 mm), and 5 were immature fish (26.6–41.5 mm) of indeterminate sex. Based on reproductive stages of females, sexual maturity occurs at sizes of 40–45 mm in this species. All females larger than 45 mm, except two, were mature. Twenty-eight females (39.8–80.6 mm) were gravid; 13 others (42.2–71.3), although not gravid, were mature with fully elongate ovaries, and in some, developed ova were evident. Seven females (21.8–47.7 mm) were immature with ovaries just undergoing elongation. Topp and Hoff (1972) also reported females of 37 and 43 mm with ovaries just undergoing elongation, whereas ovaries of a 62-mm specimen that they examined contained nearly mature ova.

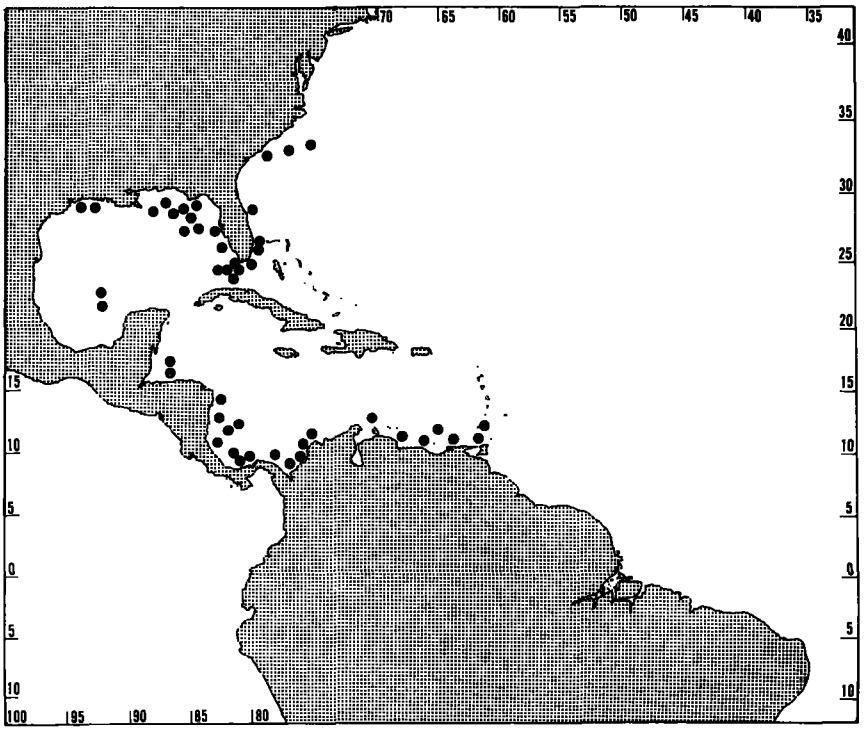


**Figure 43**

Geographic distribution of *Symphurus parvus* based on material examined (discussion of geographic distribution appears in species account).

**Geographic distribution (Fig. 43)** Neritic waters of the western North Atlantic from just south of Cape Lookout, North Carolina, south to Trinidad. Most frequently taken on inner continental shelf mud substrates off the southeastern Atlantic coast of Florida, throughout the Gulf of Mexico and Caribbean Sea off Central and South America to Trinidad, but absent from the Greater and Lesser Antilles.

Off the southeastern U.S. coast, *S. parvus* has been collected most frequently off southern Florida. Only three captures, consisting of one specimen apiece, record *S. parvus* north of this region. The northernmost record for this species is a specimen (VIMS 8832; 87 mm) taken on the continental shelf just south of Cape Lookout, North Carolina (34°23'N, 75°58'W; 80 m). One other specimen was collected off South Carolina (33°N), and the third specimen was taken at an unusually deep location (383 m) under the Gulf Stream off Daytona Beach, Florida (29°N).

*Symphurus parvus* has been collected at many inner continental shelf localities throughout the Gulf of Mexico, including areas off west Florida, the Central Gulf off Alabama and Louisiana, and the western Gulf off Texas and the Yucatan Peninsula (Springer and Bullis, 1956; this study). *Symphurus parvus* also occurs on the inner continental shelf throughout the Caribbean Sea—off Belize, Honduras, Panama, Colombia, eastern Venezuela, and Trinidad.

Ginsburg (1951) speculated that *S. parvus* would eventually be found in the West Indies. A single specimen (USNM 47657) containing a label reading *Blake* XXV is listed in the ledgers at USNM as probably having been taken from an unspecified location in the West Indies. Locality information for this specimen, however, is questionable. Eschmeyer (1965) noted many discrepancies regarding *Blake* station data between those reported by Goode and Bean (1896) and those entered in ledgers at the USNM fish collection. Because no additional locality information accompanies USNM 46757 and because station data associated with this speci-

men are unreliable, occurrence of *S. parvus* in the West Indies, based on this particular specimen, cannot be unequivocally verified. Also, because *S. parvus* is most often found on silty substrates in relatively deep neritic waters (see below), its occurrence in the West Indies would be quite restricted owing to absence of suitable soft mud and silt substrates (calcareous sediments are more widespread throughout this region) at depths where *S. parvus* usually occurs.

**Bathymetric distribution** *Symphurus parvus* occurs over a wide range of depths from 20 to 146 m; one unusual deepwater capture of a single specimen (UMML 35263) was made at 383 m (Table 10). Most specimens (107/114, 94%), however, have been collected between 31 and 110 m. Only five specimens have been taken at depths shallower than 30 m, whereas eight others were trawled at depths exceeding 100 m. Topp and Hoff (1972) reported similar capture depths (37–109 m) on the west Florida shelf for this species.

Although *S. parvus* has been collected from depths greater than 110 m, such deepwater occurrences are apparently unusual. The deepest recorded captures are for single specimens collected at 146 m and 383 m, whereas the next deepest captures are for six specimens taken between 101 and 110 m. The specimen captured at 383 m (UMML 35263) is undoubtedly *S. parvus*, despite a depth of capture considerably beyond the depth range known for the other specimens. Along with *S. parvus*, specimens of *Enchelyopus cimbrius*, *Chaunax pictus*, *Dibranchus atlanticus*, *Malacocephalus occidentalis*, *Bembrops* sp., and *Coelorhynchus carminatus*, deepwater species occurring to the edge of the continental shelf and on the upper continental slope, were also taken in the same trawl collection at this station.

**Ecology** Little is known concerning the ecology of *S. parvus*. Topp and Hoff (1972) collected this species on the west Florida shelf over a temperature range of 18.8–24°C and salinities of 33.8–36.3‰. They also remarked that *S. parvus* was not abundant anywhere, because most of their collections were of solitary individuals as were most collections (51/70) examined in this study. Eleven other collections contained two specimens each, whereas nine additional lots contained three to 16 specimens. The rarity of this species, based on trawl collections, may reflect the general inefficiency of trawls for capturing small pleuronectiform fishes, especially those that inhabit relatively deep waters, as does *S. parvus*.

**Remarks** Ginsburg (1951) noted that specimens from *Albatross* Station 2318 originally designated by Goode and Bean (1886) as "collateral types" (=paratypes in current usage) of *A. pigra* were actually specimens of *S. parvus*. Ginsburg selected three of these (USNM 74330) as paratypes of *S. parvus*. The fourth specimen, contained in the same bottle with the others, was not designated a paratype of *S. parvus* because it was on loan to P. Chabanaud (MNHN) and was not included in the original description of *S. parvus*. This specimen has been recatalogued as USNM 342239.

In examining specimens on which the original description of *A. pigra* was based, Ginsburg (1951) noted that he could not find specimens from *Albatross* station 2405. However, in his description of *S. parvus*, Ginsburg listed six specimens from *Albatross* station 2318. These specimens are now catalogued with the following numbers: USNM 84491 one specimen; USNM 152733 one specimen; USNM 74330 three specimens; and USNM 342239 one specimen. Because only four specimens were originally collected from *Albatross* station 2318 (as indicated by Goode and Bean, 1886), possibly USNM 84491 and USNM 152733, now catalogued separately (the specimens were originally in the same jar), may represent the two paratypes of *A. pigra* from *Albatross* station 2405. Examination of labels contained with the specimens and museum registers at the USNM could not resolve this problem. It appears that if labels with the specimens were mixed-up, or collection data for the specimens were mislabelled, it happened before the lot became part of the USNM collection.

If USNM 84491 (the holotype of *S. parvus*) and USNM 152733 (a paratype of *S. parvus*) are indeed the specimens from *Albatross* Station 2405 included in Goode and Bean's description of *A. pigra* (instead of *Albatross* station 2318, as presently labelled), then type locality and collection information of *S. parvus* changes from *Albatross* Station 2318 (24°25'45"N, 81°46'W; 45 fm; 15 Jan 1885) to *Albatross* Station 2405 (28°45'N, 85°02'W; 30 fm; 15 Mar 1885).

Among western Atlantic tonguefishes, *S. parvus* is most unusual in that two patterns of interdigitation of dorsal-fin pterygiophores were found in nearly equal frequencies in the specimens examined. Thirty-three of 82 (40%) specimens had a 1-4-2 pattern, whereas 35/82 (43%) had a 1-5-2 pattern. No correlations between geography, sex, or size and the observed bimodal distribution of pattern types were found. *Symphurus parvus* is one of only three species in the genus in which two ID patterns occurred in nearly equal frequencies (Munroe, 1992).

**Comparisons** Of all congeners, *S. parvus* is most similar to the western South Atlantic *S. kyaropterygium* and the western North Atlantic *S. minor*. *Symphurus parvus* can be distinguished from both

species by differences in meristic characters (see Tables 4–7). These and other differences are discussed in the "Comparisons" section of the species accounts for *S. kyaropterygium* and *S. minor*).

*Symphurus parvus* differs most notably from *S. ommaspilus* in having an irregularly shaped, dark brown, blotch on the ocular-side caudal region and in having uniformly pigmented dorsal and anal fins, whereas *S. ommaspilus* lacks the pigmented blotch on the ocular-side caudal region, and it has a single, conspicuous, ocellated spot on the posterior dorsal and anal fins. Other differences between these species include modal differences in meristic features (see Tables 4–7).

*Symphurus parvus* is similar in size and some meristic features to, and also occurs syntopically with, *S. pelicanus*. *Symphurus parvus* differs readily from this species in having an unpigmented peritoneum, dark brown blotch on the ocular-side caudal region, pupillary operculum, and 10 caudal-fin rays (vs. black peritoneum, no caudal blotch, no pupillary operculum, and 12 caudal-fin rays in *S. pelicanus*). Other differences between *S. parvus* and *S. pelicanus* are discussed in the "Comparisons" section of the account for *S. pelicanus*.

*Symphurus parvus* is not easily confused with other Atlantic tonguefishes possessing 10 caudal-fin rays (*S. plagiusa, S. jenynsi*, and *S. diomedeanus*), which have either sympatric or similar bathymetric distributions and which may be collected syntopically, because *S. parvus* has much lower meristic features (see Tables 4–9), membrane ostia in dorsal and anal fins, and a dark brown caudal blotch on the ocular side (vs. higher meristics, caudal blotch, and membrane ostia lacking in these other species). *Symphurus parvus* differs further from the sympatric *S. plagiusa* and the allopatric *S. jenynsi* in having a well-developed pupillary operculum (absent in these others). *Symphurus parvus* also lacks the conspicuous black spot on the outer surface of the ocular-side opercle, fleshy ridge on the ocular-side lower jaw, and small ctenoid scales on blind sides of the posterior dorsal- and anal-fin rays characteristic of *S. plagiusa*. *Symphurus parvus* is also easily recognized from *S. diomedeanus* because it has uniformly pigmented dorsal and anal fins lacking conspicuous spots, whereas dorsal and anal fins of *S. diomedeanus* usually have a series of conspicuous spots on posterior regions of these fins.

*Symphurus parvus* is readily distinguished from eastern Pacific congeners by its combination of a 1-4-2 ID pattern, 10 caudal-fin rays, unpigmented peritoneum, and well-developed pupillary operculum. Among these species, only *S. fasciolaris* has 10 caudal-fin rays. *Symphurus parvus* differs from this species in its lower counts (43–47 vs. 48–52 total vertebrae; 75–86 vs. 90–97 dorsal-fin rays; and 60–70 vs. 77–81 anal-fin rays in *S. fasciolaris*). It also lacks the pigmented spot on the caudal fin and combination of crossbands and rounded spots on the ocular surface present in *S. fasciolaris*.

**Figure 44**
*Symphurus ommaspilus* Böhlke, FMNH 94820, 53.6 mm SL, Belize, Glovers Reef.

## *Symphurus ommaspilus* Böhlke, 1961 (Figs. 6F, 44–45; Tables 1–10, 26) Ocellated tonguefish

?*Symphurus pusillus* (not of Goode and Bean, 1885). Kyle, 1913:145 (symmetrical larva with figure, possibly this species).

*Symphurus marginatus* (not of Goode and Bean, 1886). Metzelaar, 1919:134 (St. Eustatius Island).

*Symphurus ommaspilus* Böhlke, 1961:2 (original description with photograph; west side of southern of two Long Bay Cays, Andros Island, Bahamas). Robins and Randall, 1965:334 (Bahamas; counts, measurements). Böhlke and Chaplin, 1968:225 (Bahamas; in key, figure, comments). Munroe, 1992:370, 381 (ID pattern; geographic, bathymetric distributions).

**Diagnosis** *Symphurus ommaspilus* is easily distinguished from all congeners by the combination of 1-4-2 ID pattern; 10 caudal-fin rays; membrane ostia in dorsal and anal fins; 4 hypurals; 75–79 dorsal-fin rays; 60–64 anal-fin rays; 43–44 total vertebrae; 58–64 scales in longitudinal series; unpigmented peritoneum; well-developed pupillary operculum; teeth usually along only anterior one-half (occasionally with teeth along nearly anterior three-fourths) of margin of ocular-side premaxilla; teeth usually along only anterior one-half to three-fourths of margin of ocular-side dentary (less frequently teeth along entire margin of dentary); ocular surface pigmentation uniformly whitish without caudal blotch; blind side without pepper-dot pigmentation; dorsal and anal fins each with single ocellated spot on posterior one-fifth of fin; and small body size (maximum size ca. 60 mm).

**Description** A dwarf species attaining maximum lengths of ca. 60 mm SL. ID pattern 1-4-2 (Table 2). Caudal-fin rays 10 (Table 3). Dorsal-fin rays 75–79 (Table 4). Anal-fin rays 60–64 (Table 5). Total vertebrae 43–44 (Table 6). Hypurals 4 (28/28 specimens). Longitudinal scale rows 58–64 (Table 7). Scale rows on head posterior to lower orbit 14–17 (Table 8). Transverse scales 27–33 (Table 9).

Proportions of morphometric features presented in Table 26. Body moderately deep, maximum depth in anterior one-third of body; body depth tapering gradually beyond body midpoint. Preanal length shorter than body depth. Head relatively long and wide, considerably narrower than body depth. Head length shorter than head width (HW:HL 1.02–1.18, $\bar{x}$=1.1). Lower head lobe width considerably less than postorbital length; narrower than upper head lobe. Lower opercular lobe on ocular side narrower than upper opercular lobe. Snout long and somewhat pointed; covered with small deciduous ctenoid scales. Dermal papillae well developed on blind side of snout; occasionally extending onto anterior portion of snout on ocular side of body. Anterior nostril on ocular side long, when depressed posteriorly, usually reaching anterior margin of lower eye. Jaws short; maxilla usually extending posteriorly to vertical through midpoint of lower eye; occasionally only reaching vertical through anterior margin of lower eye. Teeth well developed on blind-side jaws; usually only anterior one-half of margin of ocular-side premaxilla with single row of slender teeth; occasionally teeth along

**Table 26**

Morphometrics for holotype (ANSP 93810) and 27 additional specimens of *Symphurus ommaspilus*. (Abbreviations defined in methods section; SL is expressed in mm; characters 2 to 14 are expressed in thousandths of SL; 15 to 21 in thousandths of HL; *n* = no of specimens measured.)

| Character | Holotype | *n* | Range | Mean | SD |
|---|---|---|---|---|---|
| 1. SL | 40.9 | 28 | 14.4–56.4 | 34.3 | 11.02 |
| 2. BD | 308 | 28 | 254–348 | 300.2 | 17.41 |
| 3. PDL | 68 | 28 | 40–87 | 58.8 | 11.08 |
| 4. PAL | 269 | 28 | 224–326 | 267.2 | 22.70 |
| 5. DBL | 927 | 28 | 846–975 | 941.5 | 25.83 |
| 6. ABL | 756 | 28 | 612–773 | 730.6 | 32.31 |
| 7. PL | 98 | 25 | 54–104 | 82.8 | 11.63 |
| 8. PA | 56 | 27 | 49–90 | 62.6 | 9.43 |
| 9. CFL | 127 | 26 | 92–160 | 128.3 | 14.16 |
| 10. HL | 235 | 28 | 196–268 | 231.4 | 13.99 |
| 11. HW | 259 | 28 | 227–292 | 253.8 | 14.62 |
| 12. POL | 137 | 28 | 119–190 | 144.9 | 13.38 |
| 13. UHL | 166 | 28 | 140–171 | 155.1 | 8.00 |
| 14. LHL | 103 | 28 | 96–135 | 111.2 | 11.81 |
| 15. POL | 583 | 28 | 546–802 | 627.1 | 46.48 |
| 16. SNL | 240 | 27 | 147–330 | 210.6 | 34.19 |
| 17. UJL | 198 | 28 | 164–277 | 205.7 | 23.31 |
| 18. ED | 115 | 28 | 114–175 | 138.4 | 16.58 |
| 19. CD | 198 | 27 | 162–274 | 206.0 | 30.69 |
| 20. OPLL | 177 | 28 | 147–277 | 196.0 | 29.31 |
| 21. OPUL | 281 | 28 | 210–346 | 279.4 | 31.45 |

nearly entire anterior three-fourths of premaxillary margin. Ocular-side dentary with teeth on anterior one-half to three-fourths of its length; less frequently with teeth along entire margin of bone. Chin depth usually slightly less than snout length. Ocular-side lower jaw without fleshy ridge. Lower eye relatively large; eyes usually equal in position, occasionally upper eye slightly in advance of lower eye. Anterior and medial surfaces of eyes usually scaleless; 2–3 scales present in narrow interorbital region. Pupillary operculum well developed. Dorsal-fin origin usually equal with vertical through midpoint of upper eye; occasionally reaching vertical through anterior margin, or rarely, posterior margin, of pupil of upper eye; predorsal length long. Basal region of dorsal-fin membrane from about seventh dorsal-fin ray and backwards, and anal-fin membrane throughout entire length of fin, with series of openings (membrane ostia) between fin rays. Scales absent on blind sides of dorsal- and anal-fin rays. Pelvic fin long; longest pelvic-fin ray, when extended posteriorly, usually reaching base of first anal-fin ray. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anus, or occasionally extending posteriorly to anal-fin origin (membrane torn in most specimens). Caudal fin moderately long. Scales large, ctenoid on both sides of body.

**Pigmentation (Fig. 44)** Body coloration generally similar for both sexes. Ocular surface generally whitish with numerous, indistinct, irregularly-shaped, darker brown chromatophores sprinkled over entire surface. Posterior one-third of body darker due to heavier chromatophore concentration; posterior darkening of body surface terminating near caudal-fin base. Occasionally dark pigment concentrated into one, or unusually, two, incomplete, and rather faint, crossbands situated at, or slightly posterior to, body midpoint. Outer surface of ocular-side opercle with same background coloration as body. Inner linings of opercles and isthmus on both sides of body unpigmented. Ocular-side lips diffusely sprinkled with faint melanophores, but without definite pigment band. Blind side off-white or yellowish. Peritoneum unpigmented.

Dorsal and anal fins with single, large, distinctly ocellated spot on fin in posterior one-fifth of body (approximately 10–14 fin rays anterior to posterior extent of each fin). Remainder of fin rays in dorsal and anal fins with variable sprinkling of brown pigment at irregular intervals, but heaviest in regions corresponding to crossbands on body. Both fin rays and membranes of dorsal and anal fins in posterior one-third of body more heavily pigmented than corresponding features in anterior region of body. Scaly portion of caudal fin with darker brown pigment, but not forming distinct spot; distal, scaleless portion of caudal fin with little, if any, pigment.

**Size and sexual maturity (Fig. 6F)** *Symphurus ommaspilus* is a dwarf species attaining lengths of about 57 mm. The majority (15/28) of individuals were much smaller (25–40 mm). Females attain somewhat larger sizes than males. The three largest specimens are gravid females measuring 56.4, 55.0, and 53.6 mm. The two largest males are substantially smaller, both only 42.7 mm. Of 25 specimens for which size-related life history information was examined, 8 were males (27.9–42.7 mm), 14 females (26.4–56.4 mm), and 3 fish (14.4–25.7 mm) were immature (sex could not be determined). Based on reproductive stages of females, sexual maturity occurs at very small sizes. Females as small as 27.7 mm were mature with fully elongate ovaries, and the smallest gravid females were 28.4 and 30.3 mm. All females, but two (26.4 and 33.6 mm), between 27 and 35 mm were sexually mature with ovaries either fully elongate, or with ovaries containing developed ova. The smallest female (26.4 mm) had ovaries just undergoing posterior elongation. The smallest specimen (14.4 mm) examined in this study was a completely metamorphosed immature fish (with little indication of any gonadal development) with completely devel-

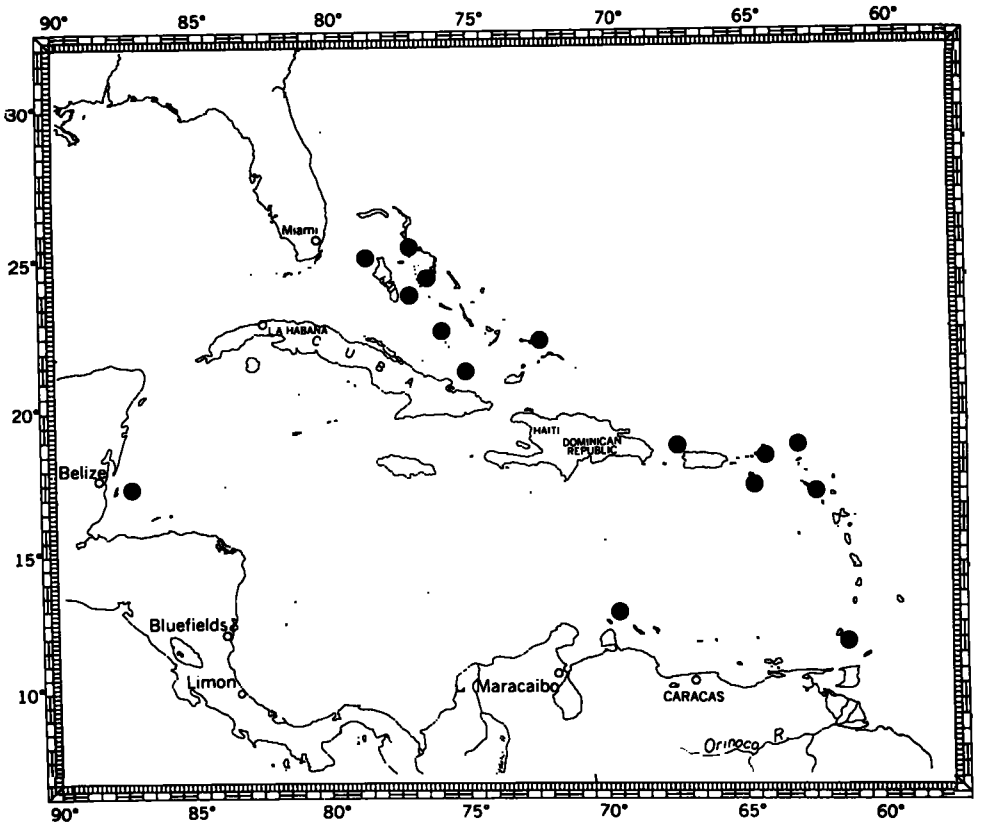


**Figure 45**

Geographic distribution of *Symphurus ommaspilus* based on material examined (discussion of geographic distribution appears in species account).

oped squamation and that had already assumed a benthic lifestyle.

**Geographic distribution (Fig. 45)** Widespread through insular regions of the Caribbean Sea, including the Bahamas, Glover's Reef, Belize, St. James in the Virgin Islands, Puerto Rico, St. Eustatius, St. Barthelemy, Curaçao, and the French West Indies. About one-half ($n$=13) of the examined specimens were collected in the Bahamas. The species has rarely been captured at reef areas along the continental margin of the Caribbean (only one citation, FMNH 94820, at Glover's Reef, Belize). Thus far, *S. ommaspilus* has not been recorded from the Florida Keys.

**Bathymetric distribution** *Symphurus ommaspilus* inhabits sandy substrates, including those in submerged beds of aquatic vegetation, in clear shallow waters (1–27 m) adjacent to coral reefs (Table 10). The majority of collections (23/24) occurred in waters shallower than 15 m, whereas the deepest reported capture is that of one specimen (ZMUC 8652) at 27 m.

**Ecology** Little is known concerning the biology of *S. ommaspilus* which is captured infrequently and generally in small numbers. The combination of small size, cryptic habits, and difficulties in sampling on substrates where *S. ommaspilus* occurs may account for its infrequent capture. Only three of 15 lots contained more than two fish (one each with 3, 5, and 7 individuals); most captures were a single fish.

**Comparisons** *Symphurus ommaspilus* most closely resembles *S. minor* and *S. parvus*, but is easily distinguished in having a single ocellated spot on both the dorsal and anal fins (absent in *S. minor* and *S. parvus)*, and it lacks the pigmented blotch on the ocular-side caudal region (present in the others). Other differences between *S. ommaspilus, S. minor*, and *S. parvus* are discussed in the "Comparisons" sections in accounts for each of these species.

*Symphurus ommaspilus* is somewhat similar to *S. diomedeanus* in that both possess 10 caudal-fin rays, well-developed pupillary operculum, and both have spotted dorsal and anal fins. However, *S. ommaspilus* has only a single ocellated spot on the posterior dorsal and anal fins, whereas *S. diomedeanus* usually

has a series of nonocellated spots on posterior portions of dorsal and anal fins. *Symphurus ommaspilus* also possesses ostia in the dorsal- and anal-fin membranes (absent in *S. diomedeanus*) and it has much lower, nonoverlapping, meristic features (75–79 dorsal-fin rays vs. 86–96 in *S. diomedeanus*; 60–64 anal-fin rays vs. 69–80; and 43–44 total vertebrae vs. 47–50 in *S. diomedeanus*). These two species also differ with respect to ID pattern (1-4-2 vs. 1-4-3 in *S. diomedeanus*) and *S. ommaspilus* is much smaller (ca. 60 mm or less), whereas *S. diomedeanus* attains 185 mm or more and does not mature until 90 mm or larger.

*Symphurus ommaspilus* is easily diagnosed from *S. plagiusa*, a species that also possesses 10 caudal-fin rays and unpigmented peritoneum, because *S. plagiusa* lacks the conspicuous ocellated dorsal- and anal-fin spots characteristic of *S. ommaspilus*. *Symphurus ommaspilus* differs further from that species in possessing a pupillary operculum and membrane ostia (both absent in *S. plagiusa*), in lacking a conspicuous black spot on the outer surface of the ocular-side opercle, a fleshy ridge on the ocular-side lower jaw, and small ctenoid scales on blind sides of dorsal- and anal-fin rays (vs. presence of a black opercular spot, fleshy ridge, dark pigmentation on isthmus and inner opercular linings, and small scales on blind sides of fin rays in *S. plagiusa*).

*Symphurus ommaspilus* differs from the western Atlantic *S. urospilus* in having ocellated spots on the dorsal and anal fins and a different caudal-fin ray count (10 vs. 11 caudal-fin rays in *S. urospilus*). Also, *S. ommaspilus* does not have an ocellated spot on the caudal fin, characteristic of *S. urospilus*. Differences between *S. ommaspilus* and other western Atlantic tonguefishes with which it might be confused are discussed in the "Comparisons" sections under species accounts for *S. arawak*, *S. pelicanus*, and *S. kyaropterygium*, respectively.

**Figure 46**

*Symphurus diomedeanus* (Goode and Bean). (**A**) UMML 35270, 136 mm SL, Venezuela 10°49'N, 63°13'W. (**B**) UMML 35271, 121 mm SL, British Guiana 8°08'N, 58°34'W.

### *Symphurus diomedeanus* (Goode and Bean, 1885) (Figs. 9D, 46–47; Tables 1–10, 27–28) Spottedfin tonguefish

*Aphoristia diomedeana* Goode and Bean, 1885:589 (original description; off Tortugas, Florida). Goode and Bean, 1896:460 (in part, more than one species included in account) (Tortugas, Florida; redescription, counts and figure of holotype; additional data on specimens from Gulf of Mexico and Caribbean). Jordan, 1886b:603 (West Indies).

*Symphurus diomedeanus*. Jordan and Goss, 1889:101 (possible geographical variety and synonym of *S. plagiusa*). Jordan and Evermann, 1898:2711 (after Goode and Bean). Evermann and Marsh, 1900:332 (in key; geographical variety of *S. plagiusa*). Chabanaud, 1939:26 (Gulf of Mexico). Longley and Hildebrand, 1941:49 (Tortugas, Florida). Munroe, 1992:371, 382 (ID pattern; geographic, bathymetric distributions).

*Symphurus sumptuosus* Chabanaud, 1948:509 (original description; Rio de Janeiro, Brazil).

*Symphurus diomedianus*. Ginsburg, 1951:194 (invalid emendation of name; North Carolina to Brazil; redescription, synonymy, figure). Hildebrand, 1954:296 (Texas, Mexico; occurrence on brown shrimp grounds; substrate preference). Hildebrand, 1955:205 (Gulf of Campeche, Mexico; occurrence on pink shrimp grounds; substrate prefer-

ence). Springer and Bullis, 1956:55 (Gulf of Mexico localities). Briggs, 1958:297 (Florida). Hoese, 1958:346 (Texas). Duarte-Bello, 1959:65 (Cuba). Cervigón, 1961:42 (Venezuela). Bullis and Thompson, 1965:34 (North Carolina, Florida). Moe and Martin, 1965:149 (off Tampa, Florida). Caldwell, 1966:84 (Jamaica). Cervigón, 1966:817 (Venezuela). Carvalho et al., 1968:3 (Brazil; in key). Moe, 1968:172 (Gulf of Mexico; reversed, partially ambicolorate specimen). Starck, 1968:31 (Alligator Reef, Florida). Struhsaker, 1969:298 (southeastern coast United States). Mago-Leccia, 1970:111 (Venezuela). Franks et al., 1972:124 (Mississippi; two specimens with ecological data). Topp and Hoff, 1972:79 (west Florida shelf; synonymy, counts, figure, distribution, ecology). Miller and Jorgenson, 1973:305 (meristic features and vertebrae counts, four specimens). Palacio, 1974:86 (Colombia). Chittenden and McEachran, 1976:94 (northwest Gulf of Mexico). Menezes and Benvegnú, 1976:148 (Brazil; redescription, counts, figure; senior synonym of *S. sumptuosus* Chabanaud, 1948, and *S. pterospilotus* Ginsburg, 1951). Chittenden and Moore, 1977:111 (110 m depth contour, central and western Gulf of Mexico). Lema and Oliveira, 1977:5 (in key). Ogren and Brusher, 1977:101 (St. Andrews Bay, Florida). Soares, 1978:24 (Rio Grande do Norte, Brazil). McCaffrey, 1981:204 (northeast Gulf of Mexico). Nonato et al., 1983:151 (São Paulo State, Brazil). Darcy and Gutherz, 1984:93 (west Florida shelf). Valdez and Aguilera, 1987:174 (Gulf of Venezuela; counts, description, figure). Cervigón et al., 1993:305 (Venezuela; descriptive characters; distribution; figure). Darovec, 1995:88 (distribution on west Florida shelf).

*Symphurus pterospilotus* Ginsburg, 1951:194 (original description, figure; Isla de Flores, Uruguay). Menezes and Benvegnú, 1976:148 (redescription, counts; junior synonym of *S. diomedeanus*). Lazzaro, 1977:69 (in key). Soares, 1978:24 (Rio Grande do Norte, Brazil). Lema et al., 1980:45 (Porto Belo and Florianopolis, Brazil; literature summary). Menni et al., 1984:202 (Uruguay; possible synonym of *S. diomedianus*).

*Symphurus diomedanus* [sic]. Corrêa et al., 1986:37 (Matinhos, Brazil; common names; figure).

*Symphurus parvus* (not of Ginsburg, 1951). Gaspar-Dillanes and Espinosa-Pérez, 1989:252 (inner continental shelf, Quintana Roo, Mexico).

*Symphurus plagiusa* (not of Linnaeus, 1766). Gaspar-Dillanes and Espinosa-Pérez, 1989:252 (inner continental shelf, Quintana Roo, Mexico).

**Diagnosis** *Symphurus diomedeanus* is distinguished from all congeners by its unique combination of: predominant 1-4-3 ID pattern; 10 caudal-fin rays; 4 hypurals; 86–96 dorsal-fin rays; 69–80 anal-fin rays; 47–50 total vertebrae; 79–96 scales in longitudinal series; well-developed pupillary operculum; unpigmented peritoneum; absence of scales on blind sides of dorsal- and anal-fin rays; absence of membrane ostia in dorsal and anal fins; absence of fleshy ridge on ocular-side lower jaw; usually with single, mostly incomplete, row of teeth extending to middle of margin of ocular-side lower jaw; ocular-side upper jaw usually without teeth (occasionally with few teeth on margin at premaxillary symphysis); ocular surface uniformly yellowish to dark brown without prominent blotches on caudal region (occasionally with faint traces of irregular number of wide, diffuse, poorly defined, crossbands); without pigmented spot on outer surface of ocular-side opercle; blind side without pepper-dot pigmentation; and posterior portions of dorsal and anal fins with series of well-developed, nonocellated spots (rarely with nonocellated spot also on caudal fin).

**Description** A relatively large species attaining sizes to ca. 207 mm SL. ID pattern usually 1-4-3 (160/218 specimens), less frequently 1-5-3 (13/218), 1-4-2 (13/218), or 1-3-4 (Table 2). Caudal-fin rays usually 10 (202/213), rarely 9, 11, or 12 (Table 3). Dorsal-fin rays 86–96, usually 88–93 (Table 4). Anal-fin rays 69–80, usually 72–77 (Table 5). Total vertebrae 47–50, usually 48–50 (215/219) (Table 6). Hypurals 4 (219/219). Longitudinal scale rows 79–96, usually 84–94 (Table 7). Scale rows on head posterior to lower orbit 16–21, usually 17–20 (Table 8). Transverse scales 34–47, usually 37–44 (Table 9).

Proportions of morphometric features presented in Table 27. Body moderately deep; maximum depth in anterior one-third of body; body depth tapering fairly rapidly posterior to midpoint. Preanal length considerably smaller than body depth. Head moderately long and narrow, considerably narrower than body depth. Head length shorter than head width (HW:HL 1.11–1.41, $\bar{x}$ = 1.2). Lower head lobe width slightly less than postorbital length; considerably narrower than upper head lobe. Lower opercular lobe of ocular side considerably wider than upper opercular lobe. Snout short and rounded; covered with small ctenoid scales. Dermal papillae well developed on snout, chin, and dorsal portion of head at base of dorsal fin on blind side of body. Anterior nostril on ocular side short, when depressed posteriorly, usually falling just short of anterior margin of lower eye. Jaws relatively short; maxilla extending posteriorly only to point between verticals through middle and anterior margin of pupil of lower eye. Ocular-side lower jaw without obvious fleshy ridge. Teeth well developed on

**Table 27**

Morphometrics for holotype (USNM 37347) and 40 additional specimens of *Symphurus diomedeanus*, including holotypes of *S. sumptuosus* (BMNH 1913.7.30:345) and *S. pterospilotus* (USNM 87770) herein regarded as junior subjective synonyms. (Abbreviations defined in methods section; SL is expressed in mm; measurements 2 to 14 are thousandths of SL; 15 to 21 are thousandths of HL; *n* = no. of specimens measured).

| Character | *diomedeanus* holotype | *sumptuosus* holotype | *pterospilotus* holotype | *n* | Range | Mean | SD |
|---|---|---|---|---|---|---|---|
| 1. SL | 137.9 | 111.5 | 115.2 | 41 | 88.8–175.0 | 131.8 | 22.91 |
| 2. BD | 302 | 310 | 299 | 41 | 268–324 | 297.4 | 11.86 |
| 3. PDL | 47 | 39 | 45 | 41 | 33–55 | 42.5 | 4.17 |
| 4. PAL | 206 | 197 | 201 | 41 | 179–238 | 208.5 | 12.63 |
| 5. DBL | 954 | 961 | 955 | 41 | 945–967 | 957.5 | 4.18 |
| 6. ABL | 787 | 781 | 796 | 41 | 751–823 | 783.2 | 18.14 |
| 7. PL | 60 | 60 | 64 | 41 | 46–64 | 54.4 | 5.20 |
| 8. PA | 55 | 66 | 61 | 40 | 28–82 | 50.3 | 11.46 |
| 9. CFL | 104 | 104 | 107 | 40 | 96–120 | 107.9 | 6.20 |
| 10. HL | 174 | 187 | 162 | 41 | 162–204 | 181.9 | 11.04 |
| 11. HW | 218 | 263 | 222 | 41 | 199–263 | 223.9 | 15.30 |
| 12. POL | 116 | 128 | 104 | 41 | 81–143 | 119.9 | 10.47 |
| 13. UHL | 138 | 153 | 149 | 41 | 122–170 | 148.5 | 10.43 |
| 14. LHL | 91 | 110 | 90 | 41 | 78–117 | 94.8 | 8.24 |
| 15. POL | 667 | 688 | 642 | 41 | 483–721 | 658.5 | 35.47 |
| 16. SNL | 175 | 173 | 187 | 41 | 130–209 | 172.5 | 17.31 |
| 17. UJL | 208 | 173 | 176 | 41 | 165–223 | 191.2 | 15.78 |
| 18. ED | 138 | 82 | 150 | 41 | 82–156 | 130.5 | 15.71 |
| 19. CD | 192 | 216 | 262 | 40 | 152–294 | 210.5 | 29.52 |
| 20. OPLL | 321 | 375 | 364 | 41 | 240–375 | 304.3 | 32.00 |
| 21. OPUL | 229 | 226 | 214 | 41 | 183–284 | 225.8 | 21.35 |

blind-side jaws. Margin of ocular-side lower jaw usually with single, mostly incomplete, row of slender teeth extending to middle of jaw; ocular-side upper jaw usually without teeth, occasionally with few teeth at margin of premaxillary symphysis. Chin depth somewhat larger than snout length. Lower eye relatively large; eyes usually equal in position, although occasionally upper slightly in advance of lower eye. Anterior and medial surfaces of eyes not covered with scales; usually 1–3 small ctenoid scales in narrow interorbital region. Pupillary operculum well developed. Dorsal-fin origin usually equal with vertical line through anterior margin of upper eye; occasionally either slightly anterior to vertical through anterior margin of upper eye, or reaching vertical through midpoint of upper eye; predorsal length long. Scales usually absent on blind sides of dorsal- and anal-fin rays; occasionally 1–2 scales at base of fin rays, especially in larger specimens. Pelvic fin short; longest pelvic-fin ray, when extended posteriorly, usually reaching base of first anal-fin ray. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anus, or occasionally extending posteriorly almost to anal-fin origin (membrane torn in most specimens). Caudal fin short. Scales large, strongly ctenoid on both sides of body.

**Pigmentation (Fig. 46, A and B)** Body coloration similar for both sexes. Ocular surface usually uniformly dark brown; occasionally with faint traces of variable number of wide, diffuse, poorly defined crossbands. Crossbands, when present, usually incomplete across body and not continued onto dorsal and anal fins; crossbands usually only slightly darker than background coloration. Specimens without crossbands usually with irregular dark mottling or dark blotches over entire ocular surface. Pupillary operculum usually dark brown or black. Specimens collected from light-colored substrates usually with uniform light brown or yellowish coloration on ocular surface, and with silvery pupillary operculum. Outer surface pigmentation of ocular-side opercle usually same as on body. Inner linings of opercles and isthmus on both sides of body unpigmented. Ocular-side upper lip usually with faint, but continuous, pigment band; ocular-side lower lip frequently spotted, but without definite band of pigment. Blind side uniformly creamy white to yellowish. Peritoneum unpigmented.

Fin rays and membranes of dorsal and anal fins on anterior two-thirds of body lightly pigmented with diffuse scattering of melanophores, but without spots or blotches. Dorsal- and anal-fin rays on posterior

one-third of body generally with more intense pigmentation than anterior fin rays, becoming variably dusky, dark brown, or occasionally black. Fin rays in posterior one-third of dorsal and anal fins usually with 1–5 conspicuous, rounded, dark brown or black spots on each fin. Topp and Hoff (1972) presented more detailed discussion of frequency of occurrence and location of spots on fins of this species in Florida waters. Spots on fin rays and membranes situated about midway between bases and distal tips of fin rays. Spots on dorsal and anal fins usually unequal in number and slightly offset from those in opposing fin. Posteriormost spot in each fin usually short distance anterior to base of caudal fin. Fin spots usually moderately or sharply contrasting to general fin pigmentation; occasionally first 1–3 spots poorly defined; spots on more posterior regions of fins generally with more well-defined, rounded shape. Melanistic specimens with fins uniformly darkly pigmented through most of length with fin spots present, although sometimes barely perceptible against background coloration. Specimens from light-colored substrates occasionally with fin spots barely perceptible without magnification. Caudal fin uniformly dark brown or black along length of fin; unusual specimens with single, rounded, nonocellated spot eccentrically placed on distal one-third of caudal fin.

**Size and sexual maturity (Fig. 9D)** *Symphurus diomedeanus* is a relatively large species, with a maximum reported size of 207 mm for a specimen collected off North Carolina (Ginsburg, 1951). This is the third largest of the Atlantic symphurine tonguefishes (only *S. jenynsi* and *S. tessellatus* are larger, see below). Males and females attain similar sizes. The largest specimen examined in this study (183 mm) is a female, whereas the next largest specimen (180 mm) is a male. Although 56 of the 324 specimens measured exceeded 150 mm, most were usually smaller than 130 mm. Topp and Hoff (1972) reported a size range of 48–174 mm (all but one specimen exceeded 100 mm), with estimated mean sizes of 149.1 mm for females and 146.8 mm for males, for *S. diomedeanus* collected off west Florida.

Among 169 specimens for which size-related life history information was summarized, 90 were females (85.3–183 mm) and 79 males (66.8–180 mm). Sexual maturation in females occurs usually between 90 and 120 mm. The smallest mature females measured ca. 89–107 mm, respectively. However, the majority of mature females ($n$=55) were 120–150 mm. Seven immature females ranged in size from 84.6 to 119 mm.

Of particular interest is the general scarcity of smaller fish in collections examined. Among 324 specimens measured, only 20 were smaller than 100 mm (57.9–98.3 mm). In fact, the smallest of specimens taken in benthic collections is 48 mm (Topp and Hoff, 1972). It seems unlikely that the absence of small *S. diomedeanus* in collections results entirely from selectivity of collecting gear (mostly trawls) for larger specimens, because specimens 75 mm and less of other tonguefish species are routinely taken in trawls. Instead, the absence of smaller size classes of *S. diomedeanus* in trawl collections may indicate that juveniles occupy different habitats than those of adults, and that these areas are not generally sampled, or are inaccessible to conventional trawling gears.

**Geographic distribution (Fig. 47)** *Symphurus diomedeanus* has the most extensive geographic distribution of any western Atlantic flatfish. It occurs on the inner continental shelf in warm temperate and tropical waters from the region just north of Cape Hatteras, North Carolina (35°23'N), along the southeastern Atlantic coast of the United States, through the Gulf of Mexico and Caribbean Sea (Ginsburg,

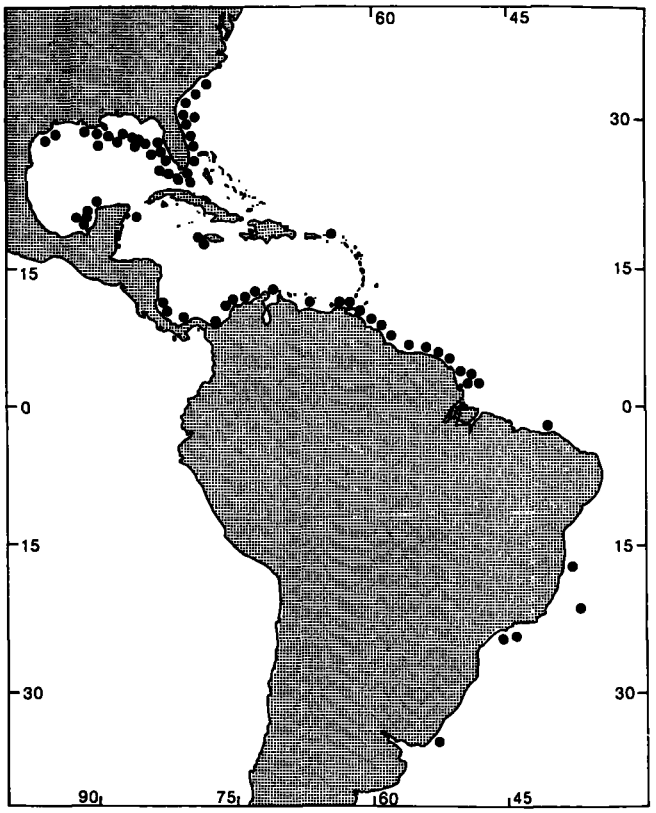


**Figure 47**

Geographic distribution of *Symphurus diomedeanus* based on material examined (discussion of geographic distribution appears in species account).

1951; Topp and Hoff, 1972), and on the inner continental shelf of South America to about Isla de Flores (34°56'S, 55°53'W), Uruguay (Ginsburg, 1951; Menezes and Benvegnú, 1976; Menni et al., 1984; Corrêa et al., 1986).

Off the southeastern United States and in the eastern Gulf of Mexico, *S. diomedeanus* is numerically the most common tonguefish in depths greater than 18 and shallower than 80 m. In a study assessing potential fishery resources along the southeastern United States (Struhsaker, 1969, Appendix B), *S. diomedeanus* was present at more than 50% of shallow stations sampled by trawls and was considered to be very common in these areas. In the Gulf of Mexico, *S. diomedeanus* occurs from the southern tip of Florida and Dry Tortugas region in the east (Topp and Hoff, 1972), to southern Texas and the Gulf of Campeche in the west (Hildebrand, 1955; Gaspar-Dillanes and Espinosa-Pérez, 1989). It has been reported to be the most common tonguefish between 37 and 73 m on the southwest Florida shelf (Topp and Hoff, 1972), whereas in the Caribbean Sea, this species has been collected at continental locations off Yucatan (Hildebrand, 1955; Topp and Hoff, 1972; this study), Nicaragua, and Panama. It is rare in the Antilles with records from only the shallow waters south of Jamaica (Caldwell, 1966) and off the Virgin Islands (Appendix). In the southern Caribbean, *S. diomedeanus* is taken commonly in shallow seas off Colombia and Venezuela (Cervigón, 1966). Along northeastern South America, there are numerous captures of this species from Guyana to northern Brazil. Although this species was recorded as far south as Isla de Flores, Uruguay (Ginsburg, 1951), Menezes and Benvegnú (1976) noted that when compared with more northern areas of Brazil, the abundance of *S. diomedeanus* diminishes substantially in waters south of about Rio de Janeiro.

**Bathymetric distribution** *Symphurus diomedeanus* occurs on a variety of inner continental shelf substrates at depths of 6–183 m (Table 10). The center of abundance for this species occurs between 21 and 80 m, where 284 out of 315 (90%) of the specimens were collected. Topp and Hoff (1972) reported a similar depth range for *S. diomedeanus* collected during cruises on the west Florida shelf. Most fish they examined were taken at 37 m or deeper. These authors also noted that *S. diomedeanus* abundance declined noticeably at both the very deepest and the shallowest stations, indicating that it inhabits a rather narrow depth range on the inner continental shelf off west Florida. The deepest recorded capture of this species is a single specimen (UMML 34377) collected at 183 m off Tortugas, Florida (Longley and Hildebrand, 1941). Other deep collections of *S. diomedeanus* recorded herein are single specimens taken at 145 m and 146 m.

As noted previously (Topp and Hoff, 1972), this species usually does not inhabit shallow inshore or estuarine areas. Only three specimens examined in this study were taken in waters 20 m or shallower (Table 10), with one specimen (UMML 35206) collected at 6 m off Key Biscayne, the shallowest capture depth. Moe and Martin (1965) collected three other specimens at 3–5 m off Tampa Bay, Florida. Cervigón (1966) reported that in Venezuelan coastal waters, *S. diomedeanus* is occasionally collected at less than 30 m, but most captures of this species typically occur in deeper waters. Occurrence of the smallest specimen (33 mm; UMML 35268) at 27 m may indicate that newly settled individuals occur in offshore habitats similar to those occupied by adults.

**Ecology** On the continental shelf off west Florida, Topp and Hoff (1972) collected *S. diomedeanus* at bottom temperatures ranging from 17.5° to 28°C and at salinities of 32.3–36.7‰. Springer and Bullis (1956) reported capturing this species on substrates with a high mud component. Hildebrand (1954) noted that in the western Gulf of Mexico the species was rarely caught on soft mud bottoms but was more common on hard bottoms, such as those comprising the snapper banks. Later (1955), he noted the capture of four specimens in the western Gulf of Mexico on substrates with a high shell and coral content. Topp and Hoff (1972) collected most specimens off west Florida on calcareous substrates, noting also that *S. diomedeanus* was not taken where appreciable proportions of quartz sand were present. The majority of specimens examined in the present study were also collected on substrates consisting of calcareous mud, calcareous sand, and those with a large component of shell hash.

Topp and Hoff (1972) reported that 49 of 140 specimens of *S. diomedeanus* examined for diet composition contained a broad spectrum of benthic invertebrates. Crustaceans, particularly small crabs, were most frequently encountered, followed in importance by polychaetes, gastropods, bivalves, gastropod eggs, and amphipods.

**Geographic variation** Variation in counts of dorsal- and anal-fin rays and total vertebrae for *S. diomedeanus* divided into 13 geographic regions (from southeastern United States to Uruguay) was comparatively small (Table 28). No significant differences in meristic characters of fishes from any segment of the geographic range were evident, although *S. diomedeanus* from the southernmost re-

**Table 28**

Geographic variation in selected meristic features of *Symphurus diomedeanus*. (Abbreviations: SEUS = southeastern United States; EGMX = Eastern Gulf of Mexico (to 91°W); WGMX = western Gulf of Mexico, including Yucatan shelf region; JAM = Jamaica; VI = Virgin Islands; PAN = Panama; COL = Colombia; VEN = Venezuela; GUY = Guyana; FG = French Guiana; NBR = Northern Brazil; SBR = Southern Brazil; URU = Uruguay; *n* = no. of fish measured.)

| Character | Area | *n* | Mean | Range | SD |
|---|---|---|---|---|---|
| Dorsal rays | SEUS | 46 | 90.9 | 88–93 | 1.44 |
| | EGMX | 64 | 90.5 | 87–94 | 1.53 |
| | WGMX | 32 | 90.3 | 88–93 | 1.12 |
| | JAM | 9 | 91.0 | 89–93 | 1.41 |
| | VI | 2 | 90.0 | 89–91 | 1.41 |
| | PAN | 1 | — | 91 | — |
| | COL | 8 | 91.4 | 89–94 | 1.92 |
| | VEN | 6 | 91.3 | 90–93 | 1.03 |
| | GUY | 6 | 91.8 | 90–93 | 1.17 |
| | FG | 11 | 91.3 | 89–92 | 1.68 |
| | NBR | 5 | 92.6 | 92–94 | 0.89 |
| | SBR | 19 | 91.4 | 90–93 | 1.16 |
| | URU | 1 | — | 93 | — |
| Anal rays | SEUS | 46 | 74.7 | 69–77 | 1.55 |
| | EGMX | 64 | 74.4 | 72–77 | 1.33 |
| | WGMX | 32 | 74.2 | 72–76 | 0.98 |
| | JAM | 9 | 75.7 | 74–80 | 1.80 |
| | VI | 2 | 73.0 | 72–74 | 1.41 |
| | PAN | 1 | — | 76 | — |
| | COL | 8 | 75.1 | 73–77 | 1.36 |
| | VEN | 6 | 75.0 | 74–76 | 0.63 |
| | GUY | 6 | 75.7 | 74–76 | 0.82 |
| | FG | 11 | 74.7 | 73–77 | 1.19 |
| | NBR | 5 | 76.6 | 75–80 | 1.95 |
| | SBR | 19 | 75.2 | 71–78 | 1.74 |
| | URU | 1 | — | 75 | — |
| Vertebrae | SEUS | 46 | 48.9 | 47–50 | 0.71 |
| | EGMX | 64 | 48.8 | 47–50 | 0.65 |
| | WGMX | 31 | 48.7 | 47–50 | 0.59 |
| | JAM | 9 | 48.8 | 48–49 | 0.44 |
| | VI | 2 | 48.5 | 48–49 | 0.71 |
| | PAN | 1 | — | 49 | — |
| | COL | 8 | 49.0 | 49 | 0.00 |
| | VEN | 6 | 49.2 | 49–50 | 0.41 |
| | GUY | 6 | 49.2 | 49–50 | 0.41 |
| | FG | 11 | 49.1 | 48–50 | 0.83 |
| | NBR | 5 | 49.0 | 48–50 | 0.71 |
| | SBR | 19 | 49.1 | 48–50 | 0.88 |
| | URU | 1 | — | 49 | — |

gions had slightly higher counts, on average, than those taken from fishes collected in northernmost extents of the species range.

[1] Steyskal, G. C. (deceased). 1989. Dep. Entomology, National Museum of Natural History, Washington, D.C. 20560. Personal commun.

**Etymology** The name *Diomedea*, from the Greek *Diomedes*, the name for a Greek hero in the Trojan War, has been used as a generic name for albatrosses (Brown, 1954). Apparently, Goode and Bean (1885b) chose this word as the stem name for this species' specific epithet because the first specimen was captured by the research vessel *Albatross*. At the time of the original description of this species, symphurine tonguefishes were placed in the genus *Aphoristia*, which is feminine in gender. To agree in gender with *Aphoristia*, Goode and Bean used the specific epithet *diomedea*. Later, when *Aphoristia* was placed in the synonymy of *Symphurus* Rafinesque (Jordan and Goss, 1889), the specific name of this species was emended to *diomedeanus* to agree in gender with the masculine *Symphurus*. This spelling (i.e. *diomedeanus*) prevailed until Ginsburg's revision (1951), in which he accidentally changed the spelling of the trivial name to *diomedianus*. Ginsburg provided no comments regarding this change, but it is noteworthy that the trivial name of the species is incorrectly spelled throughout the synonymy he provided, including the same misspelling for the original description of *Aphoristia diomedeana* Goode and Bean. Subsequent checklists (Bailey et al., 1960; Robins et al., 1991) and other references (see synonymy above) followed Ginsburg's emended spelling of the trivial name. However, Ginsburg was incorrect in changing the spelling of the stem root from *diomedea* to *diomedianus*. The correct spelling of the specific epithet is *diomedeanus*. This emendation is based on the original spelling designated by Goode and Bean and agrees in gender with *Symphurus* (Steyskal[1]).

**Remarks** Goode and Bean (1885b) described *Aphoristia diomedeana* from a single specimen collected off Tortugas, Florida. In 1896, they reported on additional specimens purportedly of this species, but that series has proved to be a mixture of species. Ginsburg (1951) discovered that the specimen (USNM 74331) from *Albatross* station 2121-2122 included in Goode and Bean's (1896) account of *S. diomedeanus* was actually an undescribed species, which he described as *S. pelicanus*, designating the specimen in USNM 74331 as a paratype. Goode and Bean (1896) also identified as *S. diomedeanus* another specimen that was collected by the *Blake* off Dominica. It is conceivable that this is the specimen now catalogued as MCZ 27968, and referred to as *S. stigmosus* (see further discussion in species account of *S. stigmosus* above).

In 1948, Chabanaud described *S. sumptuosus*, based on a single specimen collected off Rio de Janeiro, Brazil. The holotype of *S. sumptuosus* has 10 caudal-fin rays and a series of spots on the dorsal

and anal fins. In his description of *S. sumptuosus*, Chabanaud failed to compare his new species with previously described western Atlantic tonguefishes, even *S. diomedeanus*, which also possesses 10 caudal-fin rays and spotted dorsal and anal fins. Ginsburg (1951) recognized that *S. sumptuosus* was conspecific with *S. diomedeanus*, pointing out that the holotype of *S. sumptuosus* agreed with *S. diomedeanus* in the number of caudal-, dorsal-, and anal-fin rays and scales in a longitudinal series and that both nominal species possessed a series of spots on the dorsal and anal fins. Additional similarities between the holotype of *S. sumptuosus* and the holotype and other specimens of *S. diomedeanus* were found in the present study. These include the number of total vertebrae (50 in *S. sumptuosus* vs. 47–50 in *S. diomedeanus*), and ID pattern (1-4-3, both species). Both nominal species also possess a pupillary operculum and an unpigmented peritoneum, and have similar morphometric features (see Table 27). I agree with Ginsburg that *S. sumptuosus* is a synonym of *S. diomedeanus*.

In that same paper, Ginsburg (1951) described another nominal species, *S. pterospilotus*, from one specimen collected off Uruguay. Ginsburg thought this nominal species was distinct from other congeners because of its unique combination of a spot on the caudal fin, a series of spots on the dorsal and anal fins, and its 11 caudal-fin rays. He noted that, except for the number of caudal-fin rays, all other counts for this specimen exceeded those for *S. urospilus*, the only other western North Atlantic species with 11 caudal-fin rays and a spotted caudal fin. He thus considered the specimen to represent a distinct taxon. In further comparisons of his new species with other western Atlantic *Symphurus*, Ginsburg noted that fin-ray and scale counts for *S. pterospilotus* overlapped with those for *S. diomedeanus*. However, given the presence of a caudal-fin spot and differences in number of caudal-fin rays (11 vs. 10 in *S. diomedeanus*), he concluded that it was appropriate to describe *S. pterospilotus* as a distinct species.

Menezes and Benvegnú (1976) evaluated the status of all nominal tonguefish species from South American waters having 10 or 11 caudal-fin rays and spotted dorsal and anal fins. They noted that occasional specimens of *S. diomedeanus* have a partial or complete spot on the caudal fin and that some specimens have either 9 or 11 caudal-fin rays, instead of the 10 caudal-fin rays typical for this species. Menezes and Benvegnú thus noted that the characters Ginsburg used to discriminate *S. pterospilotus* from *S. diomedeanus*, namely the combination of 11 caudal-fin rays and a spot on the caudal fin in addition to spots on the posterior dorsal and anal fins, were not diagnostic of a new species, because they were also found in samples of *S. diomedeanus*, which they examined. Menezes and Benvegnú concluded, therefore, that *S. pterospilotus* Ginsburg is based on a specimen of *S. diomedeanus* featuring an unusual combination of meristic and pigmentation features.

Additional evidence supporting placement of *S. pterospilotus* in the synonymy of *S. diomedeanus* was found in this study. Although most specimens of *S. diomedeanus* possess 10 caudal-fin rays, specimens with 11 caudal-fin rays do occur (5/196 of *S. diomedeanus* examined, Table 3), albeit rarely. Also, the 49 vertebrae of the holotype of *S. pterospilotus* fall within the range of vertebrae in *S. diomedeanus* (Table 6). The two nominal species share the same ID pattern (1-4-3), both possess a pupillary operculum and unpigmented peritoneum, and both have similar morphometric features (see Table 27). On the basis of available evidence, I agree with Menezes and Benvegnú (1976) that *S. pterospilotus* Ginsburg is a junior synonym of *S. diomedeanus*, which is the only species occurring throughout the western Atlantic with the combination of 10 (rarely 9 or 11) caudal-fin rays and a series of spots on the posterior regions of the dorsal and anal fins (occasional specimens also with a spot on the caudal fin in combination with other spots on the posterior dorsal and anal fins).

**Comparisons** *Symphurus diomedeanus* is similar in ID pattern, body shape, overall size, and has meristic features that overlap, at least partially, those of several western Atlantic tonguefishes also possessing the 1-4-3 ID pattern, including *S. plagiusa*, *S. urospilus*, *S. civitatium*, *S. plagusia*, *S. tessellatus*, *S. oculellus*, and *S. caribbeanus*. *Symphurus diomedeanus* differs from these species, except *S. plagiusa*, in caudal-fin ray count (10 vs. 11 in *S. urospilus*, 12 in the others), and in modal counts for total vertebrae and dorsal- and anal-fin rays (see Tables 4–6).

In overall size and similarity of meristic features, *S. diomedeanus* most resembles *S. plagiusa*. Like *S. plagiusa*, *S. diomedeanus* has 10 caudal-fin rays and an unpigmented peritoneum but differs from this species in possessing a well-developed pupillary operculum and a variable number of conspicuous black spots on the posterior dorsal and anal fins (both features absent in *S. plagiusa*). *Symphurus diomedeanus* lacks the small ctenoid scales on blind sides of the posterior rays of the dorsal and anal fins, the fleshy ridge on the ocular-side lower jaw, and black spot on the dorsal portion of the ocular-side opercle usually present in *S. plagiusa*. *Symphurus diomedeanus* is also distinct from *S. plagiusa* in having an

unpigmented isthmus and unpigmented inner opercular linings, whereas those of *S. plagiusa* are heavily pigmented. Further differences between *S. diomedeanus* and *S. plagiusa* are modally higher counts in *S. diomedeanus* (dorsal-fin rays 86–96 vs. 81–91 in *S. plagiusa*; anal-fin rays 69–80 vs. 66–75; total vertebrae 47–50, usually 48–50 vs. 44–49, usually 45–48, in *S. plagiusa*).

*Symphurus diomedeanus* is similar to the sympatric *S. urospilus* in some meristic features and in size, and both species also possess a well-developed pupillary operculum. Besides its different caudal-fin ray count, *S. diomedeanus* differs markedly from *S. urospilus* in possessing a series of spots on posterior regions of dorsal and anal fins (only in rare instances is there ever a spot on the caudal fin and when present, the caudal spot occurs in combination with spots on posterior portions of dorsal and anal fins), whereas *S. urospilus* always possesses a single, ocellated spot on the caudal fin and lacks pigmented spots on dorsal and anal fins. Further differences are that *S. diomedeanus* has 79–96 longitudinal scales (vs. 67–82 in *S. urospilus*), and the ocular surface of *S. diomedeanus* is more or less uniformly pigmented (only occasional specimens having faint crossbands), whereas most *S. urospilus* have well-developed crossbands. The two species can also be distinguished by differences in vertebral counts (47–50, usually 48–50, total vertebrae in *S. diomedeanus* vs. 44–48, usually 45–46, in *S. urospilus*).

Some meristic features of *S. diomedeanus* overlap those of *S. civitatium, S. plagusia, S. tessellatus, S. oculellus*, and *S. caribbeanus*, which occur sympatrically, and occasionally syntopically, with *S. diomedeanus* (Munroe, 1991). *Symphurus diomedeanus* differs from these in having 10 caudal-fin rays (vs. 12 in the others), a pupillary operculum (lacking in these other species), and a series of rounded black spots on posterior rays of the dorsal and anal fins. In contrast, vertical fins of *S. civitatium, S. plagusia*, and *S. tessellatus* are more or less uniformly pigmented, without distinctive pigmented blotches or spots. Those of *S. caribbeanus* and *S. oculellus* have an alternating series of somewhat rectangular-shaped, pigmented blotches and unpigmented areas beginning in the midbody region and continuing posteriorly (inclusive of the caudal fin in *S. oculellus*), a pattern quite different from that observed in *S. diomedeanus* (dorsal and anal fins with fewer, nearly spherical spots only on posterior regions of these fins and usually exclusive of caudal fin). *Symphurus diomedeanus* also differs from *S. tessellatus* in lacking small scales on blind sides of the posterior dorsal- and anal-fin rays. It can be further distinguished from both *S. tessellatus* and *S. oculellus* because it lacks a black spot on the outer surface of the ocular-side opercle (vs. a black spot usually present on outer surface of ocular-side opercle in these other species).

Some meristic and pigmentation features of *S. diomedeanus* overlap, at least partially, those of at least 14 other species of western Atlantic tonguefishes. Among these, *S. diomedeanus* is most similar to, and occurs sympatrically with, *S. kyaropterygium, S. minor, S. parvus*, and *S. ommaspilus*. All species possess 10 caudal-fin rays and have a well-developed pupillary operculum and unpigmented peritoneum. Differences between these species are discussed in the "Comparisons" sections in accounts for *S. kyaropterygium, S. parvus, S. minor*, and *S. ommaspilus*.

*Symphurus diomedeanus* is similar in overall body shape, caudal-fin ray count, and has some meristic features that overlap partially those of *S. trewavasae*, which co-occurs with *S. diomedeanus* in the western South Atlantic. The two are easily distinguished by the presence in *S. diomedeanus* of a pupillary operculum (absent in *S. trewavasae*), and *S. diomedeanus* has spots on the dorsal and anal fins (usually), whereas *S. trewavasae* does not have spotted fins. Other differences between these species are discussed in the "Comparisons" section in the account for *S. trewavasae*.

Among eastern Pacific species of *Symphurus*, *S. diomedeanus* is most similar to *S. fasciolaris* in that both have overlapping meristic features, 10 caudal-fin rays, pupillary operculum, unpigmented peritoneum, and 1-4-3 ID pattern. *Symphurus fasciolaris*, however, lacks pigmented spots on dorsal and anal fins that characterize *S. diomedeanus*, and *S. diomedeanus* lacks the ocellated spot on the caudal fin featured in *S. fasciolaris*. In addition, none of the *S. diomedeanus* have the combination of crossbands and rounded spots on the ocular surface that is found on many *S. fasciolaris*.

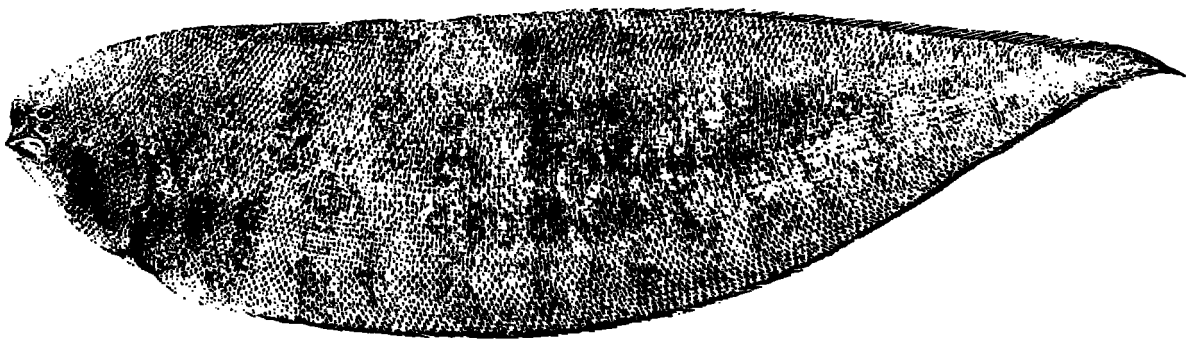

**Figure 48**
*Symphurus jenynsi* Evermann and Kendall, USNM 327835, 168 mm SL, Uruguay 35°52'S, 55°14'W.

### *Symphurus jenynsi* Evermann and Kendall, 1907 (Figs. 9G, 48–49; Tables 1–10, 29) Jenyn's tonguefish

*Plagusia* sp. Jenyns, 1840-42:140 (San Blas, coast of Patagonia; brief description; comparison with *Plagusia brasiliensis*=*S. tessellatus*, this study).

*Symphurus plagusia* (not of Schneider, in Bloch and Schneider, 1801). ?Berg, 1895:79 (Mar del Plata, Montevideo).

*Symphurus jenynsi* Evermann and Kendall, 1907:108 (original description, figure of type; probably from market at Buenos Aires). Devincenzi, 1920:135 (Río de La Plata, Uruguay; diagnosis; counts and measurements). Chabanaud, 1939:26 (market at Buenos Aires). Lahille, 1939:203 (Argentina). Chiesa, 1945:101 (Argentina, 35–39°S). Ginsburg, 1951:200 (redescription, counts, measurements, distribution). Carvalho et al., 1968:21 (southern Brazil and Argentina). Roux, 1973:176 (southern Brazil and Argentina). Lazzaro, 1973:247 (Argentina). Benvegnú, 1973:499 (southern Brazil and Uruguay). Kawakami, 1976:629 (ecological distribution, feeding habits). Menezes and Benvegnú, 1976:139 (southeastern Brazil to Argentina; redescription, photograph, counts, measurements, ecological distribution). Lema and Oliveira, 1977:6 (Santa Catarina and Rio Grande do Sul, Brazil, to northern Uruguay). Lema et al., 1980:42 (southern Brazil; synonymy). Chao et al., 1982:73 (yearround occurrence, coastal habitats in and near Lago dos Patos, Rio Grande do Sul, Brazil). Volcker and Andreata, 1982:223 (Laguna da Tijuca, Rio de Janeiro, Brazil; counts, measurements). Lucena and Lucena, 1982:55 (northern Brazil to Argentina). Menni et al., 1984:201 (Uruguay and Argentina). Chao et al., 1985:433 (Los Patos lagoon, Brazil; estuarine occurrence). Inada, 1986:316 (Argentina). Muelbert and Weiss, 1991:48 (Lago dos Patos, Brazil; larval distribution). Munroe, 1992:371, 382 (ID pattern; geographic, bathymetric distributions). Haimovici et al., 1996:36 (distribution and abundance on continental shelf off southern Brazil).

*Symphurus bergi* Thompson, 1916:414 (original description, figure; Montevideo). Devincenzi, 1920:136 (Río de La Plata, Brazil, and Uruguay; diagnosis; counts and measurements). Devincenzi, 1924–26:282 (Uruguay; counts, measurements). Chabanaud, 1939:26 (American Atlantic, Montevideo). Lahille, 1939:203 (Argentina; figure). Chiesa, 1945:102 (Argentina, 35° and 38°S). Barcellos, 1962b:12 (Rio Grande do Sul, Brazil).

*Symphurus jenynsii.* Devincenzi, 1920:136 (Uruguay; counts, measurements). Devincenzi 1924:281 (Uruguay; counts, measurements). Barcellos, 1962a:12 (Rio Grande do Sul). Menezes, 1971:61 (Santa Catarina and Rio Grande do Sul, Brazil).

*Symphurus meridionalis* Lema and Oliveira, 1977:8 (original description, figures; Rio Grande do Sul, Brazil). Lema et al., 1980:43 (Rio Grande do Sul and Porto Belo, Brazil). Lucena and Lucena, 1982:55 (in part; Brazil; specimen (MCP 8009) pre-

viously reported as *S. meridionalis* synonymized with *S. jenynsi*).

*Simphurus* [sic] *jenynsi*. Wakabara et al., 1982:67 (feeding habits; continental shelf off southern Brazil and Uruguay).

**Diagnosis** *Symphurus jenynsi* is one of the most distinctive species in the genus, easily distinguished from other congeners by the combination of: predominant 1-4-3 ID pattern; 10 caudal-fin rays; 4 hypurals; 107–115 dorsal-fin rays; 91–99 anal-fin rays; 57–60 total vertebrae; 102–119 scales in longitudinal series; unpigmented peritoneum; absence of pupillary operculum; absence of scales on blind sides of dorsal- and anal-fin rays; absence of fleshy ridge on ocular-side lower jaw; teeth absent on ocular-side lower jaw; ocular-side premaxilla with small number of teeth on anterior marginal region only; absence of membrane ostia in dorsal and anal fins; ocular surface pigmentation uniformly light to dark brown with crossbands, but without caudal blotch; faint, dusky blotch on outer surface of ocular-side opercle; blind side without pepper-dot pigmentation; and dorsal, anal, and caudal fins without spots or blotches.

**Description** The largest species in the genus attaining maximum sizes of at least 319 mm SL. ID pattern usually 1-4-3 (62/86 specimens), less frequently 1-5-3 or 1-3-4 (Table 2). Caudal-fin rays usually 10 (78/81), rarely 9 (Table 3). Dorsal-fin rays 107–115 (Table 4). Anal-fin rays 91–99 (Table 5). Total vertebrae 57–60, usually 58–59 (73/88) (Table 6). Hypurals 4 (88/88). Longitudinal scale rows 102–119, usually 104–115 (Table 7; Menezes and Benvegnú (1976) reported 106–124 longitudinal scale rows). Scale rows on head posterior to lower orbit 21–25, usually 22–24 (Table 8). Transverse scales 41–51, usually 44–48 (Table 9).

Proportions of morphometric features are presented in Table 29. Body relatively elongate, maximum depth usually at body midpoint; body depth tapering gradually posterior to midpoint. Preanal length considerably shorter than body depth. Head short and rather narrow, less than body depth. Head length less than head width (HW:HL 1.02–1.48, $\bar{x}$=1.2). Lower head lobe width usually slightly less than postorbital length; narrower than upper head lobe. Lower opercular lobe of ocular side slightly wider than upper opercular lobe. Snout short and rounded; covered with small ctenoid scales. Anterior nostril on ocular side short when depressed posteriorly, usually falling just short of anterior margin of lower eye. Dermal papillae well developed on snout, chin, and, in some individuals, dorsal portion of head near base of dorsal fin on blind side. Jaws moderately long; maxilla usually extending posteriorly to vertical through posterior margin of pupil of lower eye; occasionally extending only to vertical through midpoint of lower eye. Ocular-side lower jaw without fleshy ridge. Teeth well developed on blind-side jaws. Ocular-side lower jaw without teeth; ocular-side premaxilla with small number of slender teeth on margin of bone in region anterior to vertical through base of anterior nostril. Chin depth nearly equal with snout length. Lower eye small; eyes usually equal in position, or occasionally with upper slightly anterior to lower eye. Anterior and medial surfaces of eyes without scales; narrow interorbital region with 3–8 rows of small ctenoid scales. Pupillary operculum absent. Dorsal-fin origin far forward, usually with first dorsal-fin ray slightly anterior to vertical through anterior margin of upper eye, occasionally first dorsal-fin ray reaching only to vertical through anterior margin of upper eye; predorsal length short. Scales absent on blind sides of dorsal- and anal-fin rays. Pelvic fin short; longest pelvic-fin ray, when extended posteriorly, usually reaching base of first anal-fin ray. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anus, or occasionally extending posteriorly almost to anal-fin origin (membrane torn in most specimens). Caudal fin short. Scales large, strongly ctenoid on both sides of body.

**Pigmentation (Fig. 48)** Body coloration similar for both sexes. Ocular surface uniformly light to dark brown, with 7–20 (typically 7–10), complete and incomplete, darker brown crossbands. Crossbands begin at posterior margin of operculum and continue at irregular intervals to base of caudal fin. Crossbands do not continue onto dorsal and anal fins. Specimens lacking definite crossbands usually with irregular diffuse dark brown markings on ocular surface. Outer surface of ocular-side opercle with small, sometimes rounded, dusky blotch, usually only slightly obvious against general background coloration. Inner linings of opercles and isthmus on both sides of body pigmented. Both lips on ocular side usually lightly spotted; occasionally with light band of pigment on upper lip. Blind side off-white with yellowish pigment on body near bases of dorsal- and anal-fin rays. Peritoneum unpigmented.

Fin rays in dorsal and anal fins usually dark brown or black, except for whitish distalmost tips. Fins without distinctive spots or blotches. Anterior sections of dorsal and anal fins with fin rays and connecting membranes pale or only lightly pigmented, fin rays and membranes becoming progressively darker posteriorly; posterior two-thirds of fins almost completely dark brown or black. Some specimens with series of two to four lightly pigmented fin rays alter-

**Table 29**

Morphometrics for holotype (USNM 55573) and 30 additional specimens of *Symphurus jenynsi*, including holotypes of *S. bergi* (USNM 76852) and *S. meridionalis* (MCN 2401), herein regarded as junior subjective synonyms. (Abbreviations defined in methods section; SL is expressed in mm; measurements 2 to 14 are thousandths of SL; 15 to 21 are thousandths of HL; *n* = no. of specimens measured).

| Character | *jenynsi* holotype | *bergi* holotype | *meridionalis* holotype | *n* | Range | Mean | SD |
|---|---|---|---|---|---|---|---|
| 1. SL | 168 | 174 | 173 | 31 | 60.6–319.0 | 150.0 | 50.33 |
| 2. BD | 255 | 292 | 286 | 31 | 231–328 | 256.8 | 19.75 |
| 3. PDL | 27 | 31 | 39 | 31 | 26–51 | 38.8 | 5.70 |
| 4. PAL | 171 | 197 | 187 | 31 | 161–239 | 202.9 | 17.85 |
| 5. DBL | 973 | 969 | 961 | 31 | 949–974 | 961.2 | 5.70 |
| 6. ABL | 796 | 816 | 813 | 31 | 753–840 | 793.3 | 22.34 |
| 7. PL | 48 | — | 58 | 31 | 48–72 | 57.8 | 5.52 |
| 8. PA | — | — | 41 | 31 | 30–74 | 49.4 | 10.93 |
| 9. CFL | 73 | — | 81 | 31 | 61–111 | 83.5 | 10.93 |
| 10. HL | 155 | 156 | 166 | 31 | 133–202 | 170.6 | 12.97 |
| 11. HW | 201 | 206 | 204 | 31 | 185–231 | 203.4 | 10.68 |
| 12. POL | 107 | 112 | 74 | 31 | 69–140 | 109.1 | 14.92 |
| 13. UHL | 120 | 127 | 130 | 31 | 116–147 | 132.0 | 8.10 |
| 14. LHL | 89 | 98 | 86 | 31 | 72–101 | 86.2 | 7.22 |
| 15. POL | 690 | 717 | 442 | 31 | 442–717 | 638.3 | 60.73 |
| 16. SNL | 199 | 191 | 265 | 31 | 191–269 | 237.2 | 18.06 |
| 17. UJL | 199 | 217 | 237 | 31 | 191–268 | 231.0 | 13.89 |
| 18. ED | 84 | 88 | 77 | 31 | 74–95 | 84.4 | 5.41 |
| 19. CD | 230 | 239 | 286 | 31 | 164–370 | 249.6 | 35.61 |
| 20. OPLL | 249 | — | 286 | 31 | 177–329 | 267.6 | 31.45 |
| 21. OPUL | 199 | — | 216 | 31 | 185–308 | 234.9 | 29.41 |
| 22. UHL | 774 | 812 | 784 | 31 | 672–1016 | 777.9 | 79.47 |
| 23. LHL | 575 | 629 | 516 | 31 | 434–642 | 507.2 | 40.45 |

nating with similar number of darkly pigmented fin rays along most of length of dorsal and anal fins. Caudal fin uniformly dusky, dark brown, or black throughout nearly entire length, distalmost tips of caudal-fin rays, however, whitish.

**Size and sexual maturity (Fig. 9G)** *Symphurus jenynsi* is the largest symphurine tonguefish, attaining a maximum length of ca. 319 mm. Menezes and Benvegnú (1976) reported several individuals exceeding 250 mm and noted that this is the largest tonguefish occurring in Brazilian waters. Of 64 specimens for which size-related life history information was available, 35 were males, 22 females, and 7 were juveniles (sex unknown). Females (58.1–250 mm) were somewhat larger than males (32.2–200 mm). Sex of the largest specimen (319 mm) examined could not be determined because of degraded internal organs. Based on reproductive stages of females, sexual maturity occurs at a relatively large size in *S. jenynsi*. Although no gravid females were found, 17 females larger than 115 mm were mature with elongate ovaries. Only one (224 mm) contained developing ova. Ovaries of the six smallest females (58.1–87.7 mm) were immature and just undergoing elongation.

**Geographic distribution (Fig. 49)** In temperate waters of the western South Atlantic (Menezes and Benvegnú, 1976; Menni et al., 1984) from southeastern Brazil (usually south of 28°S latitude) to about El Rincon central Argentina (ca. 39°33'S; INIDEP uncat. collections [Diaz de Astarloa[2]]), just south of Bahia Blanca. Only two lots examined were collected north of Florianopolis, Brazil (28°21'S): one at 26°14'S (off Parana), the other at 22°27'S (near Cabo Frio). Lahille (1939) reported collecting some *S. jenynsi* from off San Blas, Argentina (40°30'S). The majority of specimens examined in the present study were caught between Santa Catarina and Uruguay.

**Bathymetric distribution** Although *S. jenynsi* has been collected from a relatively wide range of depths

[2] Diaz de Astarloa, J. 1995. Departamento de Ciencias Marinas, Facultad de Ciencias, Exactas y Naturales, Universidad Nacional de Mar del Plata, Funes 3350, (7600) Mar del Plata, Argentina. Personal commun.

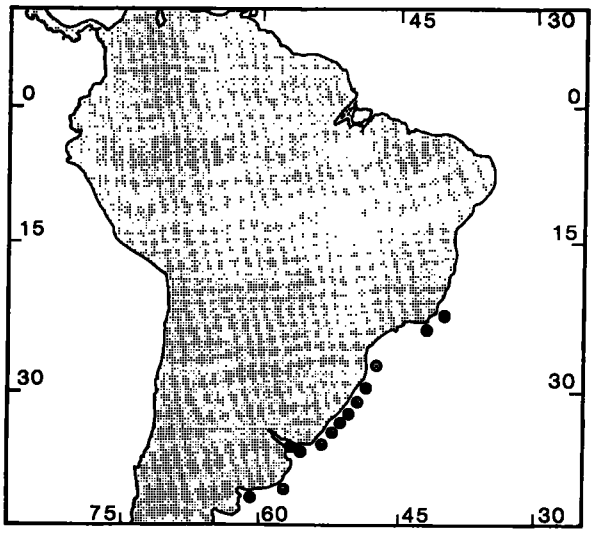


**Figure 49**
Geographic distribution of *Symphurus jenynsi* based on material examined (discussion of geographic distribution appears in species account).

(17–190 m), it is most frequently taken on mud substrates between 10 and 60 m (Menezes and Benvegnú, 1976; Haimovici et al., 1996). The majority of specimens examined in this study (46/51, 90%) were captured between 12 and 50 m (Table 10). Menezes and Benvegnú (1976) found both small (16–30 mm) and adult specimens inhabiting similar depths on the inner continental shelf. Larvae are sometimes transported into coastal lagoons; Muelbert and Weiss (1991) reported that about 0.02% of the ichthyoplankton in Patos Lagoon, Brazil, was larval *S. jenynsi*. Juveniles and small adults have also been collected in channel areas in estuarine and coastal lagoon systems (Chao et al., 1982; Volcker and Andreata, 1982; Chao et al., 1985).

**Ecology** Polychaetes are the primary food item of *S. jenynsi*, but other benthic prey, including gammaridean amphipods, cumaceans, and mysids are also eaten (Kawakami, 1976, Kawakami and Amaral, 1983). Wakabara et al. (1982) reported that *S. jenynsi* consumed eight different species of epibenthic and infaunal amphipods. They categorized this species as a "smell and touch" type of predator, noting a lack of preference among epi- or infaunal amphipod prey items consumed. Little else is known concerning the ecology of this species.

**Remarks** Jenyns (1840–42:140) provided only a brief description of a tonguefish, *Plagusia* sp. (BMNH 1933.2.28:4), collected by the *Beagle* from off San Blas, Patagonia. He compared his specimen with the description of *Plagusia brasiliensis* (=*Symphurus tessellatus*, this study) but did not formally name the species. The specimen (ca. 165 mm) has a 1-4-3 ID pattern, 59 total vertebrae, and approximately 10 caudal-, 113 dorsal-, and 96 anal-fin rays (from a radiograph), agreeing with those counts for *S. jenynsi*.

Several discrepancies exist between meristic and morphological characters reported in Evermann and Kendall's (1907) original description of *S. jenynsi* and measurements that I made on the holotype. Evermann and Kendall listed the counts for the holotype as follows: dorsal-fin rays 108; anal-fin rays 93; caudal-fin rays 12. Counts taken from a radiograph of the holotype are dorsal-fin rays 110, anal-fin rays 95, and caudal-fin rays 10. In the original description, the longitudinal scale count was listed as approximately 120, but there was no indication of how that count was made. Examination of the holotype reveals ca. 115 longitudinal scales, ca. 45 transverse scales, and 21 head scales. Menezes and Benvegnú (1976) reported 106–124 longitudinal scale rows in their specimens of *S. jenynsi*. Although Evermann and Kendall also stated that teeth were absent on the ocular-side upper jaw of the holotype, a small patch of teeth is present on the anterior margin of the ocular-side premaxilla.

In 1916, Thompson described *S. bergi* from the Montevideo region with features similar to those found in *S. jenynsi*. In his description of *S. bergi* he stated that in comparing the specimens at hand with the description of *Symphurus jenynsi* Evermann and Kendall from the same locality, the following differences are found: only in a single case does the number of dorsal-fin rays fall as low as 109, none being 108; the scales in longitudinal series vary from 100 to 114, and in no case reach 120; there are, distinctly, teeth on the margin of the ocular-side upper jaw, which is stated by Evermann and Kendall to be without teeth; the eyes are far from being "on the same line," the lower beginning below the end of the anterior third of the upper, instead of "slightly advanced"; and finally, there are not 12, but 10 caudal-fin rays. The differences are obviously great, although "the general appearances are similar." Apparently, Thompson did not actually examine the holotype of *S. jenynsi*.

Ginsburg (1951) examined types of both nominal species and concluded that they were conspecific. Subsequent authors (Menezes and Benvegnú, 1976; Lema et al., 1980; Lucena and Lucena, 1982) have also considered there to be only one species among material identified as *S. jenynsi* and *S. bergi*. Examination of radiographs of specimens, including holotypes of both nominal species as well as the entire paratype series of *S. bergi*, did not reveal any osteological differences, and the specimens have simi-

lar ID patterns and overlapping vertebral counts. These data support conclusions arrived at by earlier workers that only one valid species should be recognized among this material, *S. jenynsi* Evermann and Kendall.

In 1977, another nominal species featuring high vertebral, and dorsal- and anal-fin ray counts was described from this region when Lema and Oliveira described *S. meridionalis* from three specimens from off southern Brazil. Purported diagnostic differences between this taxon and *S. jenynsi* were presence of 11 caudal-fin rays (vs. 10 in *S. jenynsi*) and differences in eye diameter. Examination of the holotype and paratypes of *S. meridionalis* and radiographs of these types revealed that all three specimens possess 10 caudal-fin rays, not 11. Eye size for *S. jenynsi* measured in the present study ($n$=30) varied from 7.4 to 9.5% HL. Eye sizes for the three type specimens of *S. meridionalis* are also within this range. Therefore, on the basis of overall similarities in ID patterns, body shapes, meristic and morphometric features, pigmentation patterns, and relative body sizes, I conclude that *S. meridionalis* Lema and Oliveira is conspecific with *S. jenynsi*.

In another, more recent study, Volcker and Andreata (1982) also reported that *S. jenynsi* had 11 caudal-fin rays. This count is not supported by findings reported in Menezes and Benvegnú (1976) or results of this study (Table 3), where the typical count for this species is 10 caudal-fin rays.

**Comparisons** Except for similarities in caudal-fin ray number, no other shallow-water, western Atlantic species has total vertebral or fin-ray counts overlapping those observed in *S. jenynsi* (see Tables 4–7). Only some meristic features of *S. tessellatus*, which may occur sympatrically with *S. jenynsi* and *S. oculellus* (which is allopatric), approach those observed for *S. jenynsi*. Despite these superficial similarities, *S. jenynsi* is readily distinguished from both in having fewer caudal-fin rays (10 vs. 12 in these others) and by differences in other meristic features (less than 107 dorsal-fin rays, less than 90 anal-fin rays, and 55 or fewer total vertebrae in these other species). Although *S. jenynsi* sometimes has a dusky blotch on the outer surface of the ocular-side opercle, this pigment is quite different from the conspicuous black spot present on the outer opercle in *S. tessellatus* and *S. oculellus*. *Symphurus jenynsi* lacks the small scales covering the basal two-thirds of blind sides of most dorsal- and anal-fin rays in *S. tessellatus* (larger *S. jenynsi* occasionally have several small scales extending onto fin rays, but only on a few fin rays in the posteriormost region of the dorsal and anal fins).

Other Atlantic tonguefishes with meristic features similar to those of *S. jenynsi* include three deepwater species, the western Atlantic, *S. nebulosus*, and two eastern Atlantic species, *S. vanmelleae* and *S. ligulatus*. *Symphurus jenynsi* differs from these relatively small, bathyal species in the following characters (those of *S. jenynsi* listed first): caudal-fin ray count (10 vs. 12 in *S. vanmelleae;* 14 in *S. ligulatus* and *S. nebulosus*); unpigmented peritoneum (vs. black in these others); and ID pattern (1-4-3-2-2 vs. 1-2-2-2-1 or 1-2-2-1-2 in *S. vanmelleae*; 1-2-2-2-2 in *S. ligulatus* and *S. nebulosus*). These elongate, deep-sea tonguefishes also have relatively thin bodies and seldom attain sizes greater than 140 mm (usually smaller than 110 mm), whereas *S. jenynsi* is a thick-bodied species reaching 300 mm or larger.

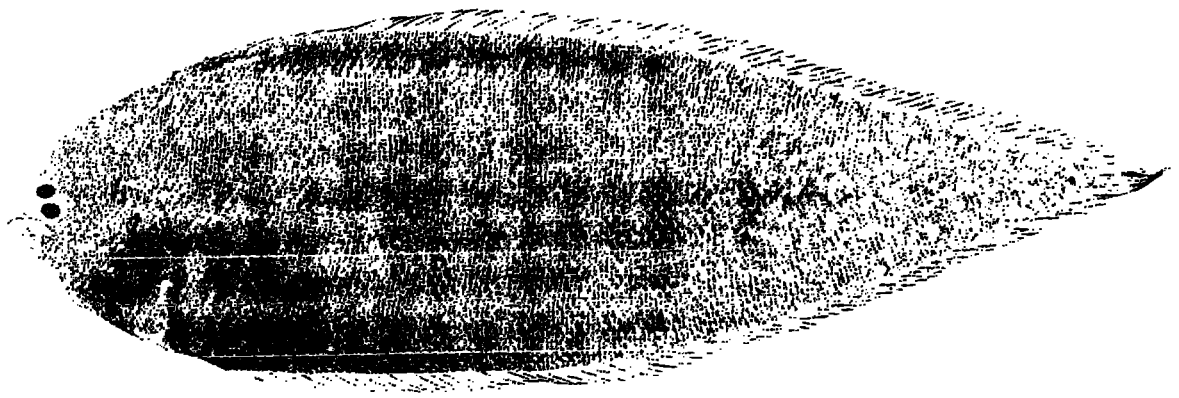

**Figure 50**
*Symphurus plagiusa* (Linnaeus), USNM 316745, 99.0 mm SL, James River, Virginia.

### *Symphurus plagiusa* (Linnaeus, 1766) (Figs. 9B, 50–51; Tables 1–10, 30–31) Blackcheek tonguefish

*Pleuronectes plagiusa* Linnaeus, 1766:455 (original description; Charleston, South Carolina).

*Plagusia fasciata* DeKay, 1842:304 (original description based on unpublished illustration by Holbrook; South Carolina). Storer, 1846:480 (after Holbrook).

*Glossichthys plagiusa.* Gill, 1861:51 (new combination).

*Apionichthys plagiusa.* Günther, 1862:490 (based on misinterpretation of Linnaeus' *Pleuronectes plagiusa*).

*Plagusia plagiusa.* Gill, 1864:215 (substitute for *Pleuronectes* Linnaeus). (*Plagusia* unavailable, preoccupied in Crustacea).

*Aphoristia ornata* (not of Lacepède, 1802). Goode and Bean, 1885a:196 (substitution name based on misinterpretation of collection information associated with Linnaean holotype).

*Aphoristia fasciata.* Jordan, 1885:395 (following Goode and Bean's (1885b) rejection of Linnaean holotype; suggested *Aphoristia* (=*Plagusia*) *fasciata* Holbrook in DeKay, 1842, as proper senior synonym).

*Aphoristia plagiusa.* Jordan, 1886a:53 (synonymized with *Aphoristia ornata* Poey (=*S. tessellatus*) from Cuba). Bean, 1891:83 (Chesapeake Bay, Virginia).

*Symphurus plagiusa.* Jordan and Goss, 1889:325 (synonymy, in key; discussion of nomenclature). Jordan and Evermann, 1898:2710 (synonymy, in key; counts, measurements, distribution). Evermann and Marsh, 1900:332 (in key; comparison with *S. plagusia* Bloch and Schneider). Linton, 1905:330, 415 (North Carolina; food habits, parasites). Hildebrand and Schroeder, 1928:177 (Chesapeake Bay; synonymy, redescription, figure; brief ecological notes). Hildebrand and Cable, 1930:476 (in part, more than one species included in description) (North Carolina; description of larval stages). Gunter, 1945:88 (Texas; temperature, salinity ranges; size distribution). Chabanaud, 1949:87 (compared with *S. plagusia*). Ginsburg, 1951:195; (in part, includes specimens of *S. tessellatus* from Cuba) (New York to Yucatan Peninsula, Mexico; redescription, counts, measurements, photograph). Siebenhaler, 1952:96 (eastern Florida, presence in shrimp bycatch). Reid, 1954:67 (Cedar Key, Florida; seasonal occurrence; temperature, salinity records; substrate preference; food habits). Hildebrand, 1954:297 (Texas; relative abundance on brown shrimp grounds). Hildebrand, 1955:204 (Gulf of Campeche, Mexico; occurrence on pink shrimp grounds). Simmons, 1957:188 (Laguna Madre, Texas; occurrence, salinity distribution). Briggs, 1958:298 (listed, Florida; geographic distribution New York to Argentina (40°S) and Gulf of Mexico). Springer and Woodburn, 1960:87 (Tampa Bay, Florida; seasonal occurrence; ecological distribution; diet). Dawson, 1962:138 (anomalies). de Sylva et al., 1962:130 (Delaware River estuary; absent in shore zone collections; rare in ichthyoplankton collections). Dawson, 1965:279 (Gulf of Mexico;

length-weight relationship). Moe and Martin, 1965:146 (off Tampa Bay, Florida; seasonal occurrence, spawning seasonality). Roessler, 1965:314 (Biscayne Bay, Florida; abundance in trawl survey). Anderson, 1968:13 (southern U.S. Atlantic coast; occurrence in shrimp bycatch). Böhlke and Chaplin, 1968:226 (Eleuthera Island and Great Bahama Bank, Bahamas; in key, description, figure). Fox and Mock, 1968:47 (Barataria Bay, Louisiana; abundance in seine collections). Jorgenson and Miller, 1968:6 (Georgia; standard length to total length conversions). Struhsaker, 1969:298 (continental shelf southeastern United States; distribution, relative abundance). Dahlberg, 1970a:260 (Georgia; reversed specimen). Dahlberg, 1970b:95 (Georgia; abnormalities). Staiger, 1970:67 (Straits of Florida; one specimen, 132 m on Pourtalès Terrace). Swingle, 1971:65 (Alabama estuaries; seasonal occurrence; ecological distribution; relative abundance). Franks et al., 1972:124 (Mississippi; size, seasonal, depth information). Topp and Hoff, 1972:79 (west Florida shelf; in key, synonymy, counts, figure; distribution; life history information). Dorfman et al., 1974:7 (first estuarine record for New Jersey). Stickney and Shumway, 1974:782 (cellulase activity). Swingle and Bland, 1974:48 (Alabama; coastal watercourses; ecological distribution). Shealy et al. 1974:127 (South Carolina estuaries; relative abundance; size distribution; ecological occurrence; length-frequency relationship). LeGrande, 1975:516 (karyotype). Menezes and Benvegnú, 1976:145 (compared with *S. trewavasae*). Olney and Grant, 1976:229 (lower Chesapeake Bay; description of early larval stages). Keiser, 1976:22, 36 (South Carolina; seasonal abundance, size range, contribution to shrimp bycatch). Stickney, 1976:202 (Georgia; food habits, nematode infections). Walls, 1976:393 (northern Gulf of Mexico; counts, measurements, pigmentation, figure). Chittenden and Moore, 1977:111 (occurrence, relative abundance at 110-m depth contour, western Gulf of Mexico). Ogren and Brusher, 1977:101 (St. Andrew Bay, Florida; seasonal occurrence, relative abundance; size distribution). Wilk et al., 1977:52 (New York Bight). Naughton and Saloman, 1978:46 (nearshore zone, St. Andrews Bay, Florida; relative abundance, seasonal occurrence). Sansón et al., 1978:11 (rare, Cuba). Wang and Kernehan, 1979:315 (Delaware estuaries; distribution; summary of early life history information with figures). Bozeman and Dean, 1980:92 (South Carolina; seasonal occurrence and relative abundance in intertidal creek). Lema et al., 1980:43 (discussion of erroneous reports from south Atlantic). McCaffrey, 1981:207 (continental shelf northeastern Gulf of Mexico; occasional element inner shelf fish fauna). Darcy and Gutherz, 1984:104 (continental shelf west Florida; rarely caught in trawls). Zimmerman and Minello, 1984:427 (Galveston Bay, Texas; seasonal occurrence vegetated and nonvegetated habitats). Cowan and Birdsong, 1985:51 (Virginia, seaside estuary; rarely taken in trawls). Deegan and Thompson, 1985:41 (Louisiana estuaries). Ross and Epperly, 1985:217 (Pamlico Sound, North Carolina). Subrahmanyam, 1985:197 (minor component of ichthyofauna, St. Marks River estuary, Florida). Wheeler, 1985:71 (clarification of holotype status). Yáñez-Arancibia et al., 1985:483 (southern Gulf of Mexico). Castro-Aguirre et al., 1986:167 (Tuxpam-Tampamachoco estuarine lagoon, Veracruz, Mexico). Gartner, 1986:141 (anomalies). Yáñez-Arancibia and Sánchez-Gil, 1986:39, 125 (southern Gulf of Mexico continental shelf; abundance, distribution). Fuentes Mata et al., 1989:261 (first record, Laguna de Sontecomapan, Veracruz, Mexico). Wenner and Sedberry, 1989:32 (coastal habitats southeastern United States; seasonal distribution, relative abundance, length-frequency information). Webster et al.[3] (South Atlantic Bight; ranked 28th in abundance of 244 taxa in trawl sampling). Brown-Peterson and Eames, 1990:231 (Indian River Lagoon, Florida; association with spoil islands). Norcross and Hata, 1990:451 (lagoons, saltmarshes eastern shore, Virginia; seasonal distribution, relative abundance of juveniles). Beatty et al.[4] (South Atlantic Bight; ranked 24th in abundance of 223 taxa in trawl sampling). Grimes and Finucane, 1991:115 (larvae in Mississippi River discharge plume). Hook, 1991:133 (South Bay, Texas). Kobelkowsky, 1991:88 (Lagunas Pueblo Viejo, Veracruz, Mexico). Reichert and Van der Veer, 1991:382 (Georgia estuary; juvenile settling, seasonal abundance, growth, population dynamics). Able, 1992:7 (New Jersey; rare in marine waters). Munroe, 1992:371, 382 (ID pattern; geographic, bathymetric distributions). Rakocinski et al., 1992:140 (Louisiana; salt marsh; distribution; microhabitat). Baltz et al., 1993:115 (Louisiana; salt marsh; distribution; microhabitat). Bonzek et al., 1993:40 (Chesapeake Bay, Virginia; seasonal distribution, abundance). Hettler and

[3] Webster, R. P., H. R. Beatty, and E. L. Wenner. 1989. Results of trawling efforts in the coastal habitat of the South Atlantic Bight, FY-1989. Final Rep. to SEAMAP-SA, South Carolina Marine Resources and Research Institute, S.C. Wildl. and Mar. Res. Dep., Charleston, SC, 66 p.

[4] Beatty, H. R., J. M. Boylan, R. P. Webster, and E. L. Wenner. 1991. Results of trawling efforts in the coastal habitat of the South Atlantic Bight, FY-1991. Final Rep. to SEAMAP-SA, South Carolina Marine Resources and Research Institute, S.C. Wildl. and Mar. Res. Dep., Charleston, SC, 52 p.

Barker, 1993:168 (North Carolina; seasonal distribution, abundance of larvae at two barrier island inlets). Schwartz et al. 1993:108 (North Carolina; abundance in dredged canal system at barrier island). ?Van der Veer et al., 1994:456 (inshore habitats, Puerto Rico; juvenile occurrence, abundance and seasonality of settlement). Darovec, 1995:89 (distribution on west Florida shelf). Toepfer and Fleeger, 1995:242 (Louisiana estuary; diets of juveniles). Franks et al., 1996:377 (north central Gulf of Mexico; prey item of juvenile cobia, *Rachycentron canadum*). Meyer and Franks, 1996:164 (north central Gulf of Mexico; food item of adult cobia, *Rachycentron canadum*). Allen and Baltz 1997:91 (Barataria Bay, Louisiana; seasonal distribution and abundance).

*Symphurus plagusia* (not of Schneider, in Bloch and Schneider, 1801). Chabanaud, 1939:26 (American Atlantic and Gulf coasts).

?*Symphurus plaguisa*. Evseenko, 1982:135 (larva in Gulf Stream waters off Nova Scotia).

**Misidentifications** Regan, 1914:23 (Brazil; specimens were *S. trewavasae*). Chabanaud, 1948b:134 (Louisiana; reversed specimen, actually *S. civitatium*). Lazzaro, 1973:245 (Argentina; probably *S. trewavasae*). Roux, 1973:176 (Brazil; probably *S. trewavasae*). Lema and Oliveira, 1977:7 (South Brazil; probably *S. trewavasae*). ?Guitart, 1978:729 (Cuba; specimen figured appears to be *S. tessellatus*). Lema et al., 1980 (South Brazil; possibly based on *S. trewavasae*). Gaspar-Dillanes and Espinosa-Pérez, 1989:252 (inner continental shelf, Quintana Roo, Mexico; actually *S. diomedeanus*). Séret and Andreata, 1992:94 (two specimens from continental shelf South Brazil; actually *S. ginsburgi*).

**Diagnosis** *Symphurus plagiusa* is distinguished from all congeners by the combination of predominant 1-4-3 ID pattern; 10 caudal-fin rays, 4 hypurals; 81–91 dorsal-fin rays; 66–75 anal-fin rays; 44–49 total vertebrae; 76–86 scales in longitudinal series; absence of well-developed pupillary operculum (small remnant of pupillary operculum may be present); unpigmented peritoneum; mostly incomplete row of teeth partially covering margin of ocular-side dentary; ocular-side premaxilla usually lacking teeth altogether (occasionally with few teeth on anterior margin of premaxilla); a fleshy ridge on posterior region of ocular-side lower jaw; scales present on both blind and ocular sides of posterior rays of dorsal and anal fins; absence of membrane ostia in dorsal and anal fins; ocular surface ranging from uniformly dull tannish to dark brown without crossbands to light or dark brown with sharply contrasting dark brown crossbands but always without pigmented blotch on caudal region of ocular surface; blind side without pepper-dot pigmentation; usually with a conspicuous black spot on outer surface of upper angle of ocular-side opercle; dorsal, anal, and caudal fins without conspicuous spots or blotches.

**Description** A relatively large species attaining maximum lengths of ca. 175 mm SL. ID pattern usually 1-4-3 (85/141 specimens), less frequently 1-4-2 (24/141) or 1-3-3 (22/141), rarely 1-5-2 (Table 2). Caudal-fin rays usually 10 (132/139), less frequently 9 or 11 (Table 3). Dorsal-fin rays 81–91, usually 84–90 (Table 4). Anal-fin rays 66–75 (Table 5). Total vertebrae 44–49, usually 45–48 (141/143) (Table 6). Hypurals 4 (143/143). Longitudinal scale rows 76–86 (Table 7). Scale rows on head posterior to lower orbit 15–19, usually 17–18 (Table 8). Transverse scales 30–39 (Table 9).

Proportions of morphometric features presented in Table 30. Body moderately deep; maximum depth in anterior one-third of body; body depth tapering gradually posterior to midpoint. Preanal length much smaller than body depth. Head moderately long and wide, somewhat narrower than body depth. Head length shorter than head width (HW:HL 1.07–1.46,

**Table 30**

Morphometrics for holotype (LS 124) and 30 other specimens of *Symphurus plagiusa*. (Abbreviations defined in methods section; SL is expressed in mm; characters 2 to 14 are expressed in thousandths of SL; 15 to 21 in thousandths of HL; *n* = no. of specimens measured.)

| Character | Holotype | *n* | Range | Mean | SD |
|---|---|---|---|---|---|
| 1. SL | 122.1 | 30 | 64.7–171.6 | 103.8 | 33.72 |
| 2. BD | 322 | 30 | 283–326 | 304.7 | 8.89 |
| 3. PDL | — | 30 | 22–51 | 38.4 | 6.23 |
| 4. PAL | — | 30 | 140–243 | 199.7 | 27.69 |
| 5. DBL | — | 30 | 933–979 | 960.6 | 11.82 |
| 6. ABL | 790 | 30 | 727–826 | 787.6 | 20.52 |
| 7. PL | — | 29 | 51–79 | 67.4 | 6.80 |
| 8. PA | — | 30 | 36–75 | 54.7 | 9.51 |
| 9. CFL | — | 30 | 94–141 | 106.6 | 9.65 |
| 10. HL | 162 | 30 | 145–210 | 192.5 | 13.73 |
| 11. HW | 210 | 30 | 212–265 | 234.9 | 14.57 |
| 12. POL | 84 | 30 | 111–145 | 128.9 | 7.93 |
| 13. UHL | 115 | 30 | 147–182 | 167.2 | 10.01 |
| 14. LHL | 93 | 30 | 91–123 | 102.5 | 7.89 |
| 15. POL | 515 | 30 | 619–842 | 671.8 | 39.31 |
| 16. SNL | 227 | 30 | 194–247 | 218.2 | 16.35 |
| 17. UJL | 242 | 30 | 180–242 | 202.8 | 14.83 |
| 18. ED | 101 | 30 | 83–126 | 101.6 | 9.81 |
| 19. CD | 136 | 30 | 213–391 | 278.7 | 39.81 |
| 20. UHL | 707 | 30 | 734–1046 | 871.8 | 78.06 |
| 21. LHL | 571 | 30 | 436–707 | 535.2 | 58.15 |

$\bar{x}$=1.2). Lower head lobe width slightly less than postorbital length; considerably narrower than upper head lobe. Snout long and somewhat rounded; covered with small ctenoid scales. Anterior nostril on ocular side short, when depressed posteriorly, usually falling just short of anterior margin of lower eye. Dermal papillae well developed on snout, chin, and dorsal portion of head at dorsal-fin base on blind side; larger specimens with dermal papillae extending onto snout of ocular side of body. Jaws relatively short; maxilla extending posteriorly almost to vertical through middle of lower eye, occasionally only reaching vertical through anterior margin of pupil of lower eye. Ocular-side lower jaw with fleshy ridge near posterior margin. Teeth well developed on blind-side jaws. Ocular-side dentary usually with single, mostly incomplete, row of slender teeth along margin; ocular-side premaxilla usually lacking teeth altogether, occasionally with small number of slender teeth on marginal portion of premaxilla anterior to vertical through base of anterior nostril. Chin depth usually slightly larger than snout length. Lower eye small; eyes usually equal in position, or occasionally upper slightly in advance of lower eye. Anterior and medial surfaces of eyes not covered with scales; usually 1–3 small, ctenoid scales in narrow interorbital region. Pupillary operculum absent (occasional specimens with upper side of iris with irregular margin that may be remnant of small, poorly developed, pupillary operculum). Dorsal-fin origin usually equal to vertical through anterior margin of pupil of upper eye, occasionally with first dorsal-fin ray reaching vertical anterior to anterior margin of upper eye; predorsal length short. Blind sides of dorsal- and anal-fin rays (especially in posterior region of fins and in larger specimens) with single row of small, well-developed ctenoid scales extending from base to point about three-fourths length of fin ray. Larger specimens also with row of small, well-developed ctenoid scales extending from base to about three-fourths length of fin rays on ocular side of body. Pelvic fin moderately long; longest pelvic-fin ray, when extended posteriorly, usually reaching base of first anal-fin ray. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anus, or occasionally extending posteriorly almost to base of anal-fin origin (membrane torn in most specimens). Caudal fin short. Scales large, strongly ctenoid on both sides of body.

**Pigmentation (Fig. 5O)** Body coloration similar for both sexes. Ocular surface uniformly dull tannish to dark brown with or without crossbands, or light to dark brown with sharply contrasting dark brown crossbands. Individuals from habitats with light-colored substrates generally with whitish ocular surface, with or without crossbands. Crossbands highly variable in number and degree of development but not continued onto dorsal and anal fins. Crossbands usually nearly completely continuous across body; those at midbody region often interrupted in midlateral region; crossbands relatively narrow covering only 3–5 scale rows. Specimens lacking crossbands with variable number of very dark, small specks scattered over ocular surface. Majority of larger specimens with large, conspicuous, black spot on upper lobe of ocular-side opercle (usually faint or absent in smaller specimens; especially evident in recently preserved material). Inner linings of opercles and isthmus on both sides of body heavily pigmented. Gill filaments with conspicuous median line of dark pigment. Ocular-side upper lip with slight pigment band; ocular-side lower lip frequently spotted, but usually without definite pigment band. Blind side uniformly creamy white; occasional specimens with band of yellow pigment on blind side along body at bases of dorsal and anal fins. Peritoneum unpigmented.

Dorsal and anal fins faintly or moderately dusky throughout their lengths, but without conspicuous spots or blotches. Dorsal- and anal-fin rays uniformly pigmented along their lengths. Membrane covering fin rays usually darker than membrane between fin rays and clearly outlining each fin ray. Caudal fin dusky throughout length, without spots or blotches.

**Size and sexual maturity (Fig. 9B)** *Symphurus plagiusa* attains a maximum standard length of ca. 174 mm (Moe and Martin, 1965). The largest specimen examined in the present study was 171 mm, but most were 120–150 mm. Of 568 fish examined, only about 4% exceeded 150 mm. Maximum total lengths of ca. 210 mm were reported for *S. plagiusa* collected on the continental shelf in the southern Gulf of Mexico and off South Carolina, respectively (Yáñez-Arancibia and Sánchez-Gil, 1986; Wenner and Sedberry, 1989). Shealy et al. (1974) provided information on length-frequency relationships for this species; Jorgenson and Miller (1968) derived formulae for converting standard length and total length measurements; and Dawson (1965) calculated a length-weight formula for this species in the Gulf of Mexico.

Among 191 specimens examined for life history information, were five fish (27.0–62.1 mm) for which sex was indeterminate, 64 were males (41.0–159 mm), and 122 (34.0–157 mm) were females. No significant differences in sizes were observed between males and females. Based on reproductive stages of females, the estimated sizes at which *S. plagiusa* matures are between 85 and 95 mm. Of 85 mature

females (85.0–157 mm), only six were smaller than 90 mm and all females larger than 100 mm were mature. Twenty-four females (94.4–157 mm) were gravid, with all but three of these exceeding 110 mm. The smallest gravid females measured 94.4, 103.0, and 103.2 mm. Thirty-seven immature females ranged in size from 34.0 to 98.1 mm. Most were smaller than 80 mm, whereas only five exceeded 85 mm.

**Geographic distribution (Fig. 51)** Shallow neritic and estuarine waters of the Atlantic coast of the United States from New York Bight and Long Island Sound, south through the Florida Keys, through the northern Gulf of Mexico to Campeche Peninsula, Mexico (Ginsburg, 1951; Hildebrand, 1955; Topp and Hoff, 1972; Castro-Aguirre et al., 1986; Fuentas Mata et al., 1989; Kobelkowsky, 1991), the Bahamas (Böhlke and Chaplin, 1968), and Cuba (Sansón et al., 1978; this study).

The geographic center of abundance for this species, based on frequency of capture and numerical abundance, occurs in estuarine and nearshore habitats from Chesapeake Bay to southern Florida, including Florida Bay, and throughout the northern Gulf of Mexico. Captures of *S. plagiusa* north of Chesapeake Bay have been sporadic. Ginsburg (1951) examined specimens from Long Island Sound; Wilk et al. (1977) and this study (see Appendix) noted specimens from the New York Bight. Wang and Kernehan (1979:317) listed the Gulf of St. Lawrence as the northernmost extension of the geographic range for *S. plagiusa*, purportedly on the basis of information in Leim (1960). However, information in Wang and Kernehan (1979) appears to be in error.

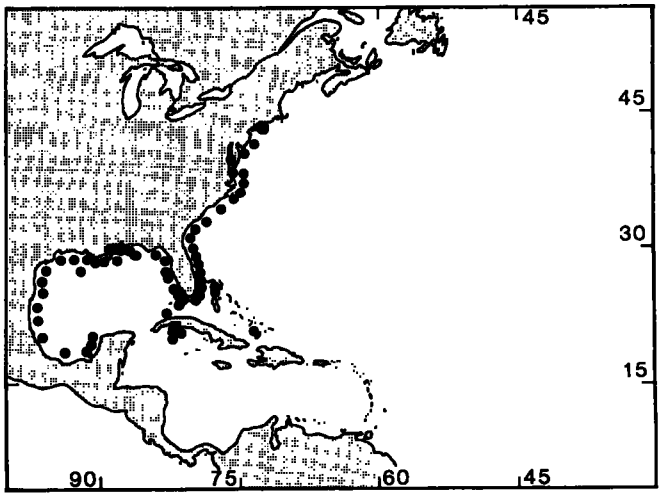


**Figure 51**

Geographic distribution of *Symphurus plagiusa* based on material examined (discussion of geographic distribution appears in species account).

Leim (1960) did not list *S. plagiusa* among unusual fishes recorded from Canadian waters, nor did Leim and Day (1959) report this species among fishes they had discussed in an earlier paper. Furthermore, subsequent compilations of information on marine fishes of Canada's Atlantic coast (Leim and Scott, 1966; Scott and Scott, 1988) have not listed *S. plagiusa* as occurring in this region.

This species was not listed among fishes occurring in New Jersey waters in studies conducted earlier this century (Fowler, 1905; 1920; 1952), and the first specimen of this species from estuarine waters of New Jersey was not reported until relatively recently (Dorfman et al., 1974). Able (1992) considered this species rare in marine waters of New Jersey. *Symphurus plagiusa* also occurs rarely in Delaware waters—only a single specimen was taken in the Delaware River by de Sylva et al. (1962), and Abbott (1878) and Fowler (1911) did not list this species for the Delaware River and Delaware Bay region. It was not listed among demersal fishes taken during seining and trawling studies of seaside bays and Delaware coastal waters (Derickson and Price, 1973; Maurer and Tinsman, 1980), but Pacheco and Grant (1965) and Campbell (1975) collected a few specimens in the Indian River estuary, and Wang and Kernehan (1979) reported collecting numerous young (16 mm and larger) on mud and mixed mud and sand substrates in the thermal plume of the Indian River Power Plant, with most specimens collected in fall and winter samples. More recent information for the Delaware Bay region (Michels[5]; Michels[6]) indicates that a small number of *S. plagiusa* are taken each year during trawling studies (usually <1% of total number of fishes trawled), but the species is uncommon there.

Farther south, Schwartz (1961; 1964) did not list this species among fishes recorded from seaside bays of southern Delaware, Maryland, and northern Virginia. Cowan and Birdsong (1985) collected only a single specimen in Wachapreague Inlet, Virginia, during the course of a one-year study, and Hildebrand and Schroeder (1928) also considered this species to be rare in waters north of Cape Hatteras. Undoubtedly, the relatively small size of *S. plagiusa* and its inaccessibility to most commercial fishing gears used in Chesapeake Bay have accounted for this species seldomly being observed in historical commercial or recreational catches from this region, because more

[5] Michels, S. F. 1993. A: Coastal finfish assessment survey, April 1, 1992–March 31, 1993, 18 p. B: Bottom trawl survey of juvenile fishes in the Delaware estuaries, 18 p. 1993 Annual Rep. for U.S. Fish Wildl. Serv. Proj. F-42-R-4. Del. Div. Fish Wildl., Dover, DE.

[6] Michels, S. F. 1992. Division of Fish and Wildlife, Richardson/Robbins Building, PO Box 1401, Dover, DE 19903. Personal commun.

recent information indicates that *S. plagiusa* is abundant in seaside estuaries behind barrier islands off the Delmarva peninsula (Norcross and Hata, 1990) where it has ranked among the ten most abundant species taken in trawls and beach seines with tickler chains. And in lower Chesapeake Bay and its lower tributaries, *S. plagiusa* has ranked sixth in numerical abundance among juvenile finfishes taken in the Bay during trawl surveys conducted over a 20-yr period (Bonzek et al., 1993).

Along southeastern and Gulf coasts of the United States and northern Mexico, *S. plagiusa* is the most common tonguefish encountered in estuarine and shallow-water environments. The southern limits of distribution for this species occur on the northwestern coast of the Yucatan Peninsula just north of Campeche (Ginsburg, 1951; Hildebrand, 1955; Castro-Aguirre et al., 1986; Fuentas Mata et al., 1989; Kobelkowsky, 1991).

Briggs (1958:298) reported that *S. plagiusa* occurred from Long Island, New York, to Argentina (40°S), but the southern portion of that reported distribution is incorrect. In addition to *S. plagiusa,* Briggs included information for *S. plagusia* and perhaps also that for *S. tesselatus and S. trewavasae.*

Beyond the North American continental margin, *S. plagiusa* has been reported from a number of localities in the Caribbean Antilles (Ginsburg, 1951; Topp and Hoff, 1972; Sansón et al., 1978; Guitart, 1978; Van der Veer et al., 1994) and coastal waters of South America (Regan, 1914; Lazzaro, 1973; Roux, 1973; Lema and Oliveira, 1977; Lema et al., 1980; Manickchand-Heileman, 1994). Several citations (Regan, 1914; Ginsburg, 1951; Lazzaro, 1973; Roux, 1973; Lema and Oliveira, 1977; Lema et al., 1980) are based on misidentifications of specimens of *S. trewavasae* (see summary in Menezes and Benvegnú, 1976) or *S. ginsburgi* (Séret and Andreata, 1992). Other purported captures of *S. plagiusa* from Caribbean localities (Jordan, 1886a:31, Jordan, 1886b:603) and South American localities have no associated voucher specimens and cannot be verified. Of specimens collected beyond coastal margins of North America and purportedly identified as *S. plagiusa*, I have seen voucher specimens of *S. plagiusa* only from the Bahamas (ANSP 101977, Eleuthera Island; ANSP 111567, 3 mi offshore Eleuthera Island; and USNM 265181, off southern Bahamas at 20°54'N, 73°33'W) and Cuba (see Appendix). *Symphurus plagiusa* apparently is uncommon in the Bahamas, as Böhlke and Chaplin (1968) noted, who took only a few specimens during extensive searches they conducted in this region.

*Symphurus plagiusa* also occurs in Cuban waters (Jordan, 1886a, Sansón et al., 1978; this study). Jordan (1886a:31) identified a tonguefish from Cuba as *Aphoristia (=Pleuronectes) plagiusa* (Linnaeus) and again (Jordan, 1886b:603) used that name in his checklist of fishes from the West Indies. Ginsburg (1951) identified two specimens collected in shallow Cuban waters as *S. plagiusa.* One specimen (USNM 37750), although it has the 10 caudal-fin rays typical for most specimens of *S. plagiusa*, has more fin rays (92 dorsal-fin rays and 78 anal-fin rays) than *S. plagiusa*; counts more typical of *S. tessellatus.* I conclude that this specimen is *S. tessellatus.* The other specimen (USNM 107365) from Siguanea Bay referred to by Ginsburg is a juvenile (61.5 mm) whose counts (caudal-fin rays 10; dorsal-fin rays 87; anal-fin rays 71; total vertebrae 46; and 74 scales in a longitudinal series), ID pattern (1-4-3), and pigmentation features, including presence of pigmentation on both sides of the isthmus, a pigmented inner lining of the ocular-side opercle, and presence of pigment (although rather faint) on the ocular-side gill filaments are all characteristic of *S. plagiusa.* However, ratios of several morphometric features expressed in thousandths of SL (BD 210; HL 218; CFL 130) or thousandths of HL (ED 119) resemble those for *S. parvus.* On the basis of similarities in meristic and pigmentation features, however, this specimen does appear to be *S. plagiusa.* Among several lots of *S. plagiusa* identified among material examined at the Instituto de Oceanologia, Havana, were seven specimens, including two mature females (one gravid) collected from both northern and southern coasts of the island. It reportedly is common on the mudflats and near grassbed habitats in the Golfo de Batabanó (Claro)[7] (Appendix). Other specimens collected from Cuba and Puerto Rico identified as *S. plagiusa* were misidentified. The specimen from Cuba identified as *S. plagiusa* and figured in Guitart (1978:729) appears to be *S. tessellatus*, and both the color description and range of fin-ray counts provided in his account of *S. plagiusa* are more similar to those of *S. tessellatus* than they are to those of *S. plagiusa.*

Van der Veer et al. (1994), using keys to coastal fishes of Georgia and nearby states (Dahlberg, 1975) as a taxonomic reference, identified juvenile tonguefishes collected from inshore habitats of Puerto Rico as *S. plagiusa.* Unfortunately, information contained in Dahlberg's book does not include all tonguefish species known from Puerto Rico. No specimens reported in Van der Veer et al. (1994) were available for examination during this study. However, among specimens from Puerto Rico that I have

[7] Claro, R. 1994. Cuban Academy of Sciences, Institute of Oceanology, Ave. 1ra. no. 18406, Rpto. Flores, Playa, C. de La Habana, Cuba. Personal commun.

identified (listed in Appendix), including five uncatalogued lots collected recently by North Carolina State University researchers from several locations in Puerto Rico listed in Van der Veer et al. (1994), none were *S. plagiusa*. These specimens were *S. plagusia*, *S. caribbeanus*, or *S. tessellatus*, common shallow-water species having widespread distribution throughout the Caribbean Antilles (Munroe, 1991). In the absence of voucher specimens, the occurrence of *S. plagiusa* in Puerto Rico is doubtful.

**Bathymetric distribution** *Symphurus plagiusa* primarily is a shallow-water species inhabiting nearshore coastal waters, coastal embayments, and estuaries (Ginsburg, 1951). Specimens examined in this study were captured at depths from <1 to 183 m (Table 10), but the majority (309/324, 95%) were collected between 1 and 30 m. Throughout the Atlantic coast region of this species' geographic range, it is usually the only tonguefish taken commonly in shallow-water embayments and estuarine environments (juvenile *S. civitatium* occasionally co-occur in Atlantic coast environments but are more abundant in Gulf of Mexico estuaries; see account for *civitatium* below) and therefore a large part of the *S. plagiusa* population is ecologically separated from other tonguefish species in this region. On the inner continental shelf where larger-size *S. plagiusa* are taken (see below), collections also frequently contain specimens of *S. civitatium* and *S. diomedeanus* (Hildebrand, 1954; this study).

*Symphurus plagiusa* undergoes ontogenetic shifts in the bathymetric environments it inhabits. All life history stages occur in nearshore and estuarine habitats, but the smallest juveniles occur in extremely shallow tidal creeks in estuarine saltmarshes (Gunter, 1945; Swingle, 1971; Shealy et al., 1974; Stickney, 1976; Ogren and Brusher, 1977; Naughton and Saloman, 1978; Reichert and Van der Veer, 1991; Baltz et al., 1993). Some newly settled juveniles have even been captured in small, intertidal tributaries (Bozeman and Dean, 1980; Rakocinski et al., 1992). As they grow, juveniles move first to deeper areas of larger estuarine creeks and rivers and then to more open and usually more saline embayments (Topp and Hoff, 1972). Baltz et al. (1993) suggested that movements of this species that are associated with increasing size may indicate ontogenetic movements to microhabitats with higher velocity water movements.

Although the majority of the *S. plagiusa* population is centered in inshore waters, the largest individuals (usually >100 mm) occur regularly in moderate depths (10–30 m) on the inner continental shelf (Struhsaker, 1969; Franks et al., 1972; Topp and Hoff, 1972; Yáñez-Arancibia and Sánchez-Gil, 1986; Wenner and Sedberry, 1989; this study). Of the *S. plagiusa* examined in the present study, most, collected in deeper waters on the continental shelf, were large individuals of over 120 mm. Larger fish (100–190 mm TL; $\bar{x}$=ca. 140 mm TL) have also been reported in the shrimp bycatch taken in coastal waters off South Carolina (Keiser, 1976). Samples of *S. plagiusa* collected in coastal waters in the South Atlantic Bight at ca. 10 m depth (Wenner and Sedberry, 1989) were almost entirely large individuals (140–210 mm TL, $\bar{x}$=140–150 mm TL), whereas smaller specimens (<100 mm TL) were unusual in trawls made at these locations. Wenner and Sedberry concluded that juveniles were not collected at deeper stations either because they occupied different habitats or because they did not recruit to the fishing gear until reaching a larger size.

Although most records of *S. plagiusa* are from waters shallower than ca. 40 m, several studies recorded this species from much greater depths. Bullis and Thompson (1965) and Franks et al. (1972) reported collecting *S. plagiusa* at 92 m, Staiger (1970) listed one specimen (62 mm) taken at 132 m on the Pourtalès Terrace (specimen not located during this study), and Chittenden and Moore (1977) listed this species among those occurring at the 110-m bathymetric contour off Louisiana and northern Texas (specimens not examined in this study). The deepest records for *S. plagiusa* examined in this study are those of one specimen (USNM 265181) taken at 183 m off the southern Bahamas (20°54'N, 73°33'W), and 25 specimens (USNM 159616) purportedly collected between 186 and 189 m (101 and 102 fm). The depth of capture for this lot is questionable, however, because coordinates for this station (RV *Silver Bay* 156, 29°04'N, 85°49'W) place it in a region where depths range between 70 and 93 m (38 and 50 fm). Because of this uncertainty, depth-of-capture data for these specimens were not included in Table 10.

**Ecology** More ecological information is available for *S. plagiusa* than for any other tonguefish. Occurrences of all postsettlement stages of *S. plagiusa*, even those taken in neritic waters, generally correspond with the distribution of substrates with a high percentage of silt or fine sand (Reid, 1954; Springer and Woodburn, 1960; Reichert and Van der Veer, 1991; Baltz et al., 1993). Preference for soft mud substrates is reflected in the almost universal occurrence of *S. plagiusa* in studied fish communities in protected waters throughout its range. In protected areas where soft substrates abound, this species is sometimes found in great abundance. Conversely, *S. plagiusa* occurs only sporadically and generally in much lower abundance in coarse sand habitats, such

as those in high energy surfzone areas (Modde and Ross, 1981), or on live-bottom areas (Topp and Hoff, 1972; McCaffrey, 1981; Darcy and Gutherz, 1984) with calcareous sands. In saltmarshes, juveniles occur where stem density of *Spartina* is low (Rakocinski et al., 1992, Baltz et al., 1993).

*Symphurus plagiusa* is the most euryhaline of North American tonguefishes, and has been recorded at salinities of 0.0–42.9‰ (Gunter, 1945; Springer and Woodburn, 1960; Tagatz,1968; Roessler, 1970; Swingle, 1971; Topp and Hoff, 1972; Shealy et al., 1974; Schwartz et al., 1981). Simmons (1957) indicated that *S. plagiusa* did not tolerate salinity much above 35‰. *Symphurus plagiusa* undergoes an ontogenetic shift in habitats in relation to salinity, with smaller juveniles occupying lower salinity regions of the estuary and larger juveniles and adults moving into higher salinity areas (Gunter, 1945; Springer and Woodburn, 1960; Swingle, 1971; Ogren and Brusher, 1977). Baltz et al. (1993) indicated that an apparent ontogenetic shift in estuarine occurrence of the species may not be a primary response to a salinity gradient (see Rakocinski et al., 1992), but rather an ontogenetic shift to higher velocity microhabitats.

From Chesapeake Bay and south through its range in the southern Gulf of Mexico, *S. plagiusa* is the most common tonguefish occurring on soft-bottom substrates and is a year-round resident in nearshore marine and estuarine waters. In fact, as Topp and Hoff (1972) noted, this species represents a significant proportion of the demersal fish community of nearly every major estuarine system through much of its range. In lower Chesapeake Bay and tributary rivers, Bonzek et al. (1993) recorded *S. plagiusa* as the sixth most abundant fish species overall in trawl surveys of primarily juvenile fishes. Here, tonguefishes, 34–204 mm TL (mean size 127 mm), were taken every month of the year and were widespread at stations along lower segments of tributary rivers and in lower Chesapeake Bay. Average catch of the species was 6.5 fish/trawl, which was second in abundance only to the hogchoker (*Trinectes maculatus*) among flatfishes.

In coastal habitats along the southeast United States, *S. plagiusa* is also very abundant (Webster et al.[3]). This species was present in all major estuarine areas and coastal regions of South Carolina sampled during a 12-month period (Shealy et al., 1974), where it ranked 13th in numerical abundance and 14th in biomass among the fishes collected. Shealy et al. (1974) considered it the most abundant tonguefish in South Carolina inshore waters, where various life history stages of *S. plagiusa* were present during every month of the year. In coastal waters of South Carolina, tonguefishes (primarily *S. plagiusa*) were reported as abundant in bycatch of penaeid shrimp fisheries from December to April and least abundant May through August and represented 2% by numbers and ranked 12th in weight of the 105 species in the fish bycatch (Keiser, 1976). At 10 m or less in nearshore environments in the South Atlantic Bight from Cape Fear, North Carolina, to St. John's River, Florida, Wenner and Sedberry (1989) recorded *S. plagiusa* as the 11th most numerous and the fifth most abundant species in biomass of all species taken during trawling. This species was widespread through the area, with occurrences at 78% of stations sampled and with fewer fish being taken in winter than for other seasons. *Symphurus plagiusa* is also listed as a year-round resident species in Georgia estuaries (Dahlberg and Odum, 1970; Hoese, 1973).

In Gulf of Mexico estuaries, *S. plagiusa* is also a common and abundant species (Springer and Woodburn, 1960; Swingle, 1971; Ogren and Brusher, 1977; Naughton and Saloman, 1978). In inshore areas of the eastern Gulf where live-bottom substrates predominate, it is less abundant. McCaffrey (1981) considered this species to be only an occasional component of the fish fauna on the inner continental shelf of the northeastern Gulf of Mexico. In contrast, *S. plagiusa* are considered very abundant in soft mud substrate estuarine environments in the northern Gulf (Gunter, 1945). At offshore locations in the western Gulf, Hildebrand (1955) noted that this species was particularly common in 14–16 m off Punta Morros, Mexico, but was less abundant on the brown shrimp grounds off Texas (Hildebrand, 1954). It was considered abundant in demersal fish communities of the southern Gulf of Mexico (Yáñez-Arancibia and Sánchez-Gil, 1986), where it ranked 26th among the 30 most abundant species occurring on the inner continental shelf of Campeche Sound.

Although catches of this species off the south Atlantic states and in the Gulf of Mexico are large enough to constitute a small percentage of industrial fisheries (Siebenhaler, 1952; Roithmayr, 1965; Anderson, 1968), most fishermen regard tonguefish as a nuisance because these small, and relatively narrow flatfishes clog fishing nets and interfere with efficiency of the gear (Topp and Hoff, 1972).

*Symphurus plagiusa* is a nondiscriminate, benthic omnivore. Throughout its life history, except for post larvae, which consume a variety of planktonic diatoms (Strickney and Shumway, 1974), blackcheek tonguefish feed close to the substrate. Lists of dietary items include a variety of benthic prey items, algae, and sand grains (Linton, 1905; Hildebrand and Schroeder, 1928; Reid, 1954; Springer and Woodburn, 1960; Stickney, 1976). Food items recorded for this

species include copepods, amphipods, ostracods, cumaceans, brachiopods, crabs, polychaetes, and pelecypods. The most extensive study of food habits of this species (Stickney, 1976) reveals that *S. plagiusa* of all sizes fed on over 40 different plant and animal taxa but primarily consumed benthic molluscs, small crustaceans, and organic matter. Plant detritus was only a minor component of the diet, indicating this material was not actively sought as a nutrient source. Possibly, *S. plagiusa* benefit from this food source, however, because low levels of cellulase activity occur in the digestive tract of this species (Stickney and Shumway, 1974). About one-half of the 588 tonguefish examined contained sand grains in their digestive tracts, implying that feeding is nondirected, senses other than vision are used in food capture, and food selection is not as precise as in other flatfishes (Stickney and Shumway, 1974). In a Louisiana estuary, juvenile *S. plagiusa* (10–49 mm) collected near the marsh-edge environment fed primarily on epibenthic and hyperbenthic harpacticoid copepods (Toepfer and Fleeger, 1995). Other lesser important items ingested by these fishes were polychaetes, bivalves, amphipods, and tanaids. Infaunal organisms such as nematodes and foraminiferans were rare in diets of these juvenile tonguefishes.

Little is known about which fishes prey upon *S. plagiusa*. However, blackcheek tonguefishes constitute a minor component of the diets of both juvenile (Meyer and Franks, 1996) and adult (Franks et al., 1996) cobia, *Rachycentron canadum*, in the north-central Gulf of Mexico, and elsewhere (Smith[8]).

Throughout its geographic range, *S. plagiusa* apparently has a protracted spawning season coinciding with periods of seasonal thermal maxima. Based on occurrence of larvae in plankton collections, spawning occurs in late spring and throughout the summer period in Chesapeake Bay (Olney and Grant, 1976). Hildebrand and Cable (1930) reported a spawning season extending from May to October, with peak spawning probably occurring in June, for *S. plagiusa* in North Carolina waters. More recently, Hettler and Barker (1993) collected *S. plagiusa* larvae during monthly sampling from May through January in inlets at two barrier islands off North Carolina. Peak densities of *S. plagiusa* larvae, however, occurred in August and September. No larvae of this species were collected February through April. Reichert and Van der Veer (1991) reported that settling of *S. plagiusa* juveniles in a Georgia estuary occurred on muddy substrates from mid-May and extended at least into September. Off Tampa, Moe and Martin (1965) reported collecting ripe fish (145–168 mm) from March through June, whereas on the west Florida shelf, Topp and Hoff (1972) noted a protracted spawning season beginning as early as February and continuing to September. Shealy et al. (1974) noted a lower abundance of this species in the South Edisto River during May to August, which they believed probably coincided with seaward spawning migration of adults.

Hildebrand and Cable (1930) described larval development purportedly of this species, but Olney and Grant (1976) reported that the specimens on which this description was based apparently included more than one species. Working with specimens taken from plankton collections in lower Chesapeake Bay, where *S. plagiusa* is the only tonguefish known to occur, Olney and Grant (1976) provided a more accurate description of larval stages and development of this species. In that study, recently hatched larvae (1.3–2.9 mm NL) represented the majority of the *S. plagiusa* larvae taken, and these were most abundant in the deepest and most saline portions of the Bay. In fact, 76% of all tonguefish larvae taken were found in salinities of over 23‰, and no larvae were collected at stations having an average salinity less than 16.5‰. Olney and Grant (1976) also emphasized that large estuaries may be more significant spawning areas for *S. plagiusa* than previously reported. Reichert and Van der Veer (1991) reported that in a tidal creek of Duplin River estuary, Georgia, all larvae of *S. plagiusa* collected in plankton samples were postmetamorphosed juveniles. Settlement occurred at sizes as small as 9 mm TL (range 9–13 mm TL), and most specimens (70%) were taken in extremely shallow water (usually 1.5 m or less).

**Geographic variation** Variation in meristic features among *S. plagiusa* segregated into seven areas of the geographic range was slight (Table 31). No clinal trends in variation were evident for any features examined, although counts of dorsal- and anal-fin rays and total vertebrae for *S. plagiusa* collected in areas of the southeastern U.S. and Gulf coasts were slightly higher than, but not significantly different from, those of *S. plagiusa* collected off Mexico. Counts for specimens from the Bahamas were lower than those of *S. plagiusa* from continental areas, but a small sample size ($n$=5) from this region prevented detailed comparisons. Ginsburg (1951) also found comparatively little geographic variation in meristic features for *S. plagiusa* he examined. He analyzed counts of dorsal- and anal-fin rays for fishes segregated into three geographic regions, Gulf of Mexico, West Florida (Key West to Tampa), and southeastern United States. *Symphurus plagiusa* from the

[8] Smith, J. 1994. Southeast Fisheries Science Center, National Marine Fisheries Service, NOAA, Beaufort, NC 28516. Personal commun.

**Table 31**

Geographic variation in selected meristic features of *Symphurus plagiusa*. Abbreviations: NEUS = northeastern United States (Delaware to Cape Hatteras, NC); SEUS = southeastern United States; EGMX = eastern Gulf of Mexico; WGMX = western Gulf of Mexico; MEX = Mexico, including Yucatan shelf region; BAH = Bahamas; *n* = no. of specimens measured.

| Character | Area | *n* | Mean | Range | SD |
|---|---|---|---|---|---|
| Dorsal rays | NEUS | 29 | 87.96 | 86–90 | 1.118 |
| | SEUS | 32 | 88.41 | 87–91 | 1.103 |
| | EGMX | 13 | 87.23 | 85–89 | 1.301 |
| | WGMX | 26 | 88.27 | 86–91 | 1.079 |
| | MEX | 28 | 85.96 | 83–91 | 2.202 |
| | BAH | 5 | 84.80 | 81–90 | 3.271 |
| | Cuba | 1 | 87 | — | — |
| Anal rays | NEUS | 29 | 72.38 | 68–75 | 1.613 |
| | SEUS | 32 | 72.53 | 71–74 | 0.983 |
| | EGMX | 13 | 71.31 | 69–73 | 1.182 |
| | WGMX | 30 | 72.03 | 70–75 | 1.299 |
| | MEX | 28 | 69.93 | 67–75 | 2.234 |
| | BAH | 5 | 69.00 | 66–73 | 2.550 |
| | Cuba | 1 | 71 | — | — |
| Vertebrae | NEUS | 29 | 47.21 | 46–48 | 0.560 |
| | SEUS | 32 | 47.16 | 46–48 | 0.677 |
| | EGMX | 13 | 46.46 | 45–48 | 0.776 |
| | WGMX | 31 | 47.03 | 46–49 | 0.658 |
| | MEX | 28 | 45.89 | 45–48 | 1.031 |
| | BAH | 5 | 45.40 | 44–47 | 1.140 |
| | Cuba | 1 | 46 | — | — |

northern Gulf of Mexico had the highest average counts, fishes from Key West to Tampa had the lowest, and those from the southeastern Atlantic coast were intermediate between average values found for tonguefishes from other regions.

**Remarks** *Pleuronectes* (=*Symphurus*) *plagiusa* is the oldest available name for a species of tonguefish, and is based on the holotype skin (LS 124) described by Linnaeus in 1766 from a specimen sent to him from South Carolina by Alexander Garden. Writing on the label is upside down in relation to the fish (see Wheeler, 1985:71), and when the label is held in correct position for reading, the fish appears to be that of a dextral species of flatfish, which it is not. The inverted label apparently confused several investigators beginning with Linnaeus (1766:455), who incorrectly placed this species in the group of dextral flatfishes assigned to *Pleuronectes*. Günther (1862:490) was also confused by the position of the writing on the label because he tentatively suggested placing *Pleuronectes plagiusa* among the dextral flatfishes, perhaps to be included in the dextral soleid (=achirid) genus *Apionichthys*.

Confusion among American authors concerning the identity and placement of Linnaeus' species began in the late 1880's with Goode and Bean's paper (1885a) on Linnaean types of American fishes. After taking measurements and counting scales on the holotype skin of *Pleuronectes plagiusa*, Goode and Bean concluded (1885a:196) that the Linnaean specimen was considerably more slender than any specimen of tonguefish from the coastal United States, and the scale count (77) was substantially lower than counts observed and reported for western Atlantic tonguefishes. In addition, they examined correspondence between Linneaus and Garden and noted that specimen No. 27 of the 1763 consignment in the Linnaean collection was an exotic, not an American species. From these observations, they deduced that this specimen was not conspecific with the common species of tonguefish found in American waters, nor did it appear that *Pleuronectes plagiusa* L. belonged to any other species of tonguefish occurring in American waters. Instead, they concluded that this specimen was probably the type of a flatfish species occurring off Africa or in waters of the Indian Ocean. With respect to the common tonguefish species occurring off the eastern and Gulf of Mexico coasts of the United States, Goode and Bean suggested that the proper name for this species should be *Aphoristia ornata* (Lacepède), which was a new combination based on *Achirus ornatus* Lacepède.

Jordan (1885:395) basically agreed with findings reported in Goode and Bean's study and also rejected the Linnaean specimen as the holotype for the common American species of tonguefish. However, Jordan disagreed with the nomenclature proposed by Goode and Bean. Instead, he rejected *Achirus ornatus* Lacepède as the next available name for the common American tonguefish and, alternatively, suggested that *Aphoristia fasciata* (Holbrook), a name based on an unpublished figure of *Plagusia fasciata* Holbrook and discussed briefly in DeKay (1842:304), was the appropriate name next available for this species. Jordan rejected *Aphoristia ornata* (Lacepède) as an available name for the American species because he believed Lacepède's species came from the West Indies and that this nominal species was distinct from the tonguefish species commonly occurring on the Atlantic and Gulf coasts of the United States. However, in this same paper, Jordan equivocated when he stated that "it [meaning Lacepède's tonguefish] may be that this *ornata* is the original *plagiusa*." This equivocation led to further confusion and also resulted in a nomenclatural entanglement for the tonguefish species described by Linnaeus from the southeastern and Gulf Coasts of the United States and for the nominal West Indian species, pur-

portedly that of a tonguefish (see below), described by Lacepède.

In their review of the flounders and soles of Europe and America, Jordan and Goss (1889:324) completely reversed the earlier position of Jordan regarding the status of the Linnaean holotype. Jordan and Goss disagreed with findings reported in Goode and Bean (1885a) and acknowledged that the tonguefish Garden had sent to Linnaeus probably originated from the United States, not from Africa or the Indian Ocean. Jordan and Goss used the new combination *Symphurus plagiusa* (Linnaeus) as the senior synonym for the common tonguefish species occurring in coastal waters of the United States and northern Mexico. Additionally, Jordan and Goss removed *Achirus ornatus* Lacepède from the synonymy of *Symphurus plagiusa* (Linnaeus) and indicated that it was doubtful to ascertain exactly as to what species the Lacepède description applied (a position held herein as well).

Following Jordan and Goss (1889), subsequent studies have continued to use *Symphurus plagiusa* (Linnaeus) as the senior synonym for the common, shallow-water, tonguefish of the eastern and Gulf of Mexico coasts of North America and northern Mexico. Although this name had wide application in studies published during the early and mid-1900's, identity and status of the holotype skin of Linnaeus' species was never definitively settled. In his revision of western North Atlantic tonguefishes, Ginsburg (1951:195) briefly addressed taxonomic and nomenclatural problems associated with the holotype skin of *Pleuronectes plagiusa* Linnaeus. Ginsburg did not directly examine the holotype skin but noted a disparity between measurements taken by Goode and Bean (1885a) on the holotype skin and those he had made on whole, preserved specimens. Ginsburg essentially agreed with Goode and Bean that, on the basis of measurements of the holotype skin of *Pleuronectes plagiusa*, this specimen did not appear to belong to the common American tonguefish species. He also stated that if the Linnaean name did not apply to the American species, then *Plagusia fasciata* DeKay was the next available name for this species. However, Ginsburg chose not to change prevailing nomenclature for this species because he believed that further study beyond his and Goode and Bean's measurements was necessary to determine the identity of the holotype skin with accuracy.

Wheeler (1985:71) settled the controversy surrounding the identity and type status of the skin. Wheeler suggested several reasons why earlier ichthyologists (Günther, 1862; Goode and Bean, 1885a) had been confused about capture location and identity of the holotype skin of *Pleuronectes plagiusa* Linnaeus. Some confusion surrounding both the origin and identity of this species arises from the writing on the label, which, as mentioned earlier, is upside down in relation to the fish. Also, it appears that Goode and Bean erred in their study of the correspondence between Garden and Linneaus that refers to the capture location of the holotype. Wheeler stated that Goode and Bean apparently read the Garden correspondence of the 1763 consignment in which specimen No. 27 was indicated as an exotic, not originating in North American waters, and they mistakenly interpreted this as reference to the holotype of *Pleuronectes plagiusa* Linnaeus. However, the holotype of *Pleuronectes plagiusa* (also No. 27) was not part of the 1763 consignment, but rather, part of the 1761 consignment from Garden. In the 1761 consignment, the holotype skin is listed as "'Pleuronectes' here called 'Taper Flounder'" and its capture location is South Carolina. Wheeler's study leaves no doubt that the specimen of *Pleuronectes plagiusa* Linnaeus 1766 represented only by the skin is the holotype for the common, shallow-water tonguefish species occurring in coastal waters along eastern and Gulf coasts of North America, and that the name used by Linnaeus has priority over all others proposed for this species.

My examination of the holotype skin (LS 124) and associated documentation for this specimen held at the Linnaean Society of London confirms conclusions arrived at by Wheeler. All meristic (ca. 86 dorsal-fin rays, ca. 74 anal-fin rays) and morphometric features (Table 30) of this specimen are within ranges reported for those of other *S. plagiusa*. This specimen has ctenoid scales on the ocular side (ca. 86 in longitudinal series contrary to the 77 reported by Goode and Bean), small ctenoid scales extending onto the ocular-side finrays, lacks teeth on the ocular-side jaws, and has the jaws extending posteriorly only to the vertical through the mideye region, as is characteristic for other specimens of *S. plagiusa*.

Walls (1976:391) suggested placing *S. civitatium* into the synonymy of *S. plagiusa* because there were partial overlaps in meristic features, pigmentation, and ecological co-occurrence between these two species. This action is unwarranted because results of this and earlier studies (Ginsburg, 1951; Munroe, 1992) have shown that these two species are distinct and are readily distinguishable by a number of features (see "Comparisons" section below).

**Comparisons** *Symphurus plagiusa* is most similar in meristic features, body shape, and overall size to the widespread, western Atlantic *S. diomedeanus* and the South Atlantic, *S. trewavasae*. *Symphurus plagiusa* is easily distinguished from *S. diomedeanus* because it lacks the well-developed pupillary operculum and darkly pigmented spots on posterior dorsal and anal fins characteristic of *S. diomedeanus*.

*Symphurus plagiusa* usually has a well-developed black spot on the outer surface of the upper lobe of the opercle and 5–6 small ctenoid scales on blind sides of posterior rays of the dorsal and anal fins (opercular spot absent in *S. diomedeanus*, and scales either absent or only 1–2 scales at bases of fin rays in *S. diomedeanus*). Other differences between these species are discussed in the "Comparisons" section of the account for *S. diomedeanus*. In number of caudal-fin rays, *S. plagiusa* agrees with *S. trewavasae* but differs from that species in many features discussed in the "Remarks" section of the account for *S. trewavasae*.

*Symphurus plagiusa* differs from *S. minor*, *S. parvus*, *S. kyaropterygium*, and *S. ommaspilus*, other Atlantic tonguefishes characterized by 10-caudal-fin rays, in lacking a pupillary operculum and membrane ostia (present in these others); in having a conspicuous black opercular spot (no opercular spot in the others), in lacking a caudal blotch on the ocular side (caudal blotch present in *S. minor*, *S. parvus*, and *S. kyaropterygium*), and *S. plagiusa* does not have conspicuous spots on the dorsal and anal fins (ocellated spot present on dorsal and anal fins in *S. ommaspilus*). Meristic features of *S. plagiusa* are much lower and completely beyond ranges of those observed in *S. jenynsi*, and *S. jenynsi* lacks scales on blind sides of dorsal- and anal-fin rays characteristic of *S. plagiusa*. Other differences between these taxa and *S. plagiusa* are discussed in the "Comparisons" sections in the respective accounts for these other species.

There is nearly complete overlap in most meristic features of *S. plagiusa* and those of the sympatric (but not syntopic) western North Atlantic *S. urospilus*. These species differ, however, in number of caudal-fin rays (10 in *S. plagiusa* vs. 11 in *S. urospilus*); *S. plagiusa* also lacks a spot on the caudal fin and usually has a conspicuous spot on the ocular-side opercle (vs. caudal-fin spot present and no spot on outer surface of ocular-side opercle in *S. urospilus*). Additionally, *S. plagiusa* lacks a well-developed pupillary operculum (present in *S. urospilus*) and has small ctenoid scales on blind sides of dorsal- and anal-fin rays that are absent in *S. urospilus*.

South of Cape Hatteras, North Carolina, and in the Gulf of Mexico, *S. plagiusa* are frequently collected with *S. civitatium*. *Symphurus civitatium*, *S. plagusia*, and *S. caribbeanus* have similar meristic features, body sizes, and somewhat similar pigmentation patterns to those observed in *S. plagiusa*. *Symphurus plagiusa* is readily distinguished from all three by number of caudal-fin rays (10 in *S. plagiusa* vs. 12 in these others) and *S. plagiusa* has 4–8 small, ctenoid scales on blind sides of posterior dorsal- and anal-fin rays (vs. scales absent, or only 1–2 scales at bases of fin rays in these others). Many *S. plagiusa* have a conspicuous black spot on the outer surface of the upper ocular-side opercle (these others lack a conspicuous black spot on outer surface of ocular-side opercle, although some *S. civitatium* and *S. caribbeanus* have a diffuse dark brown blotch on the ocular-side opercle resulting from pigment of the inner opercular lining showing through to outside). In *S. plagiusa*, inner linings of both opercles are heavily pigmented, whereas in *S. civitatium*, *S. plagusia*, and *S. caribbeanus* usually only the inner lining on the ocular-side opercle is pigmented.

*Symphurus plagiusa* also has relatively larger eyes (8.3–12.6% HL), compared with those of *S. civitatium* (7.0–11.0% HL) and *S. plagusia* (6.4–9.5% HL), and are more nearly equal in position (eyes noticeably subequal in *S. civitatium* and *S. plagusia*). In addition, in *S. plagiusa* the posterior margin of the maxilla extends posteriorly only as far as the vertical through the mideye and often only reaches the vertical through the anterior margin of the pupil of the lower eye, whereas in *S. civitatium* and *S. plagusia* the posterior margin of the maxilla usually reaches a point between verticals through the posterior margin of the pupil and the posterior margin of the eye (less frequently), or the jaws may even extend slightly beyond the vertical through the posterior margin of the lower eye in some *S. plagusia*. Another difference between *S. plagiusa* and *S. civitatium* is that in *S. plagiusa*, both sexes have uniformly pigmented dorsal and anal fins that are generally only lightly shaded or moderately dusky. In comparison, male *S. civitatium* have dorsal and anal fins that become progressively darker and become nearly completely black on their posterior extent (especially pronounced in sexually mature males). *Symphurus plagiusa* also has a pronounced longitudinal streak of black pigment running the length of the gill filaments, whereas in *S. civitatium* the gill filaments are often spotted but lack a prominent dark black band.

*Symphurus plagiusa* differs further from *S. caribbeanus* in lacking the alternating series of blotches and unpigmented areas on the vertical fins characteristic of *S. caribbeanus* (vertical fins in *S. plagiusa* uniformly pigmented without dark blotches along their lengths). *Symphurus plagiusa* has a fleshy ridge on the ocular-side lower jaw that is lacking in *S. caribbeanus*.

Among eastern Pacific *Symphurus*, meristic features and overall body shape of *S. plagiusa* overlap those of *S. williamsi*. *Symphurus plagiusa* differs from this species in number of caudal-fin rays (10 vs. 12) and ID pattern (1-4-3 vs. 1-5-3 in *S. williamsi*). *Symphurus plagiusa* differs further from *S. williamsi* because it lacks a well-developed pupillary operculum (present in *S. williamsi*) and it has a black blotch on the ocular-side opercle that is lacking in *S. williamsi*.

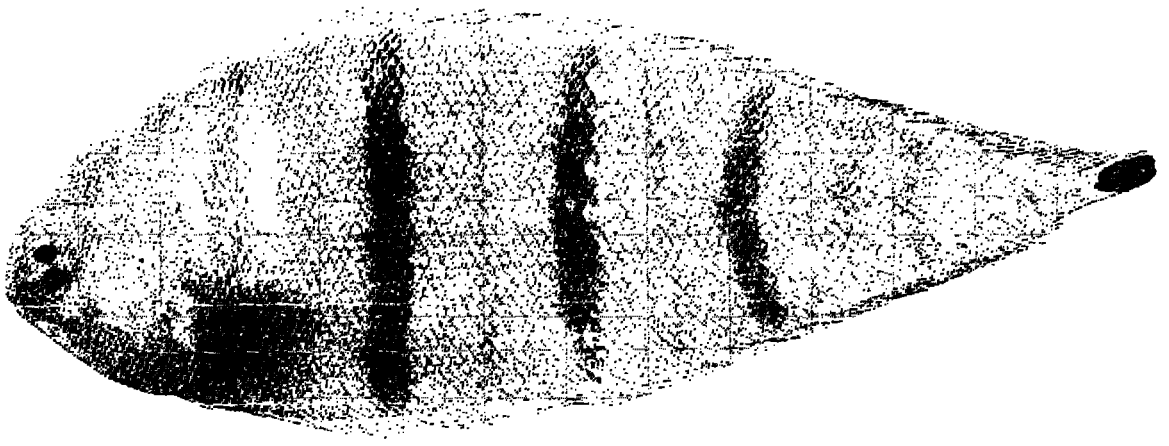

**Figure 52**
*Symphurus urospilus* Ginsburg, GMBL 76-266, 98.9 mm SL, South Carolina 32°57'N, 79°09'W.

### *Symphurus urospilus* Ginsburg, 1951 (Figs. 9A, 52–53; Tables 1–10, 32–33) Spottail tonguefish

*Symphurus urospilus* Ginsburg, 1951:193 (original description; Savannah, Georgia). Hildebrand, 1955:205 (Gulf of Campeche, Mexico; occurrence on pink shrimp grounds; substrate preference). Springer and Bullis, 1956:65 (Gulf of Mexico). Briggs, 1958:298 (Florida). Bullis and Thompson, 1965:35 (northeast Florida, Florida Keys). Moe and Martin, 1965:149 (Tampa Bay, Florida). Beaumariage, 1968:8 (St. Petersburg, Florida). Struhsaker, 1969:298 (southeast United States). Topp and Hoff, 1972:90 (continental shelf west Florida; limited ecological and life history data; distribution records). Vergara Rodriguez, 1976:6 (Cuba). Webster et al.[3] (South Atlantic Bight; ranked 70th in abundance of 244 taxa in trawls). Munroe, 1992:371, 382 (ID pattern; geographic, bathymetric distributions). Darovec, 1995:89 (distribution on west Florida shelf).

**Diagnosis** *Symphurus urospilus* is distinguished from all congeners by combination of predominant 1-4-3 ID pattern; 11 caudal-fin rays; 4 hypurals; 82–90 dorsal-fin rays; 64–74 anal-fin rays; 44–48 total vertebrae; 67–82 scales in longitudinal series; well-developed pupillary operculum; unpigmented peritoneum; fleshy ridge on ocular-side lower jaw; absence of scales on blind sides of dorsal- and anal-fin rays; absence of membrane ostia in dorsal and anal fins; partial row of teeth along margin of ocular-side lower jaw; ocular-side upper jaw usually lacking teeth altogether (occasional specimens with few teeth on anterior margin of premaxilla); ocular surface pigmentation featuring 4–11 (usually 6–10) well-developed, sharply contrasting, dark brown crossbands on head and body; absence of pigmented spot on ocular-side opercle; dorsal and anal fins without spots or blotches; and caudal fin with single, large, ocellated spot.

**Description** A relatively large species attaining maximum lengths of ca. 166 mm SL. ID pattern usually 1-4-3 (74/110 specimens), less frequently 1-4-2 (8/110) and 1-5-2 (15/110), rarely 1-3-3 or 1-5-3 (Table 2). Caudal-fin rays usually 11 (108/113), rarely 9 or 10 (Table 3). Dorsal-fin rays 82–90, usually 84–89 (Table 4). Anal-fin rays 64–74, usually 68–72 (Table 5). Total vertebrae 44–48, usually 45–46 (103/114) (Table 6). Hypurals 4 (114/114). Longitudinal scale rows 67–82, usually 71–80 (Table 7). Scale rows on head posterior to lower orbit 13–17, usually 14–16 (Table 8). Transverse scales 27–40, usually 31–40 (Table 9).

Proportions of morphometric features presented in Table 32. Body very deep, maximum depth in anterior one-third of body; body depth tapering fairly rapidly in posterior two-thirds of body. Preanal length much shorter than body depth. Head moderately long and very wide, narrower than body depth. Head

**Table 32**

Morphometrics for holotype (USNM 155225) and 54 additional specimens of *Symphurus urospilus*. (Abbreviations defined in methods section; SL in mm; characters 2 to 14 are expressed in thousandths of SL; 15 to 21 in thousandths of HL; *n* = no. of specimens measured.)

| Character | Holotype | *n* | Range | Mean | SD |
|---|---|---|---|---|---|
| 1. SL | 123.9 | 55 | 37.1–166.0 | 116.8 | 23.50 |
| 2. BD | 338 | 55 | 285–366 | 336.6 | 14.97 |
| 3. PDL | 36 | 54 | 19–52 | 33.9 | 7.47 |
| 4. PAL | 190 | 54 | 166–240 | 195.1 | 14.86 |
| 5. DBL | 964 | 55 | 941–981 | 965.6 | 8.13 |
| 6. ABL | 784 | 55 | 730–874 | 801.8 | 23.63 |
| 7. PL | 70 | 54 | 50–87 | 67.8 | 8.58 |
| 8. PA | 46 | 54 | 35–73 | 52.3 | 8.06 |
| 9. CFL | 109 | 55 | 80–139 | 117.5 | 10.04 |
| 10. HL | 188 | 54 | 155–213 | 180.6 | 10.08 |
| 11. HW | 289 | 54 | 224–308 | 267.2 | 16.93 |
| 12. POL | 121 | 54 | 76–131 | 111.2 | 11.63 |
| 13. UHL | 206 | 55 | 131–212 | 181.6 | 13.63 |
| 14. LHL | 109 | 54 | 79–115 | 100.0 | 8.15 |
| 15. POL | 644 | 54 | 439–773 | 617.7 | 56.17 |
| 16. SNL | 176 | 53 | 138–255 | 196.0 | 20.83 |
| 17. UJL | 215 | 54 | 188–261 | 220.6 | 17.37 |
| 18. ED | 116 | 53 | 102–170 | 126.0 | 12.93 |
| 19. CD | 330 | 53 | 158–391 | 280.1 | 42.60 |
| 20. OPUL | 219 | 55 | 135–268 | 214.9 | 26.78 |
| 21. OPLL | 378 | 55 | 250–427 | 331.9 | 36.80 |

length much shorter than head width (HW:HL 1.1–1.7, $\bar{x}$=1.5). Postorbital length much shorter than body depth. Lower head lobe width slightly less than postorbital length; considerably narrower than upper head lobe. Lower opercular lobe of ocular side considerably wider than upper opercular lobe. Snout short and rounded; covered with small ctenoid scales. Anterior nostril on ocular side short, when depressed posteriorly, usually falling just short of anterior margin of lower eye. Dermal papillae well developed on snout, chin, and dorsal portion of head near base of dorsal fin on blind side; dermal papillae extending onto snout region of ocular side in larger specimens. Jaws moderately long; maxilla usually extending posteriorly to vertical through middle of lower eye. Ocular-side lower jaw with distinct, fleshy ridge near posterior margin. Teeth well developed on blind-side jaws. Ocular-side lower jaw usually with single, mostly incomplete, row of slender teeth along margin; ocular-side upper jaw usually lacking teeth, occasional specimens possessing few slender premaxillary teeth anterior to vertical through base of anterior nostril. Chin depth considerably larger than snout length. Lower eye relatively large; eyes usually equal in position; occasionally upper slightly anterior to lower eye. Anterior and medial surfaces of eyes without scales; usually 1–2 small, ctenoid scales in narrow interorbital region. Pupillary operculum well developed. Dorsal-fin origin usually equal with vertical through anterior margin of upper eye; occasionally reaching slightly anterior to vertical through anterior margin of upper eye, or less frequently, only reaching vertical through midpoint of upper eye; predorsal length short. Scales usually absent on blind sides of dorsal- and anal-fin rays; occasionally with 1–2 scales at bases of posteriormost fin rays in larger specimens. Pelvic fin moderately long; longest pelvic-fin ray, when extended posteriorly, reaching base of first, or occasionally second, anal-fin ray. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anus, or occasionally extending posteriorly almost to anal-fin origin (membrane torn in most specimens). Caudal fin moderately long. Scales large, strongly ctenoid on both sides of body.

**Pigmentation (Fig. 52)** Body coloration similar for both sexes. Ocular surface usually dark brown with 4–11 (usually 6–10) well-developed, complete, sharply contrasting, dark brown crossbands on head and body. Individuals from light-colored habitats with almost whitish background coloration and strong pattern of crossbanding. Crossbands not continued onto dorsal and anal fins. Occasionally, crossbands scarcely evident in specimens with exceptionally dark ocular surface background coloration. Anteriormost crossband on head immediately posterior to eyes; second crossband on head on anterior region of opercle. Crossbands on trunk variable in number. Anterior two crossbands on body immediately posterior to opercular opening, usually darkest. Posteriormost crossband immediately anterior to base of caudal fin. Outer surface of ocular-side opercle with same pigment as that on body. Inner linings of opercles and isthmus on both sides of body unpigmented. Ocular-side upper lip with slight band of pigment; ocular-side lower lip frequently spotted, but without definite pigment band. Blind side creamy white. Peritoneum unpigmented.

Fin rays and membranes along dorsal and anal fins uniformly dark brown, darkest in regions corresponding to crossbands on body, but without defined pattern of spots or blotches. Distal portions of dorsal- and anal-fin rays unpigmented. Proximal, scaly, one-half of caudal fin occasionally with small pigmented blotch of variable intensity. Distal one-half of caudal fin with single, well-developed, ocellated, dark brown or black, spherical spot surrounded by unpigmented, whitish area, clearly evident even in smallest specimen (26.2 mm) examined. Portions of caudal-fin rays distal to ocellated spot usually unpigmented, occasionally with faint light brown pigment.

**Size and sexual maturity (Fig. 9A)** *Symphurus urospilus* is a relatively large tonguefish attaining lengths of about 166 mm. Most specimens (87/112) ranged between 101 and 150 mm. Only two specimens (166 and 150.1 mm) exceeded 150 mm. Males and females reach similar sizes, with males slightly larger. The two largest specimens examined (166 and 150 mm) were males, whereas the largest female measured 149.2 mm. Specimens smaller than 50 mm are generally rare in collections, with only four available to this study (see below). Of 108 specimens for which size-related life history information was available, there were 56 males (90.4–166 mm), 46 females (88.8–149.2), and six immature fish (25.0–56.8 mm) of undetermined sex. Based on reproductive stages of females, sexual maturity occurs at the relatively large size of ca. 100 mm. Only two of eight females 88–100 mm were mature with fully elongate or gravid ovaries (one each, respectively). Six females between 91.9 and 99.9 mm were immature with ovaries just undergoing elongation. All females >100 mm were mature with either fully elongate or gravid ovaries. The smallest gravid female was 88.8 mm, an apparently unusual specimen because the other 16 gravid females were 101–149 mm.

Of interest is the general absence of small juveniles of this species in the collections examined. Only six small fish (25.0–56.8 mm) were found. Because juveniles and adults of this species inhabit live-bottom substrates (see below), relative scarcity of small juveniles in collections may reflect the limited success of conventional trawling gear generally in capturing small flatfishes in this habitat, or it could also indicate that juveniles occur in habitats other than those usually sampled by trawling.

**Geographic distribution (Fig. 53)** A warm-temperate species with a fairly restricted and somewhat discontinuous distribution in the western North Atlantic from just south of Cape Hatteras, North Carolina, through the Gulf of Mexico to the Campeche Bank region off the Yucatan Peninsula, Mexico. There is also a single citation of this species from Cuba (Vergara Rodriguez, 1976). The occurrence of *S. urospilus* corresponds with the general distribution of live-bottom habitats in the region.

Along the southeastern Atlantic coast of the United States, *S. urospilus* ranges from south of Cape Hatteras, North Carolina, to southern Florida. In the Gulf of Mexico, it has been taken at the southern tip of Florida, including the Florida Keys and Tortugas regions, and is common in the eastern Gulf along the west Florida shelf, as far north and west as Apalachee Bay (Topp and Hoff, 1972). I did not examine specimens collected in the central Gulf of

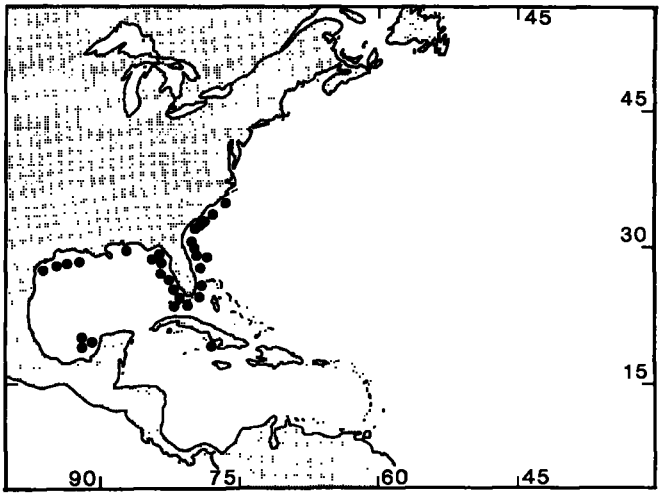


**Figure 53**

Geographic distribution of *Symphurus urospilus* based on material examined (discussion of geographic distribution appears in species account).

Mexico, but several lots taken on the inner continental shelf in the western Gulf off western Louisiana and Texas contained this species. *Symphurus urospilus* also occurs on live-bottom substrates in the Campeche Bank region of the Yucatan Peninsula, Mexico (Hildebrand, 1955; Topp and Hoff, 1972).

**Bathymetric distribution** *Symphurus urospilus* examined in this study were taken at depths of 5–324 m (Table 10). The center of abundance for this species, where 122/126 (96%) of the specimens examined in this study were captured, occurs on live-bottom substrates in the relatively narrow depth zone between 5 and 40 m. *Symphurus urospilus* has not been reported from estuarine areas, and all juveniles examined, including the two smallest specimens (25.0 and 26.2 mm), were collected on live-bottom substrates on the inner continental shelf at depths occupied by adults.

Only four *S. urospilus* examined in this study were taken deeper than 40 m (one each at 42 and 64 m, and two at 324 m). The capture depth (324 m) for two specimens in TU 14789 is very unusual for this species because it is 260 m deeper than any other recorded for the species. Depth of capture for this station appears legitimate because other fishes collected in the trawl with these tonguefishes include chlorophthalmids and macrourids, typical deep-sea species.

**Ecology** Little is known regarding the life history of *S. urospilus*. From their small samples collected on the west Florida shelf, Topp and Hoff (1972) noted that *S. urospilus* were taken at bottom temperatures

of 16.4–30.0°C and salinities of 32.8–36.2‰. Three specimens had fed on crustaceans, and one had ingested a gastropod. Topp and Hoff (1972) also noted that specimens of *S. urospilus* caught off the West Florida Shelf in September had ripe and ripening gonads, and a specimen collected in late August had developing ova. Their smallest specimen (27 mm) was collected in November, further suggesting a late summer–early fall spawning period for this species in the eastern Gulf of Mexico. Webster et al.[3] collected 457 individuals (12.8 kg) by trawling in the South Atlantic Bight. In their study, this species ranked 70th in abundance of 244 taxa collected.

**Geographic variation** Only slight variation was evident in meristic features (Table 33) examined in specimens from three different regions of the geographic range. *Symphurus urospilus* from off the southeastern United States and western Gulf of Mexico had similar counts for dorsal- and anal-fin rays and total vertebrae. Counts for these features were consistently higher in specimens from these regions than were those for *S. urospilus* from the eastern Gulf of Mexico.

**Table 33**

Geographic variation in selected meristic features of *Symphurus urospilus*. Abbreviations: SEUS = southeastern United States; EGMX = eastern Gulf of Mexico; WGMX = western Gulf of Mexico including Yucatan shelf region; *n* = no. of specimens measured.

| Character | *n* | Area | Mean | Range | SD |
|---|---|---|---|---|---|
| Dorsal rays | 20 | SEUS | 86.6 | 84–90 | 1.35 |
| | 70 | EGMX | 85.0 | 82–88 | 1.24 |
| | 26 | WGMX | 87.3 | 84–89 | 1.25 |
| Anal rays | 20 | SEUS | 70.4 | 67–72 | 1.14 |
| | 70 | EGMX | 69.0 | 64–71 | 1.27 |
| | 26 | WGMX | 71.0 | 68–74 | 1.37 |
| Vertebrae | 20 | SEUS | 45.8 | 45–47 | 0.52 |
| | 70 | EGMX | 45.2 | 44–46 | 0.51 |
| | 26 | WGMX | 46.3 | 45–48 | 0.60 |

**Comparisons** *Symphurus urospilus* is one of the most distinctive species in the genus. Its unique combination of 11 caudal-fin rays, pupillary operculum, spotted caudal fin, and ID pattern distinguishes this species from all congeners. Other western Atlantic species with spotted fins differ in caudal-fin ray count (*S. diomedeanus* and *S. ommaspilus* have 10 caudal-fin rays) and either lack a caudal spot altogether, or if a caudal spot is present (occasionally in *S. diomedeanus*), there are spots present also on the dorsal and anal fins. Other differences between *S. urospilus* and these species are discussed in the "Comparisons" sections in accounts for *S. ommaspilus* and *S. diomedeanus*.

The eastern Pacific *S. melasmatotheca* and *S. undecimplerus*, the only other congeners with 11 caudal-fin rays, also have a pupillary operculum. *Symphurus urospilus* differs from both in peritoneal color (unpigmented vs. black or spotted in these other species), its spot on the caudal fin (absent in these others), in its mostly nonoverlapping fin-ray and vertebral counts (82–90 dorsal-fin rays vs. 90–98 in *S. melasmatotheca* and 97–105 in *S. undecimplerus*; 64–74 anal-fin rays vs. 74–80 in *S. melasmatotheca* and 80–87 in *S. undecimplerus*; and 44–48 total vertebrae vs. 49–52 in *S. melasmatotheca* and 52–56 in *S. undecimplerus*), and ID pattern (1-4-3 vs. 1-5-3 in these others).

The eastern Pacific species, *S. fasciolaris*, also has a prominent spot on the caudal fin and a 1-4-3 ID pattern reminiscent of features in *S. urospilus*. Despite these similarities, these are otherwise distinctive species differing in many characteristics. *Symphurus fasciolaris* has 10 caudal-fin rays, more dorsal- (90–97) and anal-fin rays (75–80), and more total vertebrae (48–52) than does *S. urospilus*. Additionally, this species usually has a series of rounded spots in addition to crossbands on the ocular surface, whereas *S. urospilus* lacks rounded spots on the ocular surface.

**Figure 54**
*Symphurus caribbeanus* Munroe, Holotype, USNM 313487, 101 mm SL, male, Puerto Rico.

## *Symphurus caribbeanus* Munroe, 1991 (Figs. 8H, 54–55; Tables 1–10, 34)

*Symphurus plagusia* (not of Schneider, in Bloch and Schneider, 1801). Ginsburg, 1951:220 (in part; Fox Bay, Panama; specimens in USNM 81654 included in account of *S. p. plagusia*). Austin and Austin, 1971:38 (in part; Guayanilla, Puerto Rico; food habits; nine specimens from UPRM 2926).

*Symphurus caribbeanus* Munroe, 1991:280 (original description; Greater Antilles, Central America to Colombia; diagnosis; synonymy; counts, measurements, photograph; in key; bathymetric distribution; size and sexual maturity). Munroe, 1992:371, 382 (ID pattern; geographic, bathymetric distributions). Cervigón et al., 1993:306 (Venezuela).

**Diagnosis** *Symphurus caribbeanus* is distinguished from all congeners by the following combination of characters: predominant 1-4-3 ID pattern; 12 caudal-fin rays; 4 hypurals; 89–96 dorsal-fin rays, usually 92–96; 74–80 anal-fin rays; 48–51, usually 49–50, total vertebrae; 78–89 scales in longitudinal series; unpigmented peritoneum; relatively large eye (82–110 HL) without pupillary operculum; absence of scales on blind sides of dorsal- and anal-fin rays; absence of fleshy ridge on ocular-side lower jaw; ocular-side upper and lower jaws usually with small patch of teeth along only anterior one-third of jaw margins, or lacking teeth; relatively short jaws usually extending to vertical through posterior margin of pupil of lower eye or occasionally extending to vertical through posterior margin of lower eye; dorsal-fin origin usually reaching, or occasionally slightly anterior to, vertical through anterior margin of upper eye; ocular-surface pigmentation dark brown to almost yellow, usually with 10–15 narrow, irregularly complete, sharply contrasting, dark brown crossbands on head and trunk, but without caudal blotch; outer surface of ocular-side opercle without dark blotch; inner lining of opercle and isthmus heavily pigmented on ocular side, unpigmented on blind side; entire dorsal and anal fins with alternating series of blotches and unpigmented areas; and caudal fin either uniformly darkly pigmented, or with alternating series of pigmented blotches and unpigmented areas through its length.

**Description** A medium-size species attaining maximum lengths of ca. 122 mm SL. ID pattern usually 1-4-3 (69/84 specimens), less frequently 1-3-3 (8), 1-3-4 (4), or 1-4-4 (2) (Table 2). Caudal-fin rays usually 12 (81/85), less frequently 10, 11, or 13 (Table 3). Dorsal-fin rays 89–96, usually 92–96 (Table 4). Anal-fin rays 74–80 (Table 5). Total vertebrae 48–51, usually 49–50 (76/82) (Table 6). Hypurals 4 (75/75). Longitudinal scale rows 78–89 (Table 7). Scale rows on head posterior to lower orbit 17–22, usually 19–21 (Table 8). Transverse scales 36–44 (Table 9).

Proportions of morphometric features presented in Table 34. Body relatively deep, with greatest depth in anterior one-third of body; body depth tapering relatively rapidly posterior to body midpoint. Preanal length shorter than body depth. Head wide, nar-

**Table 34**

Morphometrics for holotype (USNM 313487) and 20 paratypes of *Symphurus caribbeanus*. (Abbreviations defined in methods section; SL is expressed in mm; characters 2 to 14 are expressed in thousandths of SL; 15 to 21 in thousandths of HL; *n* = no. of specimens measured.)

| Character | Holotype | *n* | Range | Mean | SD |
|---|---|---|---|---|---|
| 1. SL | 100.5 | 21 | 40.1–121.9 | 84.5 | 22.40 |
| 2. BD | 317 | 21 | 277–320 | 300.6 | 12.14 |
| 3. PDL | 34 | 21 | 29–48 | 36.2 | 5.45 |
| 4. PAL | 219 | 21 | 191–261 | 223.0 | 15.89 |
| 5. DBL | 966 | 21 | 952–972 | 964.3 | 5.70 |
| 6. ABL | 792 | 21 | 751–820 | 781.0 | 18.89 |
| 7. PL | 62 | 21 | 51–75 | 63.2 | 6.56 |
| 8. PA | 45 | 21 | 35–63 | 47.6 | 6.62 |
| 9. CFL | 106 | 21 | 87–116 | 102.4 | 7.56 |
| 10. HL | 194 | 21 | 185–224 | 199.2 | 10.94 |
| 11. HW | 239 | 21 | 220–268 | 240.0 | 11.03 |
| 12. POL | 123 | 21 | 119–143 | 133.6 | 6.72 |
| 13. UHL | 141 | 21 | 141–184 | 164.6 | 32.23 |
| 14. LHL | 112 | 21 | 84–112 | 98.6 | 26.51 |
| 15. POL | 636 | 21 | 632–744 | 671.6 | 28.72 |
| 16. SNL | 231 | 21 | 193–255 | 218.4 | 18.47 |
| 17. UJL | 251 | 21 | 195–253 | 231.3 | 15.96 |
| 18. ED | 103 | 21 | 82–110 | 97.4 | 7.18 |
| 19. CD | 267 | 21 | 227–305 | 259.8 | 19.74 |
| 20. OPLL | 359 | 21 | 241–359 | 291.8 | 32.23 |
| 21. OPUL | 236 | 21 | 162–274 | 199.4 | 27.34 |

rower than body depth. Head short; considerably shorter than head width (HW:HL= 1.1–1.3, $\bar{x}$=1.2). Lower head lobe width less than postorbital length; considerably narrower than upper head lobe. Lower opercular lobe of ocular side considerably wider than upper opercular lobe. Snout moderately long and pointed (Fig. 54), covered with small ctenoid scales. Anterior nostril usually not reaching anterior margin of lower eye when depressed posteriorly. Dermal papillae well developed, but not particularly dense, on snout and chin regions on blind side of head. Jaws long; maxilla usually reaching posteriorly to vertical through posterior margin of pupil, or occasionally posterior margin, of lower eye. Ocular-side lower jaw without distinct, fleshy ridge (Fig. 3E). Teeth well developed on blind-side jaws. Upper and lower jaws on ocular side usually with small patch of teeth only on anterior one-third of jaw margins, or lacking teeth. Chin depth larger than snout length. Lower eye relatively small; eyes usually slightly subequal in position with upper usually slightly in advance of lower eye. Anterior and medial surfaces of eyes not covered with scales; usually 1–3 small ctenoid scales in narrow interorbital region. Pupillary operculum absent. Dorsal-fin origin usually reaching, or occasionally slightly anterior to, vertical through anterior margin of upper eye. Blind sides of dorsal- and anal-fin rays without scales. Pelvic fin short; longest pelvic-fin ray, when extended posteriorly, usually reaching base of first, or occasionally second, anal-fin ray. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anus, or occasionally extending posteriorly almost to anal-fin origin (membrane torn in most specimens). Caudal fin short. Scales moderate in size, strongly ctenoid on both sides of body.

**Pigmentation (Fig. 54)** Pattern of body pigmentation generally similar for both sexes at all sizes, but mature males with more intense pigmentation on body and posterior portions of dorsal and anal fins. Ocular surface dark brown to almost yellow; usually with 10 to 15 narrow, irregularly complete, sharply contrasting, darker brown crossbands on head and trunk. Crossbands not continued onto dorsal and anal fins. Anteriormost band on head immediately posterior to eyes. Second band crossing head just anterior to opercular opening. Crossbands on trunk variable in number, usually 3–6 scale rows wide. First band crossing body immediately posterior to opercular opening. Posteriormost band slightly anterior to caudal-fin base, irregularly complete. Blind side off-white. Peritoneum unpigmented. Outer surface of ocular-side opercle with general background pigmentation as body. Dorsal margin of ocular-side opercle sometimes with dusky blotch due to dark pigmentation of inner lining of opercle showing through to outer surface. Inner lining of opercle and isthmus heavily pigmented on ocular side; unpigmented on blind side. Slight band of pigment on ocular-side upper lip; ocular-side lower lip frequently spotted, but without definite band of pigment.

Pigmentation of dorsal and anal fins generally similar in both sexes, but usually more intense in males. Except for anteriormost portion of dorsal fin, entire dorsal and anal fin with alternating series of dark blotches and unpigmented areas. Blotches variable in shape, most frequently nearly rectangular; extending from base almost to distal tip of fin rays; blotches usually covering 2 to 5 fin rays alternating with 2 to 4 lightly pigmented fin rays. Caudal fin either uniformly darkly pigmented, or with alternating series of pigmented blotches and unpigmented areas throughout length of fin.

**Size and sexual maturity (Fig. 8H)** Adult *S. caribbeanus* range in size from ca. 71 to 130 mm and this species is one of the smallest members of the *S. plagusia* complex. Size-related life history information is derived from data taken from 89 specimens. Males and females attain similar sizes. The largest female fish measured is gravid (122 mm); the larg-

est male was 130 mm. There were 44 males (52.9–130 mm), 39 females (55.6–122 mm), and 6 immature fish (24.4–43.8 mm) among material examined. On the basis of reproductive stages of females, this species matures at 70–80 mm. There were 30 mature females ranging in size from 71.8 to 122 mm. All females larger than 80 mm were mature. The smallest mature female (71.8 mm) was unusual because six of seven others in this size range (ca. 70–80 mm) had undeveloped gonads. Of 39 females, nine, ranging from 55.6 to 79.1 mm, were immature with only partially elongate ovaries. The smallest immature females (55.6, 56.9 mm) had only partially elongate ovaries, whereas some larger immature females (58.1–79.1 mm) had more developed ovaries, but without obviously developing ova.

**Geographic distribution (Fig. 55)** Widely distributed in the Caribbean Sea. *Symphurus caribbeanus* has been collected along coastal margins of Central and northern South America and off islands fringing the Caribbean Sea. This species has been collected at St. Martin and Cuba, but most specimens examined were taken at Puerto Rico and Haiti. This species has been collected at coastal locations in Nicaragua, Costa Rica, Panama, and Colombia.

**Bathymetric distribution** *Symphurus caribbeanus* inhabits sand and mud substrates in shallow water. Of 95 specimens for which depth information was available, the majority (79/95, 83%) were collected in 20 m or less (Table 10), and approximately half in waters less than 10 m. All life stages are represented in the shallowest collections. The deepest capture (29 m) is for one lot (UMML 34341) comprising 16 individuals.

**Ecology** Other than depth of occurrence and geographic distribution, little is known about ecological requirements of this species. Austin and Austin (1971) included nine specimens of *S. caribbeanus* (identified as *S. plagusia*) in their survey of feeding habits of fishes inhabiting mangrove areas in southwestern Puerto Rico. These specimens (30–104 mm) had fed mostly on polychaetes and small, benthic crustaceans, and individuals collected at night had undigested food in their stomachs, suggesting nocturnal feeding.

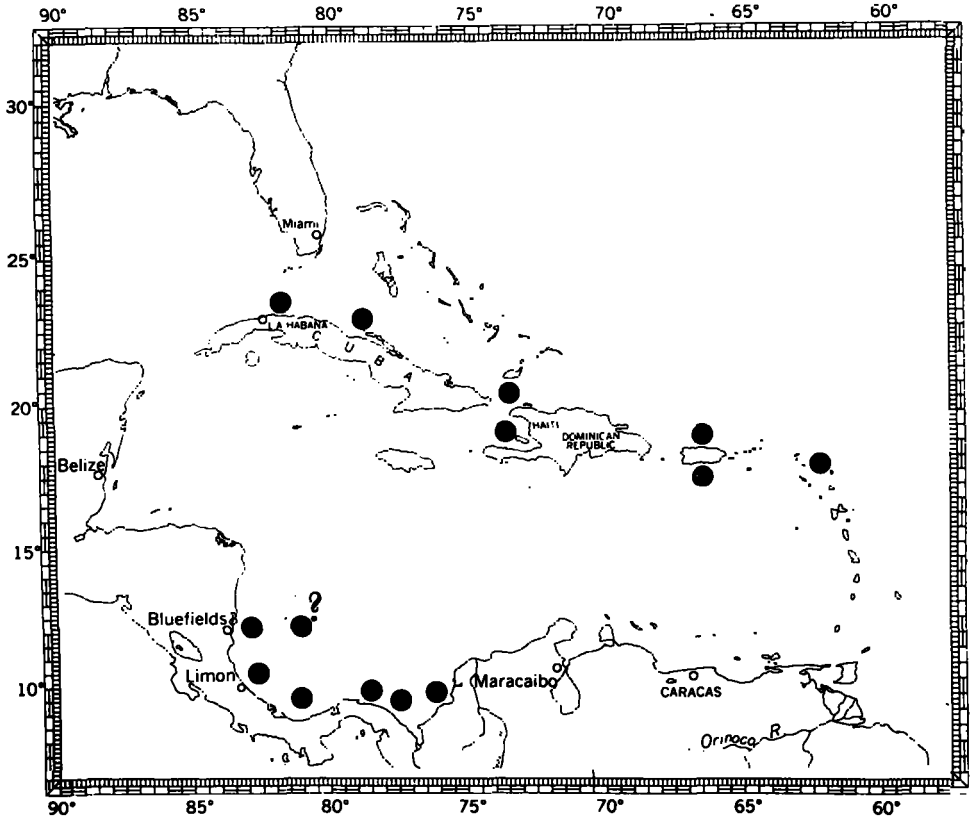


**Figure 55**

Geographic distribution of *Symphurus caribbeanus* based on material examined (discussion of geographic distribution appears in species account).

**Comparisons** Among western Atlantic tonguefishes, *S. caribbeanus* most closely resembles other members of the *S. plagusia* complex (Munroe, 1991) and occurs sympatrically with *S. plagusia* and juvenile and subadult *S. tessellatus*. Meristic values of *S. caribbeanus* overlap almost completely with those of *S. plagusia*. The two species can be distinguished, however, by the absence, in *S. caribbeanus*, of the fleshy ridge on the ocular-side lower jaw (present in *S. plagusia*; see Fig. 3, D and E). *Symphurus caribbeanus* usually has numerous, prominent crossbands on the body, and vertical fins have an alternating series of blotches and unpigmented areas, which are especially well developed posteriorly. In contrast, *S. plagusia* is generally uniformly colored with only slight evidence of crossbanding, and the fins are uniformly colored. *Symphurus caribbeanus* has a more pointed snout with a distance between upper eye and dorsal-fin base usually slightly less than twice the eye diameter, versus a squarish snout with distance from upper eye to dorsal-fin base usually larger than twice the eye diameter in *S. plagusia* (compare Figs. 54 and 60). The body shape of *S. caribbeanus* is rounded, with a pronounced taper posterior to dorsal-fin rays 25–35 (vs. somewhat elongate in *S. plagusia* with a more gradual taper). Additionally, *S. caribbeanus* has a slightly larger eye (8.2–11% HL, usually 9.0–10.0% HL) in comparison with that of *S. plagusia* (usually 7.0–9.0% HL).

*Symphurus tessellatus*, especially juveniles and small adults (to about 150 mm), are superficially similar in overall body shape, relative eye size, and body pigmentation (crossbanding) to *S. caribbeanus*. However, *S. caribbeanus* is easily distinguished from *S. tessellatus* in lacking the black spot on the outer surface of the ocular-side opercle and scales on blind-side dorsal and anal fins (both present in *S. tessellatus*), and *S. tessellatus* has the posterior dorsal and anal fins, as well as the caudal fin, uniformly darkly pigmented without alternating blotches and unpigmented areas and often has black pigment patches on the blind side of the body. In contrast, the posterior regions of the vertical fins of *S. caribbeanus* have alternating dark blotches and unpigmented areas without a progressive darkening in coloration posteriorly in these fins, and the blind side of the body lacks black pigment patches. *Symphurus caribbeanus* also has modally lower counts than *S. tessellatus* (total vertebrae 49–50 vs. 50–53 in *S. tessellatus*; dorsal-fin rays 89–96 vs. 91–102; anal-fin rays 74–80 vs. 77–86; 78–89 vs. 81–96 longitudinal scales).

*Symphurus caribbeanus* differs considerably from *S. civitatium* and *S. oculellus*. There is almost complete overlap in several meristic features between *S. civitatium* and *S. caribbeanus*, however, *S. civitatium* has a fleshy ridge on the ocular-side lower jaw (absent in *S. caribbeanus*; see Fig. 3, D and E) and has lower modal counts for total vertebrae (47–49 vs. 49–50 in *S. caribbeanus*), dorsal-fin rays (86–93 vs. 89–96), and anal-fin rays (70–78 vs. 74–80). *Symphurus caribbeanus* has numerous, well-developed crossbands and vertical fins with an alternating series of blotches and unpigmented areas in individuals of both sexes. In contrast, *S. civitatium* also has narrow crossbands with uniformly colored fins (becoming progressively darker in posterior portions of sexually mature males). *Symphurus caribbeanus* also has a more pointed snout with only a narrow space between the upper eye and dorsal-fin base (vs. square snout with space between upper eye and dorsal-fin base usually greater than twice the eye diameter in *S. civitatium*; compare Figs. 54 and 56).

From *S. caribbeanus*, *S. oculellus* differs in having much higher meristic values (52–55 total vertebrae vs. 48–51 in *S. caribbeanus*; 97–106 dorsal-fin rays vs. 89–96; 81–89 anal-fin rays vs. 74–80 in *S. caribbeanus*). *Symphurus caribbeanus* lacks the black blotch on the ocular-side opercle and fleshy ridge on the ocular-side lower jaw (see Fig. 3, D and E) present in *S. oculellus*. *Symphurus oculellus* also has a deeper body (231–297 SL, $\bar{x}$=274) compared with that of *S. caribbeanus* (277–320 SL, $\bar{x}$=301).

Meristic values of *S. caribbeanus* overlap with those of 11 other Atlantic species of *Symphurus*. *Symphurus caribbeanus* is readily distinguished from seven deepwater Atlantic species with similar meristic values (*S. marginatus*, *S. piger* and *S. stigmosus*, occurring in the Gulf of Mexico and Caribbean Sea, two western North Atlantic species, *S. pusillus* and *S. billykrietei*, the western South Atlantic *S. ginsburgi*, and the eastern Atlantic *S. nigrescens*) in ID pattern (1-4-3 vs. 1-3-2 in the others) and peritoneal pigmentation (unpigmented vs. dark black, visible through both sides of abdominal wall in the others).

Three shallow-water, western Atlantic species, *S. diomedeanus*, which occurs sympatrically with *S. caribbeanus*, and the allopatric *S. plagiusa* and *S. urospilus*, have meristic features similar to those of *S. caribbeanus*. *Symphurus caribbeanus* differs from these in caudal-fin ray count (12 vs. 10 in *S. diomedeanus* and *S. plagiusa*, 11 in *S. urospilus*) and pigmentation of the vertical fins. Other differences between *S. caribbeanus* and these species are discussed in the "Comparisons" sections in respective species accounts.

Meristic values of *S. caribbeanus* overlap with those of six eastern Pacific species possessing either a 1-4-3 or 1-5-3 ID pattern. *Symphurus caribbeanus* differs from *S. leei*, *S. atricaudus*, *S. melanurus*, *S.*

*williamsi*, *S. fasciolaris*, and *S. melasmatotheca*. in lacking a pupillary operculum (present in the others). Of these, *S. caribbeanus* appears most similar to *S. williamsi* but differs in lacking small, ctenoid scales on blind-side dorsal- and anal-fin rays (present in *S. williamsi*) and in having pigmented blotches in the dorsal and anal fins (vs. dorsal and anal fins without blotches in *S. williamsi*).

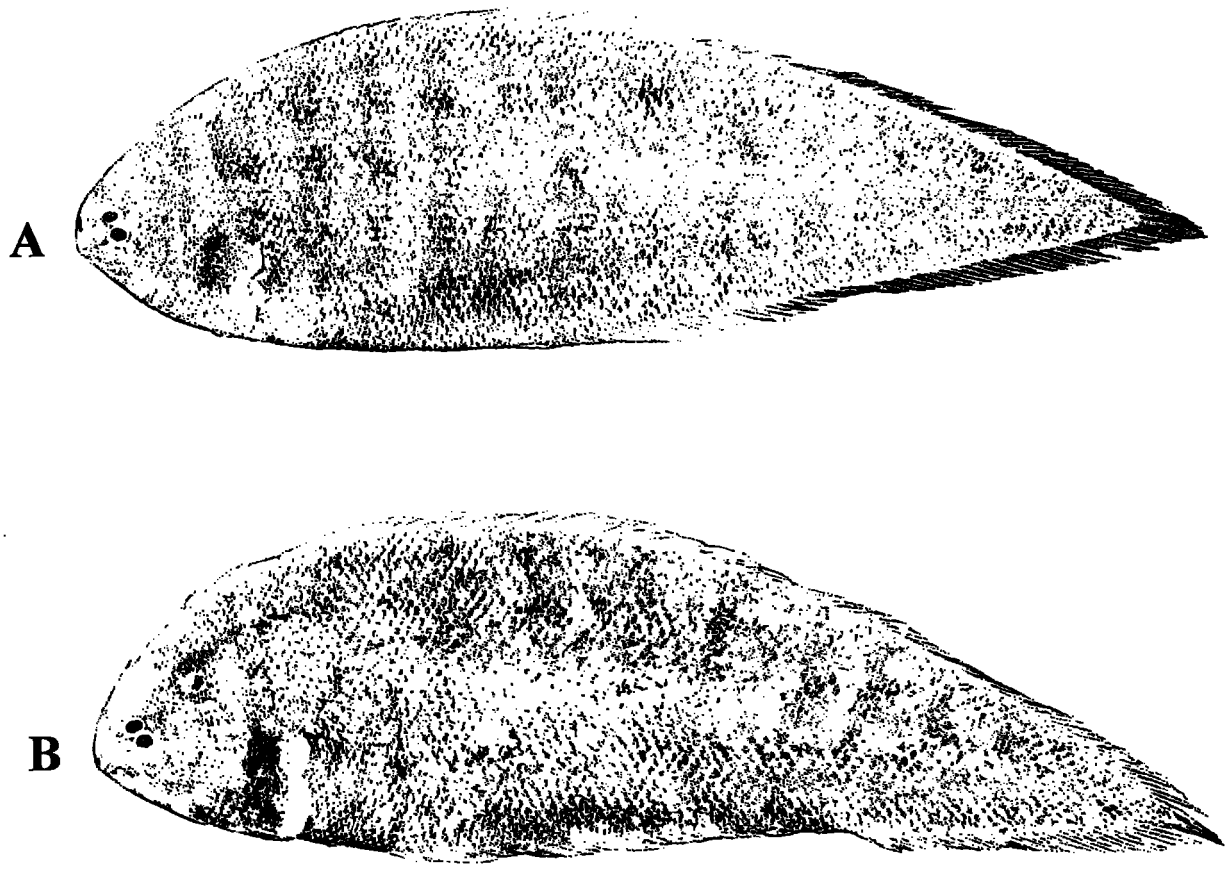


**Figure 56**
*Symphurus civitatium* Ginsburg, FMNH 46369, Gulf of Mexico 19°48'N, 91°20'W. (**A**) male, 130 mm SL; (**B**) female, 133 mm SL.

### *Symphurus civitatium* Ginsburg, 1951 (Figs. 9C, 56–57; Tables 1–10, 35–36)

*Symphurus piger* (not of Goode and Bean, 1886). Baughman, 1950:137 (inner harbor, Freeport, Texas).

*Symphurus civitatum* Ginsburg, 1951:198 (original description, counts, figure, in key; Gulf of Mexico and southeastern coasts United States). Hildebrand, 1954:297 (western Gulf of Mexico; abundance; depth distribution). Hildebrand, 1955:205 (Gulf of Campeche, Mexico; occurrence on pink shrimp grounds). Springer and Bullis, 1956:65 (Gulf of Mexico; *Oregon* stations). Reséndez Medina, 1979:646 (El-Carmen-Machona Redonda and Terminos lagoons, northern Mexico). Lema et al., 1980:42 (Uruguay; based on specimen misidentified by Lazzaro (1977) as *S. ginsburgi*).

*Symphurus civitatus*. (see "Remarks" about emendation of specific name). Briggs, 1958:297 (North Carolina to Florida and widespread in Gulf of Mexico). Roithmayr, 1965:22 (component of industrial bottomfish catch in north central Gulf of Mexico). Struhsaker, 1969:298 (rarely occurring [<10% of the tows] in demersal fish community, continental shelf from North Carolina to central Florida). Swingle, 1971:65 (offshore, Alabama). Topp and Hoff, 1972:78 (general absence on west Florida shelf; geographical distribution). Miller and Jorgenson, 1973:305 (meristic features of four specimens). Chittenden and McEachran, 1976: 93, 99 (abundance on continental shelf of northwestern Gulf of Mexico). Walls, 1976:390 (northern Gulf of Mexico; counts, figure, in key; suggested synonymy with *S. plagiusa*). Schwartz et al., 1981:32 (Cape Fear River, North Carolina). McCaffrey, 1981:204 (in part; abundance and distribution in northeastern Gulf of Mexico). Darcy and Gutherz, 1984:104 (west Florida continental shelf).

Alvarez-Guillén et al., 1985:132 (Carmen Inlet, Terminos Lagoon, Mexico; occurrence). Yáñez-Arancibia et al., 1985:155 (cyclic visitor, Carmen Inlet, Terminos Lagoon, Mexico). Yáñez-Arancibia and Sánchez-Gil, 1986:128 (captures, southern Gulf of Mexico; review of biology). Warlen and Burke, 1990:455 (uncommon occurrence in fall and winter samples, Newport River estuary, North Carolina). Hettler and Barker, 1993:168 (North Carolina; seasonal distribution and abundance of larvae at barrier island inlets).

*Symphurus civitatium.* Munroe, 1991:263 (Cape Hatteras, North Carolina, to Yucatan Peninsula, Mexico; emendation of trivial name; redescription; diagnosis; synonymy; counts, measurements, photograph; in key; bathymetric distribution; size and sexual maturity). Munroe, 1992:371, 382 (ID pattern; geographic, bathymetric distributions). Allen and Baltz, 1997:91 (Barataria Bay, Louisiana; seasonal distribution and abundance).

**Diagnosis** *Symphurus civitatium* is identified by the combination of predominant 1-4-3 ID pattern; 12 caudal-fin rays; 4 hypurals; 86–93 dorsal-fin rays; 70–78 anal-fin rays; 46–50, usually 47–49, total vertebrae; 66–83, usually 74–82, scales in longitudinal series; unpigmented peritoneum; absence of pupillary operculum; relatively small eye (70–110 HL, $\bar{x}$=88); fleshy ridge on ocular-side lower jaw; relatively short jaws usually extending posteriorly to vertical through middle of pupil of lower eye, or sometimes extending to vertical through posterior margin of pupil of lower eye; only anterior regions of ocular-side dentary and premaxilla with teeth along margins (premaxilla on ocular side occasionally lacking teeth); dorsal-fin origin usually situated at vertical anterior to front margin of upper eye, or occasionally only reaching vertical through anterior margin of pupil of upper eye; scales usually absent on blind sides of dorsal- and anal-fin rays (occasionally with 1–3 small scales at bases of fin rays, but without scales distally on fin rays); ocular surface pigmentation usually light to dark brown, occasionally with 6–14, narrow, dark brown crossbands, but without caudal blotch; outer surface of ocular-side opercle without black blotch, pigmentation usually same as on body (some specimens with dusky blotch on upper opercular lobe as consequence of pigment on inner lining of ocular-side opercle showing through to outer surface); inner lining of ocular-side opercle and isthmus usually heavily pigmented, that of blind side usually unpigmented; blind side without pepper-dot pigmentation; dorsal and anal fins considerably darker posteriorly, without spots and without alternating series of pigmented blotches and unpigmented areas; caudal fin without spots or blotches.

**Description** A relatively large species reaching maximum lengths of ca. 152 mm SL. ID pattern usually 1-4-3 (128/171 specimens), less frequently 1-4-2 (19/171), or 1-5-2 (7/171) (Table 2). Caudal-fin rays usually 12 (164/172), infrequently 11 (Table 3). Dorsal-fin rays 86–93 (Table 4). Anal-fin rays 70–78 (Table 5). Total vertebrae 46–50, usually 47–49 (171/175) (Table 6). Hypurals 4 (171/171). Longitudinal scale rows 66–83, usually 74–82 (Table 7). Scale rows on head posterior to lower orbit 16–20, usually 17–19 (Table 8). Transverse scales 26–39, usually 31–38 (Table 9).

Proportions of morphometric features presented in Table 35. Body relatively deep; with greatest depth in anterior one-third; body depth tapering gradually posterior to midpoint. Preanal length shorter than body depth. Head wide, width somewhat less than body depth. Head length shorter than head width (HW:HL 1.0–1.5, $\bar{x}$=1.2). Lower head lobe width less than postorbital length; considerably narrower than upper head lobe. Ocular-side lower opercular lobe considerably wider than upper opercular lobe on ocular side. Snout short; somewhat square (Fig. 56); covered with small ctenoid scales. Dermal papillae well developed on snout and chin regions of blind side of body. Anterior nostril on ocular side, when depressed

**Table 35**

Morphometrics for holotype (USNM 155227) and 29 additional specimens of *Symphurus civitatium*. (Abbreviations defined in methods section; SL is expressed in mm; characters 2 to 14 are expressed in thousandths of SL; 15 to 21 in thousandths of HL; *n* = no. of specimens measured.)

| Character | Holotype | *n* | Range | Mean | SD |
|---|---|---|---|---|---|
| 1. SL | 110.3 | 30 | 48.8–149.3 | 108.6 | 24.96 |
| 2. BD | 304 | 30 | 247–328 | 306.9 | 16.42 |
| 3. PDL | 43 | 29 | 22–46 | 34.5 | 6.78 |
| 4. PAL | 210 | 30 | 147–238 | 202.4 | 19.75 |
| 5. DBL | 957 | 30 | 925–982 | 963.0 | 13.22 |
| 6. ABL | 787 | 30 | 745–891 | 797.9 | 31.36 |
| 7. PL | 68 | 30 | 49–85 | 63.0 | 8.83 |
| 8. PA | 39 | 26 | 33–74 | 44.7 | 10.23 |
| 9. CFL | 124 | 29 | 87–124 | 108.6 | 9.32 |
| 10. HL | 200 | 30 | 170–219 | 191.3 | 11.55 |
| 11. HW | 240 | 30 | 212–271 | 238.3 | 14.42 |
| 12. POL | 134 | 30 | 117–187 | 134.3 | 13.64 |
| 13. UHL | 159 | 30 | 139–184 | 158.9 | 11.60 |
| 14. LHL | 103 | 30 | 87–118 | 103.9 | 6.86 |
| 15. POL | 670 | 30 | 645–740 | 692.0 | 27.45 |
| 16. SNL | 204 | 30 | 169–231 | 206.4 | 13.84 |
| 17. UJL | 272 | 30 | 181–289 | 227.7 | 24.14 |
| 18. ED | 81 | 30 | 70–110 | 87.8 | 10.26 |
| 19. CD | 308 | 29 | 225–331 | 267.9 | 30.55 |
| 20. OPLL | 371 | 29 | 253–388 | 321.3 | 34.80 |
| 21. OPUL | 217 | 29 | 178–329 | 230.0 | 34.86 |

posteriorly, not reaching anterior margin of lower eye. Jaws long; posterior margin of maxilla usually reaching to vertical through middle of pupil of lower eye or sometimes to vertical through posterior margin of pupil of lower eye. Ocular-side lower jaw with distinct, fleshy ridge near posterior margin (Fig. 3D). Teeth well developed on blind-side jaws. Margin of ocular-side dentary with single row of slender teeth on anterior one-third of jaw. Anterior one-third of ocular-side premaxillary margin with only short row of teeth, or occasionally, lacking teeth altogether. Chin depth somewhat larger than snout length. Lower eye relatively small; eyes slightly subequal in position with upper slightly in advance of lower eye. Anterior and medial surfaces of eyes not covered with scales; usually 1–3 small ctenoid scales in narrow interorbital space. Pupillary operculum absent. Dorsal-fin origin (Fig. 3D) usually situated at vertical anterior to anterior margin of upper eye; occasionally only reaching vertical through anterior margin of pupil of upper eye. Scales usually absent on blind sides of dorsal- and anal-fin rays; occasionally with 1–3 small scales at bases of fin rays, but without scales distally on fin rays. Pelvic fin short; longest pelvic-fin ray, when extended posteriorly, usually reaching base of first, or occasionally second, anal-fin ray. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anus, or occasionally extending posteriorly almost to anal-fin origin (membrane torn in most specimens). Caudal fin short. Scales large, ctenoid on both sides of body.

**Pigmentation (Fig. 56, A–B)** Body coloration generally similar for both sexes (dichromatic differences in pigmentation are discussed below). Ocular surface light to dark brown; sometimes with dark brown crossbands continuous across head and body. Crossbands, when developed, narrow, 6 to 14 in number, sometimes sharply contrasting (especially in mature females), otherwise faint and barely perceptible against dark body coloration. Crossbands not continued on dorsal and anal fins. First band crossing head short distance anterior to opercular opening. Trunk crossbands 3 to 6 scale rows wide. Two posteriormost bands immediately anterior to caudal-fin base often conjoined. Dorsal margin of outer surface of ocular-side opercle often with dusky blotch due to dark pigmentation of inner lining of opercle showing through to outer surface. Inner lining of opercle and isthmus on ocular side usually heavily pigmented; lining of blind-side opercle and blind-side isthmus usually unpigmented. Band of pigmentation usually developed on ocular-side upper lip; lower lip on ocular side frequently spotted, but usually without definite band. Blind side off-white. Peritoneum unpigmented.

Pigmentation of dorsal and anal fins generally similar in both sexes, but usually more intense in males. Dorsal- and anal-fin rays on anterior two-thirds of body streaked with brown pigment similar in shade and intensity to body color. Fin rays completely pigmented other than for unpigmented extreme distal tips. Membranes of anterior three-fourths of fins unpigmented. Caudal fin and dorsal and anal fins on posterior one-third of body more heavily pigmented and considerably darker than anterior two-thirds of fin. Fin membranes on posterior quarter of body heavily pigmented. Basal one-third of caudal fin more lightly pigmented than rest of fin. Tips of middle caudal-fin rays unpigmented, or with tips of middle caudal-fin rays streaked with pigment, but membrane unpigmented.

**Size and sexual maturity (Fig. 9C)** A relatively large tonguefish, *S. civitatium* attains sizes of about 152 mm. Males and females attain similar sizes. The largest fish examined, a female (152 mm), was only slightly larger than the largest male (149 mm). Most specimens ranged in size from 80 to 140 mm. Of 188 fish for which size-related life history information was available, there were 102 males (75.5–149.3 mm), 86 females (83.4–152 mm), and 10 immature fish (22.0–57.3 mm) of indeterminate sex. On the basis of reproductive stages of females, this species matures at sizes usually larger than 90 mm. Of 86 females examined, only 3 (83–95 mm) were immature. The two smallest gravid females were 80–90 mm, whereas the majority of gravid females were usually larger (91–140 mm).

**Geographic distribution (Fig. 57)** Western North Atlantic from Cape Hatteras, North Carolina, to the Yucatan Peninsula, Mexico. There is a single record for this species from Bermuda (ANSP 137573). In the Gulf of Mexico, *S. civitatium* occurs most commonly west of Apalachicola Bay in northern Florida (Springer and Bullis, 1956; Chittenden and McEachran, 1976; McCaffrey, 1981). It is one of the most commonly collected tonguefishes on terrigenous sand substrates on the inner continental shelf in the Gulf of Mexico from Alabama to Texas (Hildebrand, 1954). Along the Mexican coast, this species occurs on sandy substrates as far south as coastal lagoons (Lagunas el Carmen y La Machona, Laguna de Terminos) in Tabasco and Campeche, Mexico (Hildebrand, 1955; Reséndez Medina, 1979; Alvarez-Guillén et al., 1985; Yáñez-Arancibia and Sánchez-Gil, 1986), and on the continental shelf of the southern Gulf of Mexico (Cabo Rojo, Veracruz, to Sabuncuy, Yucatan Peninsula, Mexico).

Collection data for specimens from this study reveal an absence of this species from the western Florida shelf. Only two collections record this species from the Tortugas region off southern Florida. Topp and Hoff (1972) also noted the general absence of this species along the west Florida shelf and found just a single record for *S. civitatium* in the eastern Gulf of Mexico (St. Joseph Bay; from Ginsburg, 1951). Neither their efforts during the *Hourglass* cruises on the continental shelf off west Florida nor other studies (Moe and Martin, 1965; Ogren and Brusher, 1977; Naughton and Saloman, 1978) yielded this species. Furthermore, Darcy and Gutherz (1984) reported taking only a single specimen during 338 10-min bottom trawls in 9 to 193 m on the west Florida shelf.

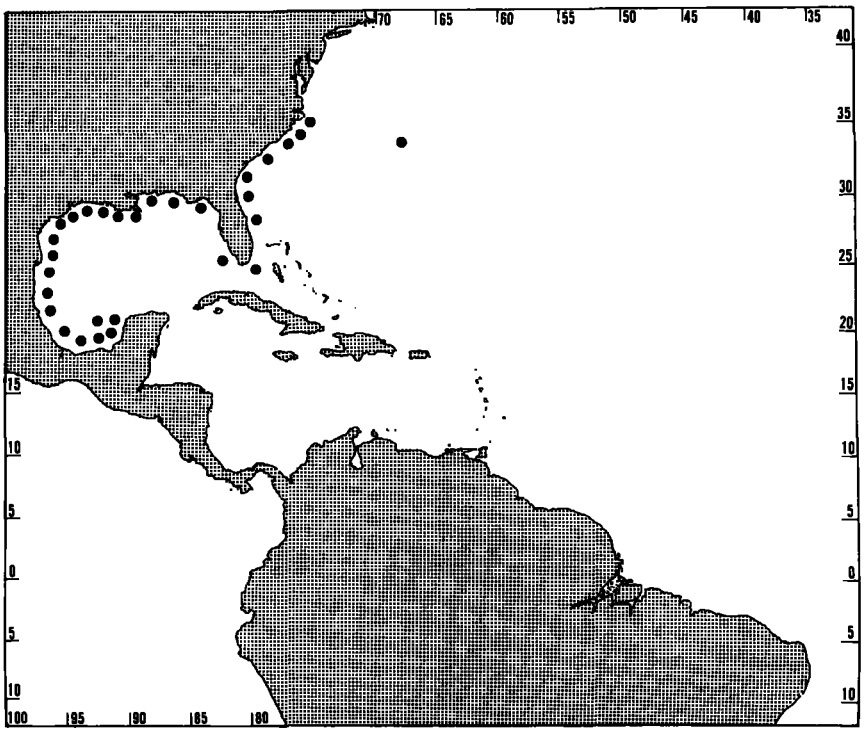


**Figure 57**

Geographic distribution of *Symphurus civitatium* based on material examined (discussion of geographic distribution appears in species account).

*Symphurus civitatium* occurs on sand or silt substrates through its range. The geographic and bathymetric distributions of this species apparently coincide with the distribution of terrigenous, quartzite sandy and silty substrates on the inner continental shelf. The scarcity of this species on the west Florida shelf and Yucatan Peninsula may reflect the strikingly different substrate compositions there. Along the west Florida shelf, Topp and Hoff (1972) reported that substrates consist of lithified sediments of cemented lime, including 1) nearshore deposits of cemented shell beachrock, 2) limestone, ranging from soft marl to conglomeritic and foraminiferal limestone, 3) small patches of living and dead coral, and 4) calcareous algae, primarily in depths ranging from 55 to 92 m. They noted that substrates off the Yucatan Peninsula are similar in composition to those of the west Florida shelf. In contrast, in the central and western Gulf of Mexico from the Mississippi Delta to Cabo Rojo, Veracruz, where *S. civitatium* is very abundant, substrates on the inner shelf consist largely of terrigenous quartzite sands, silts, and clays delivered primarily by Mississippi and Rio Grande rivers (van Andel, 1960). Hildebrand (1954) noted that although this species was very common on sand substrates in the western Gulf region, it was not taken on the "24–10 grounds" where "most of the bottom is mud, some of it is soft mud and a small part is shell."

Substrate preference may affect the distribution of *S. civitatium* in coastal seas off the southeastern United States. The depth of occurrence (11–40 m, see below) for adult *S. civitatium* apparently coincides with sand-silt substrates on the inner portions of the shelf, and this species is absent from live-bottom habitats occurring at similar depths (Struhsaker, 1969).

The specimen of *S. civitatum* reported by Lazzaro (1977:69) from the continental shelf off Uruguay is neither this species nor any other of the *Symphurus plagusia* complex (Munroe, 1991). The body shape evident in the photograph, meristic features, and great depth of occurrence (183 m) indicate that the specimen is probably *S. ginsburgi*.

**Bathymetric distribution** Although *S. civitatium* has been collected over a wide depth range (1–73 m), the center of abundance of adults, based on overall frequency of capture and general abundance, occurs between 11–45 m (Table 10). Approximately 98% (214/218) of the adult specimens examined in the present study were captured at these depths. The deepest captures were at 73 and 62 m, where a single fish was taken each time. It is unusual for adult *S. civitatium* to occur in shallow, inshore regions. The 130 fish examined in this study collected shallower than 10 m were juveniles (22–66 mm) from North Carolina and Louisiana estuaries. Other studies in

North Carolina have recorded this species from shallow-water environments. For example, Schwartz et al. (1981) collected a few specimens in the Cape Fear River estuary but listed the species as rare in this area. It was also uncommon in fall and winter sampling of larval fishes in the Newport River estuary (Warlen and Burke, 1990), and only small numbers were taken in ichthyoplankton collections at two barrier island inlets in North Carolina (Hettler and Barker, 1993).

Of 430 specimens of tonguefishes examined from estuarine waters of North Carolina in the present study, all but nine were *S. plagiusa*. Most juvenile *S. civitatium* co-occurred in samples with juvenile *S. plagiusa*. On the basis of the low frequency of occurrence of *S. civitatium* in these samples (ca. 2% of total specimens), I concur with Schwartz et al. (1981) that *S. civitatium* is rare in inshore waters in North Carolina estuaries. However, although rare in North Carolina estuaries, this species is perhaps more abundant in estuaries farther south along coastal Georgia and northern Florida, where *S. civitatium* occur in greater abundance offshore. In some estuaries along the Gulf coast west of the Mississippi, such as Barataria Bay, Louisiana, juvenile *S. civitatium* are more abundant in some inshore areas than are juveniles of *S. plagiusa* (Allen and Baltz, 1997). The possibility that two co-occurring species of *Symphurus* can be present in estuarine samples of tonguefishes should be recognized in studies conducted in these areas along the southeast and Gulf coasts, and the seasonal occurrence, abundance, and fate of juvenile *S. civitatium* in these estuarine areas needs further investigation. Deepwater captures (80–187 m) reported by McCaffrey (1981) for specimens purported to be *S. civitatium* taken on the continental shelf in the northeastern Gulf of Mexico are questionable because they are based on more than one species (Munroe, 1991), and not all specimens could be located for inclusion in this study.

**Geographic variation** Scarcely any variation was observed in dorsal- and anal-fin ray counts, and counts of total vertebrae of *S. civitatium* from five different areas of the geographic range (Table 36).

**Remarks** Munroe (1991:266) discussed justification for the emended spelling of the specific epithet for this species. The "Material examined" section in the account of *S. civitatium* in Munroe (1991) lists 148 paratype specimens counted but not measured. The 148 actually refers to the total number of specimens from which meristic information was taken. Only the first 36 specimens, i.e. those that were clearly demarcated from the others, are actual paratypes of this species. Remaining specimens listed in the counted section were specifically indicated as "nontypes." The corrected list of material studied is presented below (see Appendix).

**Table 36**

Geographic variation in selected meristic features of *Symphurus civitatium*. Abbreviations: SEUS = southeastern United States; EGMX = eastern Gulf of Mexico; WGMX = western Gulf of Mexico; MEX = Mexico, including Yucatan shelf region; BERM = Bermuda; *n* = no. of specimens measured.

| Character | Area | *n* | Mean | Range | SD |
|---|---|---|---|---|---|
| Dorsal rays | SEUS | 23 | 89.83 | 86–92 | 1.614 |
| | EGMX | 23 | 89.83 | 88–92 | 1.193 |
| | WGMX | 73 | 90.16 | 87–92 | 1.155 |
| | MEX | 48 | 90.21 | 86–93 | 1.443 |
| | BERM | 1 | 91 | — | — |
| Anal rays | SEUS | 23 | 74.26 | 71–76 | 1.214 |
| | EGMX | 24 | 74.25 | 73–76 | 0.989 |
| | WGMX | 74 | 74.31 | 70–77 | 1.249 |
| | MEX | 48 | 74.33 | 72–78 | 1.310 |
| | BERM | 1 | 75 | — | — |
| Vertebrae | SEUS | 23 | 47.96 | 47–49 | 0.562 |
| | EGMX | 25 | 47.92 | 47–49 | 0.702 |
| | WGMX | 76 | 47.93 | 46–50 | 0.699 |
| | MEX | 48 | 48.02 | 47–49 | 0.688 |
| | BERM | 1 | 48 | — | — |

**Comparisons** *Symphurus civitatium* is most similar to, but has a completely allopatric distribution from, the Caribbean and South Atlantic species, *S. plagusia*, and differs from that species in its modally lower meristic features (total vertebrae modally 47–49 vs. 49–51 in *S. plagusia*; dorsal-fin rays 86–93 vs. 89–97; anal-fin rays 70–78 vs. 73–81); and degree of development of sexually dimorphic coloration. In *S. civitatium*, there is considerably more pronounced sexual dimorphism in pigmentation. Females tend to have well-developed crossbands on the body, whereas in males the crossbands are less conspicuous. In male *S. civitatium*, posterior portions of dorsal and anal fins are noticeably darkened with black pigment (black pigment absent in females). In contrast, in *S. plagusia*, both sexes are more or less uniformly pigmented with only slight evidence of banding on the body, and with vertical fins of both sexes uniformly colored with no darkening in the posterior portion of the body.

Despite overlap in certain meristic values, *S. civitatium* and *S. tessellatus* are quite distinctive. The easiest way to distinguish these species is by noting that *S. civitatium* has a well-developed fleshy ridge on the ocular-side lower jaw (absent in *S. tessellatus*;

compare Fig. 3, D and E), lacks a black spot on the ocular-side opercle, has an unpigmented or only lightly pigmented inner opercular lining on the blind side, and when present on the body, crossbands are faint and narrow, whereas *S. tessellatus* has a bold pattern of wide crossbands, a heavily pigmented inner opercular lining, and a well-developed, black opercular spot. Other distinctions between these species include the absence of scales on blind sides of dorsal- and anal-fin rays of *S. civitatium* (present in *S. tessellatus* larger than about 60 mm), usually fewer vertebrae (total vertebrae 47–49 versus 50–53 in *S. tessellatus*), and modally lower meristic features: dorsal-fin rays 86–93 versus 91–102 (usually 93–101) in *S. tessellatus*; anal-fin rays 70–78 versus 77–86; scales in a longitudinal series 66–83 versus 81–96.

*Symphurus civitatium* is similar to *S. oculellus* with respect to small eye size, and presence of a fleshy ridge on the ocular-side lower jaw. It differs from this species, however, in its much lower counts (46–50 total vertebrae versus 52–55 in *S. oculellus*; dorsal-fin rays 86–93 versus 97–106; anal-fin rays 70–78 versus 81–89) and pigmentation pattern. *Symphurus civitatium* has a relatively uniform body coloration with faint crossbands, uniformly pigmented fins without blotches and no pigment spot on the outer opercle (vs. sharply contrasting crossbands, pigmented blotches alternating with unpigmented areas in dorsal and anal fins, and black spot on outer opercle in *S. oculellus*). Furthermore, in *S. civitatium*, the first dorsal-fin ray is usually located along a vertical anterior to the upper eye, whereas in *S. oculellus*, the dorsal-fin origin usually extends anteriorly only to the vertical through the anterior margin or mid-eye region of the upper eye.

Some meristic values of *S. civitatium* overlap those of 11 other species of Atlantic tonguefishes. *Symphurus civitatium* occurs sympatrically with *S. diomedeanus* and *S. plagiusa* and may sometimes be collected with these species. Differences between *S. civitatium* and these species are discussed in the "Comparisons" sections for *S. plagiusa* and *S. diomedeanus*. Excluding differences in caudal-fin ray counts, there is almost complete overlap in meristic features between *S. civitatium* and the sympatric (but not syntopic) western North Atlantic species, *S. urospilus*. Differences between *S. civitatium* and *S. urospilus* are discussed in the "Comparisons" section in the account for *S. urospilus*.

Meristic values of *S. civitatium* overlap those of five eastern Pacific species, *S. atricaudus*, *S. melanurus*, *S. williamsi*, *S. fasciolaris*, and *S. melasmatotheca*, possessing either a 1-4-3 or 1-5-3 ID pattern. Of these, *S. civitatium* is most similar to *S. melanurus* in that both possess a fleshy ridge on the ocular-side lower jaw, and in both the first dorsal-fin ray reaches the vertical equal with or anterior to the anterior margin of the upper eye. *Symphurus civitatium* lacks a pupillary operculum (weakly developed pupillary operculum usually present in *S. melanurus*), has fewer longitudinal scales (66–83 vs. 89–108 in *S. melanurus*), and *S. civitatium* has an unpigmented or only lightly pigmented inner lining on the blind-side opercle (vs. darkly pigmented inner lining on blind-side opercle in *S. melanurus*).

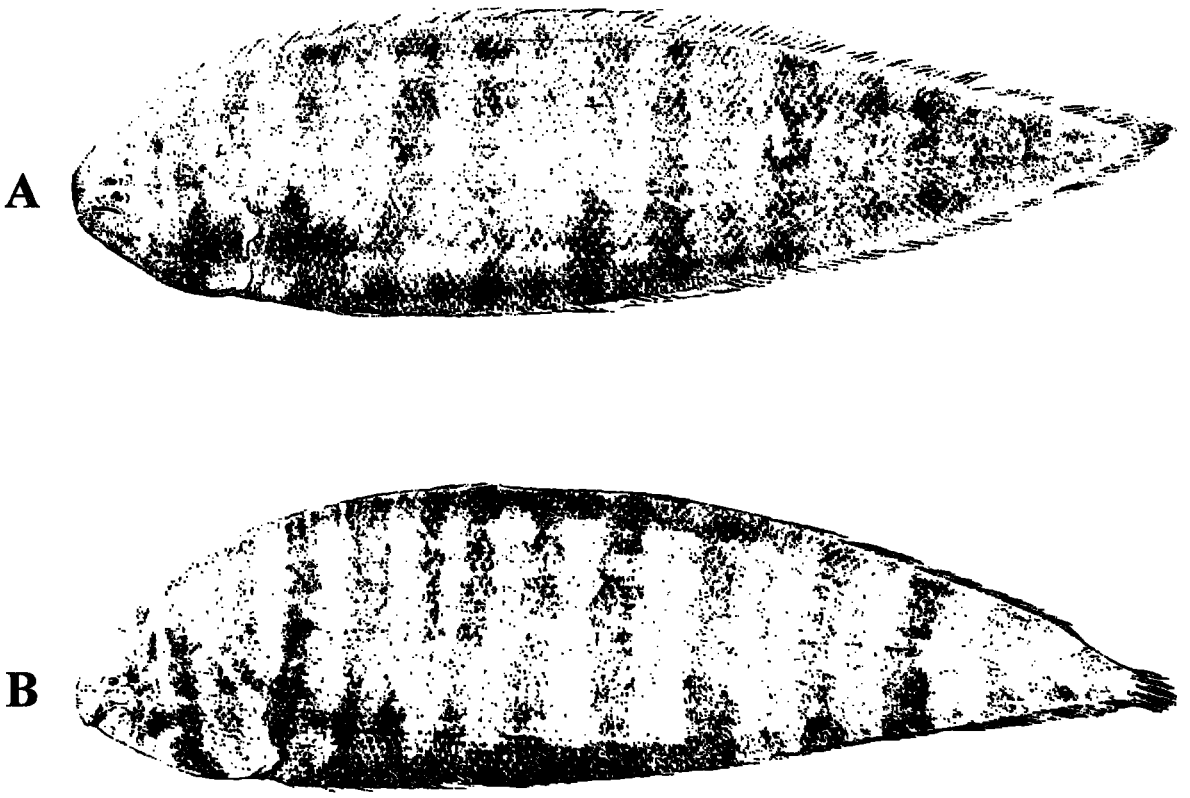


**Figure 58**

*Symphurus oculellus* Munroe. (**A**) Holotype, USNM 159606, 144 mm SL, male, 6°24'N, 55°00'W. (**B**) USNM 313515, 151 mm SL, female, 6°21'N, 54°28'W.

## *Symphurus oculellus* Munroe, 1991 (Figs. 9E, 58–59; Tables 1–10, 37)

*Symphurus atricaudus* (not of Jordan and Gilbert, 1880). Puyo, 1949:179 (French Guyana; counts, color description, poor figure; distinguished from *S. plagusia*).

*Symphurus oculellus* Munroe, 1991:276 (original description; Guyana to northeast Brazil; diagnosis; synonymy; counts, measurements, photograph; in key; bathymetric distribution; size and sexual maturity). Munroe, 1992:371, 382 (ID pattern; geographic, bathymetric distributions). Cervigón et al., 1993:306 (Venezuela).

**Diagnosis** *Symphurus oculellus* is distinguished from all congeners by the following combination of characters: predominant 1-4-3 ID pattern; 12 caudal-fin rays; 4 hypurals; 97–106 dorsal-fin rays; 81–89, usually 83–88, anal-fin rays; 52–55, usually 53–54, total vertebrae; 84–97, usually 86–93, scales in longitudinal series; unpigmented peritoneum; absence of pupillary operculum; lacking small scales on blind sides of dorsal- and anal-fin rays; prominent fleshy ridge on ocular-side lower jaw; relatively long jaws with maxilla usually extending posteriorly to vertical through posterior margin of pupil of lower eye, occasionally extending to or slightly beyond vertical through posterior margin of lower eye; margin of ocular-side dentary usually with mostly incomplete row of teeth; premaxillary margin on ocular side either lacking teeth, or with very short row of teeth on anterior one-third; relatively small eye (68–104 HL, $\bar{x}$=84); dorsal-fin origin usually at or occasionally slightly anterior to vertical through anterior margin of upper eye; ocular surface pigmentation dark to light brown with 10–14 well-developed, sharply contrasting, somewhat narrow, dark brown crossbands on head and trunk, but without pigmented blotch on caudal region of body; outer surface of ocular-side opercle with dark melanophores in diffuse circular pattern or with melanophores coalesced into some-

what rounded pigment spot; inner lining of opercle and isthmus more heavily pigmented on ocular surface than blind side; blind side without pepper-dot pigmentation; and dorsal, anal, and caudal fins with alternating series of pigmented blotches and unpigmented areas.

**Description** A relatively large species attaining maximum lengths of ca. 189 mm SL. ID pattern usually 1-4-3 (55/64 specimens), infrequently 1-3-4 (2), 1-5-3 (3), 1-4-2 (2) or 1-3-3 (2) (Table 2). Caudal-fin rays 12 (59/63 specimens), less frequently 11 (Table 3). Dorsal-fin rays 97–106 (Table 4). Anal-fin rays 81–89, usually 83–87 (Table 5). Total vertebrae 52–55, usually 53–54 (55/63) (Table 6). Hypurals 4 (63/63). Longitudinal scale rows 84–97, usually 86–93 (Table 7). Scale rows on head posterior to lower orbit 19–23 (Table 8). Transverse scales 36–42 (Table 9).

Proportions of morphometric features presented in Table 37. Body relatively elongate, with greatest body depth from vertical through anal-fin rays 10–15 posteriorly to midpoint of body; body depth tapering gradually posterior to body midpoint. Preanal length shorter than body depth. Head wide, somewhat narrower than body depth. Head length shorter than head width (HW:HL=1.1–1.5, $\bar{x}$=1.2). Lower head lobe width less than postorbital length; considerably narrower than upper head lobe. Lower opercular lobe of ocular side wider than upper opercular lobe. Snout (Fig. 58, A–B) moderately long, slightly rounded or truncate, covered with small ctenoid scales. Anterior nostril not reaching anterior margin of lower eye when depressed posteriorly. Dermal papillae well developed, but not particularly dense, on snout and chin regions of blind side of head, occasionally extending onto ocular-side snout. Jaws long; posterior margin of maxilla usually reaching to vertical through posterior margin of pupil of lower eye, occasionally to or slightly beyond vertical through posterior margin of lower eye. Ocular-side lower jaw with distinct, fleshy ridge near posterior margin (Fig. 3D). Teeth well developed on blind-side jaws. Margin of ocular-side dentary usually with single, mostly incomplete row of slender teeth; ocular-side premaxillary margin either lacking teeth, or with very short row of teeth along no more than one-third of premaxilla anterior to vertical through base of anterior nostril. Chin depth slightly larger than snout length. Lower eye relatively small; eyes slightly subequal in position with upper usually slightly in advance of lower eye. Anterior and medial surfaces of eyes not covered with scales; usually only 1–3 small, ctenoid scales in narrow interorbital region. Interorbital space sometimes equalling one-half diameter of lower eye. Pupillary operculum absent. Dorsal-fin origin usually at, or occasionally slightly anterior to, vertical through anterior margin of upper eye; predorsal length short. Scales absent from distal two-thirds of blind sides of dorsal- and anal-fin rays, occasionally with one or two scales occurring sporadically on blind sides of some dorsal- and anal-fin ray bases. Pelvic fin short; longest pelvic-fin ray extending posteriorly to base of first, or occasionally second, anal-fin ray. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anus, or occasionally extending posteriorly to anal-fin origin (membrane torn in most specimens). Caudal fin short. Scales large, ctenoid on both sides of body.

**Table 37**

Morphometrics for holotype (USNM 159606) and 13 paratypes of *Symphurus oculellus*. (Abbreviations defined in methods section; SL is expressed in mm; characters 2 to 14 are expressed in thousandths of SL; 15 to 21 in thousandths of HL; *n* = no. of specimens measured.)

| Character | Holotype | *n* | Range | Mean | SD |
|---|---|---|---|---|---|
| 1. SL | 144.1 | 14 | 75.8–164 | 142.5 | 21.09 |
| 2. BD | 271 | 14 | 231–297 | 274.5 | 17.19 |
| 3. PDL | 32 | 13 | 32–47 | 38.6 | 4.13 |
| 4. PAL | 199 | 14 | 189–243 | 205.6 | 13.32 |
| 5. DBL | 968 | 13 | 953–968 | 961.4 | 4.13 |
| 6. ABL | 795 | 14 | 765–837 | 793.7 | 18.74 |
| 7. PL | 53 | 12 | 40–64 | 54.3 | 6.08 |
| 8. PA | 37 | 12 | 20–60 | 41.2 | 12.62 |
| 9. CFL | 90 | 14 | 80–99 | 88.9 | 5.53 |
| 10. HL | 180 | 14 | 168–218 | 182.3 | 11.58 |
| 11. HW | 209 | 14 | 198–281 | 216.8 | 21.37 |
| 12. POL | 126 | 14 | 112–153 | 124.8 | 9.38 |
| 13. UHL | 140 | 14 | 126–151 | 139.4 | 6.81 |
| 14. LHL | 98 | 14 | 79–111 | 92.9 | 8.13 |
| 15. POL | 700 | 14 | 651–722 | 683.8 | 20.64 |
| 16. SNL | 204 | 14 | 190–227 | 209.0 | 11.67 |
| 17. UJL | 254 | 14 | 221–258 | 238.3 | 11.74 |
| 18. ED | 69 | 14 | 68–104 | 84.3 | 10.52 |
| 19. CD | 277 | 14 | 214–291 | 248.4 | 23.62 |
| 20. OPLL | 308 | 14 | 264–341 | 292.3 | 23.77 |
| 21. OPUL | 200 | 14 | 174–246 | 210.6 | 20.39 |

**Pigmentation (Fig. 58, A and B)** Body coloration similar for both sexes. Ocular surface dark to light brown with 10–14 (usually 10–12), well-developed, sharply contrasting, somewhat narrow, dark brown crossbands on head and trunk. Anteriormost crossband on head immediately posterior to eyes; second crossband situated short distance (usually only 3–4 scales) posteriorly. Throughout most of their vertical extent, two anteriormost bands usually separate; several specimens with first two crossbands coalesced on ventral portion of opercle forming wide,

somewhat circular spot. Crossbands on head somewhat narrower than those on mid- and posterior portions of body. Number of crossbands on trunk variable, differing in degree of completeness, especially in region between opercular opening to point about two-thirds of trunk length. Some bands on body complete, continuous on dorsal and anal fins as dark brown blotches. Posteriormost crossband situated short distance from caudal-fin base, somewhat expanded and slightly arched. Blind side creamy white. Peritoneum unpigmented. Blind-side ovarian membrane (visible only by dissection) spotted with small melanophores. Outer surface of ocular-side opercle with dark melanophores in diffuse pattern or with melanophores sometimes coalesced into somewhat rounded pigment spot. Inner lining of opercle and isthmus more heavily pigmented on ocular surface; blind-side inner opercle with pigmentation restricted to small band of pepper-dot melanophores along ventral margin. Isthmus on blind side not heavily pigmented, but often with pepper-dot pattern of melanophores. Pigment band well developed on ocular-side upper lip; lower lip frequently spotted, but without well-defined pigment band.

Dorsal, anal, and caudal fins with alternating series of blotches and unpigmented areas. Dorsal fin scarcely pigmented in anterior one-half of body; with series of alternating blotches and unpigmented areas beginning at approximately body midpoint and continuing to posterior of fin. Anterior one-fourth of anal fin without blotches; posterior three-fourths with pattern of alternating blotches and unpigmented areas as in dorsal fin. Blotches in dorsal and anal fins are 3–5 finrays wide (including adjoining membrane). Both dorsal and anal fins with blotches coalescing in posterior one-sixth of fins and forming continuous pigmentation band on fins. Posterior portions of fins becoming gradually darker; blotches, although still present, much more difficult to discern. Distal two-thirds of caudal fin heavily pigmented; proximal one-third relatively lightly pigmented. Caudal fin of most specimens not uniformly pigmented; small cluster of rays (usually 2–4) in middle of fin more lightly pigmented giving appearance of alternating darkly and lightly pigmented areas. Smaller number of specimens with entire caudal fin heavily pigmented without pattern of alternating darkly and lightly pigmented areas.

**Size and sexual maturity (Fig. 9E)** *Symphurus oculellus* is a relatively large tonguefish, attaining sizes of about 190 mm. Most specimens were between 130 and 160 mm. No significant differences were found between the sexes in overall size. The largest specimen examined (sex not determined) was 189 mm; the largest male and female measured were 181 and 180 mm. Among 76 specimens examined for life history information, 39 were males (82.2–181 mm), 32 females (75.8–180 mm), and 5 specimens were of unknown sex. On the basis of reproductive stages of females, this species attains sexual maturity at about 110 mm. All females larger than 111 mm had elongate ovaries. The smallest female, an immature fish of 75.8 mm, had only partially elongate ovaries. The next smallest female was 111 mm and had small developing ova in the gonads. All other females were larger than 130 mm, had elongate ovaries, and were considered sexually mature.

**Geographic distribution (Fig. 59)** A tropical species with a fairly restricted distribution along the inner continental shelf of northeastern South America from Guyana (57°W) to northeastern Brazil (2°S, 40°W) where the majority of specimens have been collected. All but one specimen (UMML 12265; 2°20'S) were collected north of the Amazon outflow. Because little systematic sampling has been conducted on the inner continental shelf off equatorial Brazil, it is not known whether *S. oculellus* occurs more frequently in areas immediately south of the mouth of the Amazon.

**Bathymetric distribution** *Symphurus oculellus* occurs on mud substrates at moderate shelf depths (7–110 m) and does not appear to use nearshore habitats or estuarine environments as nursery areas. Most specimens (76/81; 94%) were collected between 11 and 70 m (Table 10); only three specimens (76–

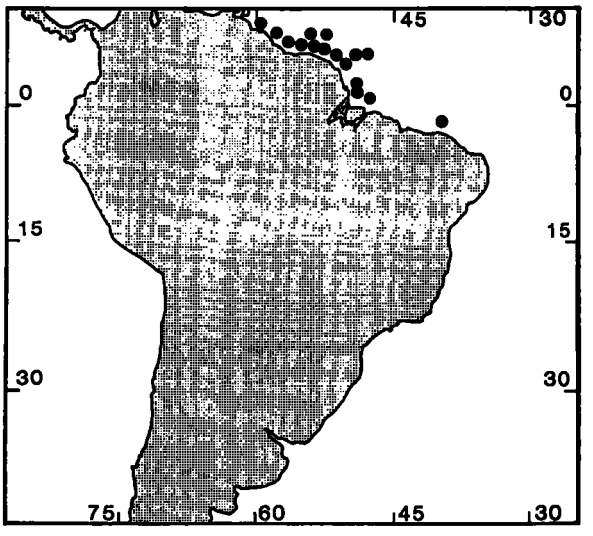


**Figure 59**

Geographic distribution of *Symphurus oculellus* based on material examined (discussion of geographic distribution appears in species account).

189 mm) were collected from depths greater than 70 m. At the shallower depths, *S. oculellus* is occasionally collected with adult *S. tessellatus*; however, size differences between the two species in these collections are quite striking. All *S. tessellatus* collected with *S. oculellus* were large adults (>130 mm), whereas the *S. oculellus* were a mixture of sizes, with juveniles as small as 78 and 82 mm.

**Remarks** Discussion of the synonymy for this species was provided in Munroe (1991:276).

**Comparisons** *Symphurus oculellus* most closely resembles and is largely sympatric with *S. tessellatus*, *S. diomedeanus*, and *S. plagusia*. Differences between *S. oculellus* and *S. diomedeanus* are presented in the "Comparisons" section of the account for *S. diomedeanus*. *Symphurus oculellus* differs from *S. tessellatus* in lacking the 4–8 small, but well-developed, scales on blind-side dorsal- and anal-fin rays characteristic of *S. tessellatus* (especially evident in specimens larger than 70 mm), a smaller eye (68–104, $\bar{x}$=84 HL vs. 79–114, $\bar{x}$=95 HL in *S. tessellatus*), and higher meristic values (dorsal-fin rays 97–106 vs. 91–102 in *S. oculellus*; anal-fin rays 81–89 vs. 74–86; total vertebrae usually 53–54 vs. 50–53). *Symphurus tessellatus* also lacks the fleshy ridge on the ocular-side lower jaw that is usually present and well developed in *S. oculellus* (compare Fig. 3, D and E). And, the posterior extension of the jaws is slightly less extensive in *S. tessellatus*, reaching only to about the vertical through the posterior margin of the pupil or posterior margin of the lower eye. In *S. oculellus*, the jaws extend farther backwards reaching a vertical through the posterior margin of the eye, and in many specimens the jaws extend slightly posterior to the vertical through the posterior margin of the lower eye.

*Symphurus oculellus* has 10 to 14 (usually 10–12), narrower, crossbands; *S. tessellatus* generally has about nine, wide, dark-brown crossbands. In *S. oculellus*, the dorsal and anal fins are not uniformly dark brown or black but, instead, in the posterior two-thirds of the dorsal and anal fins there is an alternating series of blotches and unpigmented areas, and the blind-side inner opercular lining and isthmus are much more lightly pigmented than corresponding structures on the ocular surface of the body. In *S. tessellatus*, the caudal fin and the posterior third of the dorsal and anal fins are usually dark brown or black and without alternating series of blotches and unpigmented areas, and the isthmus and inner opercular lining on the blind side are heavily pigmented, similar to those on the ocular side of the body.

*Symphurus oculellus* is also similar to *S. plagusia* with respect to small eye size and presence of a fleshy ridge on the ocular-side lower jaw. It differs from this species, however, in its much higher counts (52–55 total vertebrae vs. 47–51 in *S. plagusia;* dorsal-fin rays 97–106 vs. 89–97; anal-fin rays 81–89 vs. 73–81) and pigmentation pattern. *Symphurus oculellus* has sharply contrasting crossbands, pigmented blotches alternating with unpigmented areas in the dorsal and anal fins, and a black spot on outer opercle (vs. a relatively uniform body coloration with faint crossbands, uniformly pigmented fins without blotches and no pigment spot on the outer opercle in *S. plagusia*). Furthermore, in *S. plagusia*, the first, and occasionally the second, rays of the dorsal fin are usually located along a vertical line anterior to the upper eye, whereas in *S. oculellus*, the dorsal-fin origin usually extends anteriorly only to the vertical through the anterior margin or mideye region of the upper eye. Differences in morphometrics between the two species are that *S. oculellus* has a narrower body (231–297 SL vs. 278–319 SL in *S. plagusia*) and attains larger sizes (up to 190 mm vs. largest of only 131 mm in *S. plagusia*).

*Symphurus oculellus* is similar to *S. civitatium* with respect to small eye size and presence of a fleshy ridge on the ocular-side lower jaw. Differences between these species are discussed in the "Comparisons" section under the species account for *S. civitatium*.

There are seven eastern Pacific *Symphurus* with similar ID patterns, comparable fin-ray counts, or pigment patterns reminiscent of those observed in *S. oculellus*. Of these seven species, only *S. chabanaudi* and *S. elongatus* are similar to *S. oculellus* in lacking a pupillary operculum. Many meristic features of *S. oculellus* completely overlap those of the eastern Pacific *S. chabanaudi*. *Symphurus oculellus* differs from *S. chabanaudi*, however, in lacking the 4–8 small, but well-developed scales on blind-side dorsal- and anal-fin rays prominent in *S. chabanaudi*, especially those larger than 60 mm; in having a somewhat smaller eye (1.2–1.9, $\bar{x}$=1.5 SL in *S. oculellus* vs. 1.7–2.3, $\bar{x}$=1.9 SL), and *S. oculellus* has a well-developed fleshy ridge on the ocular-side lower jaw (absent in *S. chabanaudi*). The jaws in *S. oculellus* extend posteriorly to the vertical through the posterior margin of the lower eye, and in many specimens the jaws actually extend slightly beyond the posterior margin of the eyes, whereas in *S. chabanaudi* the posterior extension of the jaws reaches only to a vertical through the posterior margin of the pupil or the posterior margin of the lower eye. *Symphurus oculellus* also differs from *S. chabanaudi* in the relative frequencies of specimens

possessing 1-5-3 and 1-4-3 ID patterns. *Symphurus chabanaudi* has a much higher frequency of occurrence of the 1-5-3 ID pattern (50% of individuals examined) compared with only 30% with a 1-4-3 pattern. In contrast, 55 of 64 (86%) of the *S. oculellus* examined had a 1-4-3 pattern and only three specimens possessed a 1-5-3 pattern. *Symphurus chabanaudi* also differs from *S. oculellus* in that this species generally has about nine, wide, dark-brown crossbands compared with the more numerous (10–14, usually 10–12), narrower bands in *S. oculellus*. In addition, in *S. oculellus* the posterior two-thirds of the dorsal and anal fins usually have alternating series of blotches and unpigmented areas, whereas in *S. chabanaudi* the posterior third of the dorsal and anal fins, and the caudal fin, are usually uniformly dark brown or black without alternating blotches and unpigmented areas.

There is almost complete overlap in fin-ray and vertebral counts between those of *S. oculellus* and *S. elongatus*, however, these species are otherwise distinct. *Symphurus oculellus* has prominent crossbands on the body and a dark blotch on the ocular-side opercle, whereas in *S. elongatus* the body is uniformly pigmented without crossbands and a prominent blotch on the ocular-side opercle is wanting.

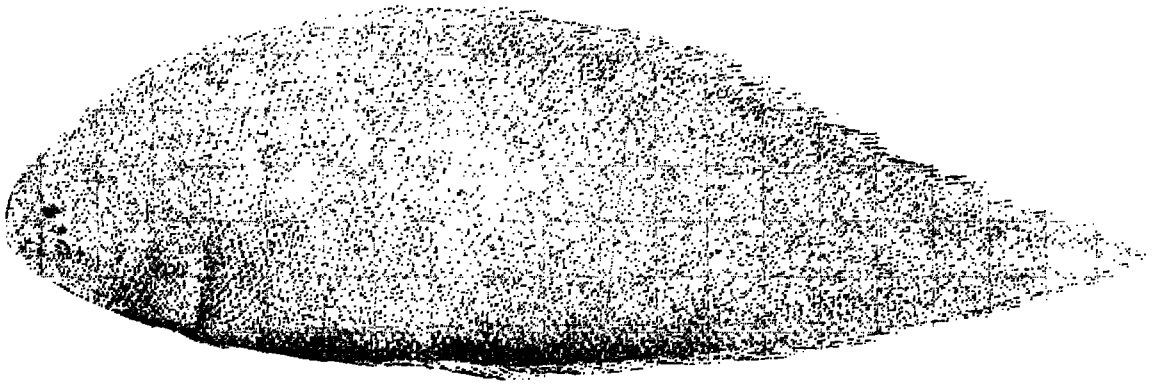

**Figure 60**
*Symphurus plagusia* (Schneider), Neotype, ANSP 132030, female, 103.2 mm SL, Puerto Yabucoa, Puerto Rico.

## *Symphurus plagusia* (Schneider, in Bloch and Schneider, 1801) (Figs. 8G, 60–61; Tables 1–10, 38)

*Plagusia* Browne, 1756 (Jamaica; nonbinomial; suppressed (Opinion 89 [Hemming and Noakes, 1958:9], Plenary Powers for nomenclatorial purposes, Direction 32. Published 17 May 1956).

*Pleuronectes plagusia* Browne,1789:445 (Jamaica; nonbinomial; suppressed (Opinion 89 [Hemming and Noakes, 1958:9], Plenary Powers for nomenclatorial purposes, Direction 32. Published 17 May 1956). Cuvier, 1816:224 (listed). Cuvier, 1829:344 (listed).

*Pleuronectes plagusia* Schneider, in Bloch and Schneider, 1801:162 (original description based on Browne, 1789).

?*Achirus ornata* (nomen dubium) Lacepède, 1802: 659, 663 (original description of tonguefish donated to France by Holland, but of uncertain identity and geographic origin).

*Aphoristia ornata*. Kaup, 1858:107 (in part) (new combination; synonymized with *Plagusia tessellata* Quoy and Gaimard, 1824). Günther, 1862:490 (in part) (synonymy; meristics; synonymized with *Plagusia tessellata* Quoy and Gaimard,1824). Poey, 1868:409 (in part) (Cuba; synonymy). Poey, 1875–1876:182 (in part) (Cuba; synonymy). Goode and Bean, 1885a:196 (in part; substitute name for *Pleuronectes plagiusa* Linnaeus, 1766). Jordan 1885:395 (in part; possible synonymy of *A. ornata* Lacepède, 1802, with *Pleuronectes plagiusa* Linnaeus, 1766; *Aphoristia ornata* Lacepède, 1802 from Jamaica distinct from *A. fasciata* [=*Plagusia fasciata*] Holbrook in DeKay, 1842).

*Aphoristia plagiusa* (not of Linnaeus, 1766). Jordan, 1886a:31 (Cuba; equals *A. ornata* of Poey). Jordan, 1886b:603 (in part) (West Indies; equals *A. ornata* of Poey).

*Symphurus plagusia*. Jordan and Goss, 1889:100 (in part) (West Indies to Brazil; synonymy, nomenclature; comparison with *S. plagiusa*; synonymized with *Plagusia tessellata* Quoy and Gaimard, 1824). Eigenmann and Eigenmann, 1891:73 (in part; east coast South America, West Indies; synonymy). Jordan and Evermann, 1898:2709 (in part; synonymy, counts, measurements, redescription; after Jordan and Goss). Evermann and Marsh, 1900:332 (in part; in key). Meek and Hildebrand, 1928:1005 (in part; Panama; synonymy; counts, measurements, redescription; distribution records). Chabanaud, 1939:26 (Antilles). Chabanaud, 1940:182 (descriptive osteology). Fowler, 1941:146 (in part; Brazilian localities). Chabanaud, 1949:82 (mouth of Amazon River; synonymy; redescription, counts, measurements, scales; figures; radiograph). Boeseman, 1956:197 (Suriname). Duarte-Bello and Buesa, 1973:234 (in part; Cuba; synonymy). Menezes and Benvegnú, 1976:142 (in part; Brazil; recommended re-examination of Ginsburg's diagnoses of two subspecies). Guitart, 1978:728 (in part; Cuba; in key, figure, meristic features, color description; finray counts probably include another species). Rosa, 1980:222 (in part; Paraíba, Brazil; nearshore, estuarine habitats). Lema et al., 1980:44 (in part; southern Brazil; synonymy).

Corrêa et al., 1986:37 (Brazilian localities; common names; figure). Garzon-F., 1989:158 (Bahia de Portete, Colombia; abundance). Munroe, 1991:256 (Greater Antilles and Central America to southern Brazil; redescription, diagnosis, designation of neotype; nomenclature; synonymy; counts, measurements, photograph; in key; bathymetric distribution; size and sexual maturity). Munroe, 1992:371, 382 (ID pattern; geographic, bathymetric distributions).

*Symphurus plagusia plagusia.* Ginsburg, 1951:199 (in part; synonymized with *Plagusia tessellata* Quoy and Gaimard, 1824; description and diagnoses of subspecies; four species included in material studied). Cervigón, 1961:42 (Venezuela). Carvalho et al., 1968:22 (in part; Antilles, Central America to Brazil; brief description; in key). Palacio, 1974:87 (in part; Colombia; counts; suggested reexamination of subspecies status). Lema and Oliveira, 1977:6 (Brazil; in key; suggested synonymy of *Pleuronectes plagusia*, *Plagusia tessellata*, and *Symphurus civitatium*). Soares, 1978:23 (in part; northern Brazil).

?*Symphurus plagusia* (Linnaeus, 1766). Valdez and Aguilera, 1987:175 (in part; Gulf of Venezuela; description, figure).

**Misidentification** Séret and Andreata, 1992:94 (southern Brazil; 640 m; five specimens actually *S. marginatus*).

**Diagnosis** *Symphurus plagusia* is distinguished from all congeners by the following combination of characters: predominant 1-4-3 ID pattern; 12 caudal-fin rays; 4 hypurals; 89–97 dorsal-fin rays; 73–81 anal-fin rays; 47–51, usually 49–51, total vertebrae; 79–89 scales in longitudinal series; absence of pupillary operculum; unpigmented peritoneum; fleshy ridge on ocular-side lower jaw; ocular-side dentary without teeth, or with short row of small teeth developed only on anterior one-half to one-third of jaw margin; anterior region of ocular-side premaxilla usually with small, mostly incomplete row of teeth along margin; relatively small, spherical eye (64–95 HL, $\bar{x}$=82); moderately long jaws, usually extending posteriorly to vertical line through posterior margin of lower eye, less frequently to vertical through posterior margin of pupil or slightly posterior to posterior margin of lower eye; dorsal-fin origin far forward, usually at vertical through anterior margin of upper eye, or with first and sometimes second rays inserting anterior to vertical through anterior margin of upper eye; scales absent on blind sides of dorsal- and anal-fin rays; ocular surface pigmentation usually uniformly light brown or yellowish, occasionally with 8–14, narrow, faint crossbands, but without blotch on caudal region; outer surface of ocular-side opercle without black blotch, pigmentation usually same as on body (some specimens with dusky blotch on upper opercular lobe as a consequence of pigment on inner lining of ocular-side opercle showing through to outer surface); inner lining of ocular-side opercle and isthmus dusky to dark brown, that of blind side usually unpigmented or occasionally with small patch of pepper-dot pigmentation on ventral margin; blind side without pepper-dot pigmentation; dorsal and anal fins uniformly pigmented, without spots or blotches and without progressive darkening or alternating series of pigmented blotches and unpigmented areas posteriorly; caudal fin without spots or blotches.

**Description** A medium-size species attaining maximum sizes of ca. 130 mm SL. ID pattern usually 1-4-3 (33/44 individuals), less frequently 1-3-3 (5), 1-3-4 (3), or 1-4-2 (2) (Table 2). Caudal-fin rays usually 12 (41/44), infrequently 10, 11, or 13 (Table 3). Dorsal-fin rays 89–97, usually 91–96 (Table 4). Anal-fin rays 73–81, usually 75–79 (Table 5). Total vertebrae 47–51, usually 49–51 (39/44 specimens) (Table 6). Hypurals 4 (43/43). Longitudinal scale rows 79–89 (Table 7). Scale rows on head posterior to lower orbit 18–22, usually 18–20 (Table 8). Transverse scales 35–43 (Table 9).

Proportions of morphometric features presented in Table 38. Body relatively deep, with greatest depth in anterior one-third of body; body depth tapering fairly gradually posterior to midpoint. Preanal length shorter than body depth. Head wide, somewhat narrower than body depth. Head length usually much shorter than head width (HW:HL=1.2–1.3, $\bar{x}$=1.2). Lower head lobe narrow, its width nearly equal to postorbital length; considerably narrower than upper head lobe. Lower opercular lobe of ocular side considerably wider than upper opercular lobe. Snout moderately long, somewhat square (Fig. 60), covered with small ctenoid scales. Dermal papillae well developed on snout and chin regions on blind side of body. Anterior nostril on ocular side short, when depressed posteriorly, usually falling just short of anterior margin of lower eye. Jaws long; maxilla usually reaching posteriorly to vertical through posterior margin of lower eye, less frequently only reaching to vertical through posterior margin of pupil or vertical slightly posterior to posterior margin of lower eye. Ocular-side lower jaw with distinct, fleshy ridge near posterior margin (Fig. 3D). Teeth well developed on blind-side jaws. Ocular-side dentary without teeth or with short row of small teeth developed only on anterior one-half to one-third of margin; pre-

**Table 38**

Morphometrics for neotype (ANSP 132030) and 14 nontype specimens of *Symphurus plagusia*. (Abbreviations defined in methods section; SL is expressed in mm; characters 2 to 14 are expressed in thousandths of SL; 15 to 21 in thousandths of HL; *n* = no. of specimens measured.)

| Character | Neotype | *n* | Range | Mean | SD |
|---|---|---|---|---|---|
| 1. SL | 103.2 | 14 | 57.4–130.3 | 98.8 | 22.29 |
| 2. BD | 304 | 14 | 278–319 | 292.1 | 13.05 |
| 3. PDL | 30 | 14 | 23–50 | 32.9 | 6.87 |
| 4. PAL | 222 | 14 | 166–244 | 209.3 | 18.60 |
| 5. DBL | 970 | 14 | 950–977 | 967.1 | 6.87 |
| 6. ABL | 776 | 14 | 758–802 | 785.6 | 15.38 |
| 7. PL | 64 | 14 | 51–73 | 63.6 | 5.76 |
| 8. PA | 48 | 14 | 38–60 | 50.0 | 7.00 |
| 9. CFL | 98 | 14 | 88–111 | 100.3 | 7.13 |
| 10. HL | 196 | 14 | 174–216 | 189.6 | 11.98 |
| 11. HW | 239 | 14 | 218–256 | 236.4 | 13.25 |
| 12. POL | 130 | 14 | 110–143 | 125.9 | 9.26 |
| 13. UHL | 142 | 14 | 125–186 | 160.1 | 15.93 |
| 14. LHL | 107 | 14 | 81–115 | 96.8 | 10.22 |
| 15. POL | 663 | 14 | 630–714 | 665.8 | 25.18 |
| 16. SNL | 228 | 14 | 205–250 | 229.1 | 15.62 |
| 17. UJL | 213 | 14 | 200–250 | 227.6 | 14.99 |
| 18. ED | 79 | 14 | 64–95 | 81.9 | 9.57 |
| 19. CD | 213 | 14 | 222–374 | 275.1 | 40.32 |
| 20. OPLL | 272 | 14 | 250–346 | 296.9 | 29.10 |
| 21. OPUL | 223 | 14 | 169–272 | 211.9 | 27.24 |

maxilla on ocular side usually with small, single, mostly incomplete row of slender teeth on margin anterior to vertical equal with anterior nostril. Chin depth slightly larger than snout length. Lower eye small, spherical; eyes slightly subequal in position with upper usually slightly in advance of lower eye. Anterior and medial surfaces of eyes not covered with scales; usually 1–2 small ctenoid scales in narrow interorbital region. Pupillary operculum absent. Dorsal-fin origin far forward (Fig. 3D), usually at vertical through anterior margin of upper eye, or with first and sometimes second dorsal-fin rays inserting anterior to vertical through anterior margin of upper eye. Scales absent on blind sides of dorsal- and anal-fin rays. Pelvic-fin short; longest pelvic-fin ray reaching base of first, or occasionally second, anal-fin ray. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anus or occasionally extending posteriorly almost to anal-fin origin (membrane torn in many specimens). Caudal-fin length moderate. Scales large, ctenoid on both sides of body.

**Pigmentation (Fig. 6O)** Body coloration similar for both sexes. Ocular surface usually uniformly light brown or yellowish, occasionally with 8–14, narrow, faint crossbands. Crossbands not continued onto dorsal and anal fins; mostly complete in anterior trunk region; on rest of body obvious only as vertical markings at body margin along dorsal- and anal-fin bases. Blind side creamy white. Peritoneum unpigmented. Pigmentation of outer surface of ocular-side opercle usually same as that of body; occasionally with dusky blotch on upper opercular lobe due to pigment on inner lining of ocular-side opercle showing through to outer surface. Inner lining of opercle and isthmus on ocular side usually dusky; some specimens with dark brown pigmentation on inner opercular lining; inner opercle and isthmus on blind side usually unpigmented or occasionally with small patch of pepper-dot pigmentation on ventral margin. Usually with slight pigment band on ocular-side upper lip and diffuse pattern of melanophores on lower lip.

Dorsal and anal fins dusky throughout their lengths; fin rays streaked with pigment darker brown than that of connecting membrane, thereby clearly outlining each fin ray; sometimes with alternating series of darker pigmented rays (usually 2–3 in succession) separated by about 4–5 successive, lighter pigmented rays. Basal half (scale-covered) of caudal fin dark brown; fin rays in distal one-half of caudal fin streaked with darker pigment than connecting membrane.

**Size and sexual maturity (Fig. 8G)** *Symphurus plagusia* is a medium-size species attaining sizes of about 130 mm. Males and females attain similar sizes. The largest of five males examined in this study was 130 mm; the largest of 24 females was only slightly smaller (127 mm). Sexual maturity occurs at a relatively large size in this species. All females larger than 80 mm were mature. All but two females smaller than 80 mm were immature with gonads undergoing elongation without ripening ova or with ovaries barely elongating.

**Geographic distribution (Fig. 61)** Widely distributed in shallow waters of the tropical western Atlantic. In the northern portion of its range, this species occurs in Puerto Rico, Cuba, and Hispaniola but is unknown from the Bahamas (Böhlke and Chaplin, 1968). Along the continental margin of Central America, *S. plagusia* has been collected at Belize, Nicaragua, Costa Rica, and Panama, whereas farther south it ranges along the Atlantic coast of Colombia, and coastal regions of Guyana, Suriname, Tobago, and Brazil as far south as Rio de Janeiro.

**Bathymetric distribution** *Symphurus plagusia* is a shallow-water species (1–51 m) most commonly inhabiting mud substrates between the shoreline and 10 m (Table 10), where 21/26 (81%) of specimens ex-

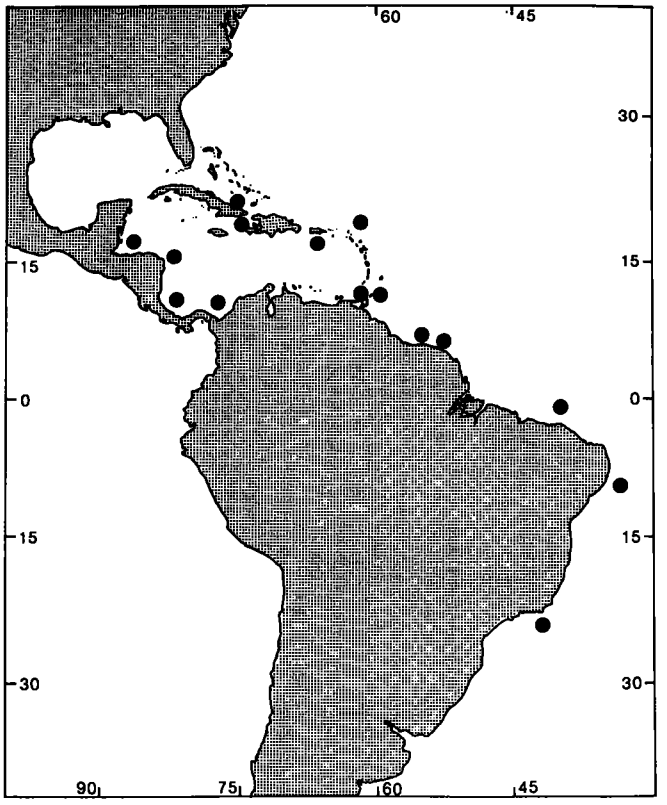


**Figure 61**

Geographic distribution of *Symphurus plagusia* based on material examined (discussion of geographic distribution appears in species account).

amined were taken. All life history stages occur in these shallow areas and only occasionally were individuals taken at deeper locations (one specimen at 51 m, three specimens at 40 m, and one specimen at 37 m). Little is known concerning the biology of *S. plagusia*. Its general rarity in collections indicates that it occurs in rarely sampled habitats.

**Remarks** Discussion of nomenclature, synonymy, and designation of a neotype was provided in Munroe (1991). UMML 34347 was incorrectly listed in Munroe as having been collected off Panama. The correct locality information for this specimen is off Guyana at 7°42'N, 57°32'W.

**Comparisons** Of western Atlantic tonguefishes, *S. plagusia* most closely resembles *S. civitatium*. Differences between these species are discussed in the "Comparisons" section in the account for *S. civitatium*. Differences between *S. plagusia* and *S. oculellus* were discussed in the "Comparisons" section of the account for *S. oculellus*.

*Symphurus plagusia* of all sizes are usually collected with juveniles and small adults of *S. tessellatus*. Despite overall similarities in meristic features, the two species are quite distinctive. The ocular surface of *S. plagusia* is uniformly colored with only faint, narrow crossbands in some individuals, it has a well-developed fleshy ridge on the ocular-side lower jaw (Fig. 3D), and this species lacks a striking black pigment spot on the outer opercle (some individuals have a diffuse blotch on inner opercle where pigmentation on inner surface of ocular-side opercle shows through), and the inner opercular lining on the blind side is relatively unpigmented. In *S. tessellatus*, in contrast, all individuals have a bold pattern of wide crossbands, a prominent black spot on the outer surface of the opercle and a heavily pigmented inner opercular lining on the blind side, and this species lacks a fleshy ridge on the ocular-side lower jaw (Fig. 3E). *Symphurus plagusia* also has a smaller eye (6.4–9.5, $\bar{x}$=8.2% HL vs. 7.9–11.4, $\bar{x}$=9.5% HL in *S. tessellatus*) and lacks small ctenoid scales on posterior fin rays on the blind side of the dorsal and anal fins present in *S. tessellatus* larger than about 70 mm. *Symphurus plagusia* also has modally lower meristic values (total vertebrae 49–51 vs. 50–53 in *S. tessellatus*; dorsal-fin rays 89–97 vs. 91–102, usually 93–101; anal-fin rays 73–81 vs. 77–86).

*Symphurus plagusia* differs further from *S. tessellatus* in having an almost squarish snout, which contrasts with the more pointed snout of *S. tessellatus* (compare Figs. 60 and 62). Also, in *S. plagusia*, the dorsal-fin origin is usually anterior to the vertical through the eye whereas in *S. tessellatus* the dorsal-fin originates slightly more posteriorly, usually above the anterior margin of the pupil of the upper eye, or even as far back posteriorly as the mideye region. Viewed from the blind side, the more posterior location of the dorsal-fin origin in *S. tessellatus* is apparent in the number of rays occurring along the dorsal margin of the body immediately above the space between the two nostrils. In *S. tessellatus* usually only the first dorsal-fin ray occurs above the space between the nostrils, whereas the second dorsal-fin ray lies immediately above the posterior nostril or is placed even slightly posterior to the posterior nostril. In *S. plagusia*, usually the first two dorsal-fin rays occur along the dorsal margin in the space between the nostrils, and in many specimens, the first dorsal-fin ray is actually situated anterior to the vertical equal with the anterior nostril. In *S. plagusia*, the jaws usually extend to the posterior margin of the lower eye or, in some cases, actually extend slightly beyond the posterior margin of the lower eye, whereas in *S. tessellatus*, the jaws usually reach only to the middle, rarely to the posterior margin, of the lower eye.

These two species also differ significantly in overall body size and size at sexual maturation. *Sym-*

*phurus plagusia* is a medium-size tonguefish reaching a maximum known body size of about 130 mm and attaining sexual maturity as small as 80 mm. *Symphurus tessellatus* is a much larger species attaining maximum known lengths of 220 mm and does not attain sexual maturity until reaching approximately 120 mm.

Some meristic values of *S. plagusia* overlap those of 11 other species of Atlantic tonguefishes. *Symphurus plagusia* occurs sympatrically, and occasionally syntopically, with *S. diomedeanus* but differs from this species in having 12 caudal-fin rays (vs. 10 in *S. diomedeanus*) and in lacking the series of dark spots on posterior rays of the dorsal and anal fins and the pupillary operculum that are present in *S. diomedeanus*. Other differences between these species are discussed in the "Comparisons" section in the account of *S. diomedeanus*.

*Symphurus plagusia* can be distinguished from *S. plagiusa*, which has an allopatric distribution in the western North Atlantic, in having 12 versus 10 caudal-fin rays. *Symphurus plagusia* also lacks the well-developed black pigment spot on the outer surface of the ocular-side opercle (present in *S. plagiusa*), and in larger (>60 mm) *S. plagiusa*, there are 4–8 ctenoid scales on blind-sides of the dorsal- and anal-fin rays (scales usually absent altogether, or occasionally 1–2 scales along bases of fin rays in *S. plagusia*). Other differences between these species are discussed in the "Comparisons" section in the account of *S. plagiusa*.

Meristic values of *S. plagusia* overlap with those of six eastern Pacific species possessing either a 1-4-3 or 1-5-3 ID pattern (Munroe, 1992). Of these, *S. plagusia* is most similar to *S. melanurus* in that both possess a fleshy ridge on the ocular-side lower jaw, and both have the first dorsal-fin ray reaching a vertical equal with, or anterior to, the anterior margin of the upper eye. The two species are distinguished in that *S. plagusia* lacks a pupillary operculum (vs. a weakly developed pupillary operculum usually present in *S. melanurus*), has fewer scales in longitudinal series (79–89 vs. 89–108 in *S. melanurus*), has a lightly pigmented inner lining on the blind-side opercle (vs. darkly pigmented inner lining on the blind-side opercle in *S. melanurus*), and in *S. plagusia* the posterior dorsal and anal fins and the caudal fin are not darker than the anterior regions (vs. progressive darkening in posterior dorsal and anal fins and darkly pigmented caudal fin in *S. melanurus*).

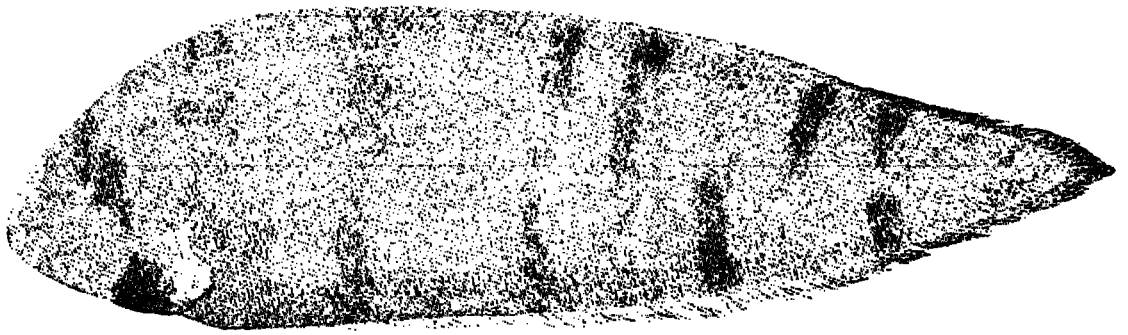

**Figure 62**

*Symphurus tessellatus* (Quoy and Gaimard), USNM 159536, female, 177 mm SL, Surinam 6°41'N, 54°17'W.

## *Symphurus tessellatus* (Quoy and Gaimard, 1824) (Figs. 9F, 62–63; Tables 1–10, 39–40)

*Plagusia tessellata* Quoy and Gaimard, 1824:240 (original description; Rio de Janeiro Bay [= Guanabara Bay], Brazil; counts, color description).

*Plagusia brasiliensis* Agassiz in Spix and Agassiz, 1831:89 (original description; Bahia, Brazil; counts, color figure). Castelnau, 1855:79 (brief description, figure). Whitehead and Myers, 1971:495 (nomenclature and dating of Spix and Agassiz's Brazilian Fishes). Kottelat, 1984:150 (in type catalogue, MHNN). Kottelat, 1988:79 (nomenclature, type status of species described in Spix and Agassiz's Brazilian Fishes).

*Aphoristia ornata.* Kaup, 1858:106 (in part; South America; synonymy). Günther, 1862:490 (in part; Atlantic coasts of tropical America; synonymized with *S. plagusia* Schneider, in Bloch and Schneider, 1801; brief description; counts). Kner, 1865-67:292 (Rio de Janeiro, Brazil).

*Symphurus plagusia* (not of Schneider, in Bloch and Schneider, 1801). Jordan and Goss, 1889:324 (in part; West Indies to Rio de Janeiro, Brazil; synonymy; in key; brief redescription; nomenclature). Berg, 1895:79 (in part; Mar del Plata-Montevideo; counts include those for *S. jenynsi*). Jordan and Evermann, 1898:2709 (in part; after Jordan and Goss, 1889). Evermann and Marsh, 1900:332 (West Indies to Brazil; common; in key; synonymy; redescription, counts, measurements; comparison with *S. plagiusa*). Thompson, 1916:416 (in part; after Jordan and Goss; counts, measurements, brief color description). Devincenzi, 1920:135 (Río de la Plata, Uruguay; counts, measurements; distinguished from *S. jenynsi*). Devincenzi, 1924–26:281 (Uruguay; counts). Meek and Hildebrand, 1928: 1005 (in part; Panama; color description; counts). Beebe and Tee-Van, 1928:77 (Haiti; color description with figure; size). Puyo, 1949:178 (in part; French Guyana; figure, counts, color description). Lowe-McConnell, 1962:694 (in part; British Guiana). Caldwell, 1966:84 (offshore localities, Jamaica). Cervigón, 1966:816 (Venezuela; probably *S. tessellatus* based on high meristic features, color description, and large sizes reported). Palacio, 1974:87 (in part; Colombia; specimens misidentified as *S. p. plagusia*). Menezes and Benvegnú, 1976:142 (Brazil; synonymized with *S. plagusia*). Soares, 1978:23 (Rio Grande do Norte, Brazil; counts, color description, figure). Lema et al., 1980:44 (Río de la Plata region, Rio Grande do Sul, Brazil; synonymy). Rosa, 1980:222 (in part; nearshore and estuarine habitats, Paraíba, Brazil). Lucena and Lucena, 1982:56 (southern Brazil). Matsuura, 1983:463 (French Guiana, Suriname; counts, measurements, color photograph).

*Aphoristia fasciata* (not of DeKay, 1842). Goode and Bean, 1896:458 (Jamaica; in key; figured).

*Symphurus plagusia tessellata.* Ginsburg, 1951:199 (diagnosis and description of subspecies; Brazil-Uruguay). Ringuelet and Arámburu, 1960:91 (Argentina; in key; figure; synonymy). Carvalho et al., 1968:22 (in part; northern Brazil; synonymy; in key; brief description). Lazzaro, 1973:247 (southern Brazil and Uruguay; in key). Palacio 1974:87 (north of Puerto, Colombia). Lazzaro, 1977:70 (Uruguay; in key). Lema and Oliveira, 1977:7 (Santa Catarina, Brazil; in key). Menni et al., 1984:201

(Uruguay and Argentina; partial synonymy; common names).

*Symphurus pterospilotus* (not of Ginsburg, 1951). Lema and Oliveira, 1977:7 (in part; southern Brazil).

*Symphurus tessellatus* (Quoy and Gaimard). Munroe, 1991:269 (Greater Antilles and Central America to Uruguay; removed from synonymy of *S. plagusia* (Schneider, in Bloch and Schneider); redescription and diagnosis; nomenclature; synonymy; counts, measurements, photograph; in key; bathymetric distribution; size and sexual maturity). Munroe, 1992:371, 382 (ID pattern; geographic, bathymetric distributions). Cervigón et al., 1993:305–306 (Venezuela; descriptive characters; distribution; figure).

**Diagnosis** *Symphurus tessellatus* is distinguished from all congeners by the following combination of characters: predominant 1-4-3 ID pattern; 12 caudal-fin rays; 4 hypurals; 91–102 dorsal-fin rays; 74–86, usually 78–84, anal-fin rays; 48–54, usually 50–53 total vertebrae; 81–96, usually 83–93 scales in longitudinal series; unpigmented peritoneum; moderately large eye (79–114 HL, $\bar{x}$=95) without pupillary operculum; 4–8 small ctenoid scales on blind sides of dorsal- and anal-fin rays (best developed on fin rays in posterior one-third of body in specimens larger than 70 mm); lacking fleshy ridge on ocular-side lower jaw; moderately long jaws usually extending to vertical through middle or posterior margin of pupil of lower eye; margin of ocular-side dentary usually with single, mostly incomplete row of teeth; premaxilla on ocular side either lacking teeth or with very short row of teeth on anterior margin; dorsal-fin origin reaching vertical through anterior margin of upper eye, or occasionally only reaching vertical through middle of upper eye; ocular-surface pigmentation dark to light brown, with 5–9 well-developed, sharply contrasting, relatively wide, dark brown crossbands on head and trunk, but without pigmented blotch on caudal region of body; distinct, dark brown or black, almost spherical blotch on outer surface of ocular-side opercle; inner lining of opercle and isthmus heavily pigmented on both sides of body; dorsal and anal fins without an alternating series of pigmented blotches and unpigmented areas and without spots; anterior dorsal- and anal-fin rays usually streaked with brown pigment; dorsal- and anal-fin rays and membranes on posterior two-thirds of body becoming progressively darker posteriorly; males with posteriormost regions of fins almost uniformly black, whereas in females, posterior portions of fins, although darker than anterior regions, usually dark brown and not as intensively pigmented as in mature males; caudal fin without spots or blotches.

**Description** A large species attaining maximum sizes to 220 mm SL. ID pattern (Table 2) usually 1-4-3 (209/278 specimens), less frequently 1-5-3 (15), 1-4-2 (11), or 1-3-3 (10). Caudal-fin rays usually 12 (249/273), less frequently 10, 11, or 13 (Table 3). Dorsal-fin rays 91–102, usually 93–101 (Table 4). Anal-fin rays 74–86, usually 78–84 (Table 5). Total vertebrae 48–54, usually 50–53 (275/282) (Table 6). Hypurals 4 (273/273). Longitudinal scale rows 81–96, usually 83–93 (Table 7). Scale rows on head posterior to lower orbit 18–23, usually 20–22 (Table 8). Transverse scales 38–45 (Table 9).

Proportions of morphometric features presented in Table 39. Body relatively elongate, only moderately deep; with greatest depth usually occurring in anterior one-third of body; body depth tapering fairly gradually posterior to midpoint. Preanal length considerably shorter than body depth. Head wide, somewhat narrower than body depth. Head length shorter than head width (HW:HL=1.1–1.4, $\bar{x}$=1.2). Lower head lobe width somewhat less than postorbital length; narrower than upper head lobe. Lower opercular lobe on ocular side wider than upper opercular lobe. Snout moderately long and somewhat pointed; covered with small ctenoid scales. Dermal papillae well developed, but not particularly dense, on snout

**Table 39**

Morphometrics for 22 specimens of *Symphurus tessellatus*. (Abbreviations defined in methods section; SL is expressed in mm; characters 2 to 14 are expressed in thousandths of SL; 15 to 21 in thousandths of HL; *n* = no. of specimens measured).

| Character | *n* | Range | Mean | SD |
|---|---|---|---|---|
| 1. SL | 22 | 97.9–203 | 145.0 | 27.66 |
| 2. BD | 22 | 247–312 | 280.2 | 18.82 |
| 3. PDL | 22 | 32–48 | 41.7 | 4.48 |
| 4. PAL | 22 | 181–227 | 204.7 | 10.58 |
| 5. DBL | 22 | 952–968 | 958.3 | 4.48 |
| 6. ABL | 22 | 771–876 | 798.0 | 22.90 |
| 7. PL | 22 | 44–73 | 59.0 | 6.47 |
| 8. PA | 22 | 27–56 | 41.5 | 6.01 |
| 9. CFL | 22 | 72–118 | 90.9 | 10.36 |
| 10. HL | 22 | 170–199 | 186.6 | 7.37 |
| 11. HW | 22 | 193–247 | 218.6 | 15.58 |
| 12. POL | 22 | 117–135 | 125.9 | 5.38 |
| 13. UHL | 22 | 113–163 | 143.3 | 12.03 |
| 14. LHL | 22 | 80–114 | 97.8 | 10.56 |
| 15. POL | 22 | 593–723 | 674.9 | 25.07 |
| 16. SNL | 22 | 196–231 | 215.7 | 9.25 |
| 17. UJL | 22 | 222–278 | 248.1 | 15.58 |
| 18. ED | 22 | 79–114 | 95.2 | 10.06 |
| 19. CD | 22 | 173–322 | 245.0 | 31.85 |
| 20. OPLL | 22 | 243–359 | 306.8 | 31.68 |
| 21. OPUL | 22 | 161–252 | 205.7 | 24.03 |

and chin regions on blind side of body, occasionally extending onto ocular-side snout. Anterior nostril, when depressed posteriorly, not reaching anterior margin of lower eye. Jaws long; maxilla usually reaching posteriorly to point between verticals through middle and posterior margin of pupil of lower eye. Ocular-side lower jaw lacking fleshy ridge (Fig. 3E). Teeth well developed on blind-side jaws. Margin of ocular-side dentary usually with single, mostly incomplete row of slender teeth; margin of ocular-side premaxilla either with very short row of teeth anterior to vertical through base of anterior nostril or lacking teeth altogether. Chin depth slightly larger than snout length. Lower eye moderately small; eyes slightly subequal in position with upper usually slightly in advance of lower eye. Anterior and medial surfaces of eyes not covered with scales; usually 1–3 small ctenoid scales in narrow interorbital region. Pupillary operculum absent. Dorsal-fin origin usually reaching vertical through anterior margin of upper eye, or occasionally only reaching vertical line through middle of upper eye; predorsal length short. Four to eight scales present on blind sides (Fig. 4A) of dorsal- and anal-fin rays (best developed on fin rays in posterior one-third of fin of specimens larger than 70 mm). Pelvic fin short; longest pelvic-fin ray, when extended posteriorly, usually reaching base of first anal-fin ray, or occasionally falling short of that point. Posteriormost pelvic-fin ray connected to body by delicate membrane terminating immediately anterior to anus, or occasionally extending posteriorly almost to anal-fin origin (membrane torn in most specimens). Caudal fin short. Scales large, strongly ctenoid on both sides of body.

**Pigmentation (Fig. 6Z)** General pattern of body pigmentation similar in both sexes at all sizes but usually more intense in sexually mature males. Males, especially those in breeding condition (collected with gravid females), usually with more intense banding, dark black fins, dark black spot on ocular-side opercle, and some specimens with irregularly shaped, black pigment patches on posterior one-half of blind side of body. In contrast, mature females also with crossbands, but less conspicuous than in males and with posterior portions of fins dark brown but usually not black. Females lack black pigment patches on blind side observed in males.

Ocular-surface background pigmentation ranging from dark to light brown. Body usually with 5–9 (usually 5–7) well-developed, sharply contrasting, relatively wide, dark brown crossbands on head and trunk. First two bands relatively consistent in position; first crossing head immediately posterior to eyes; second crossing body immediately behind opercular opening. Crossbands on trunk variable in number and degree of completeness, especially those between opercular opening and point about equal to two-thirds of trunk length. Males usually with 3–4 well-developed and lesser number of incomplete bands along trunk. Two posteriormost bands, just anterior to caudal-fin base, slightly arched and usually darker than others on body. Blind side usually uniformly creamy white; some mature males with irregular patches of black pigment on caudal one-third of blind side. Peritoneum unpigmented. Outer surface of ocular-side opercle usually with distinct, dark brown or black spot on ventral margin slightly anterior to posterior margin of opercle. Opercular spot ranging from almost spherical to dorsoventrally elongate black blotch covering most of lower opercle. Intensity of pigmentation in spot maximally developed in sexually mature adults. Inner linings of opercles and isthmus on both sides of body heavily pigmented. Pigment band well developed on ocular-side upper lip; ocular-side lower lip frequently spotted, but without well-defined band.

Anterior dorsal- and anal-fin rays usually streaked with brown pigment, more heavily pigmented than connecting membranes. Fin rays and membranes of dorsal and anal fins on posterior two-thirds of body becoming increasingly darker posteriorly. Males with posteriormost regions of fins almost uniformly black, whereas in females, posterior portions of fins, although darker than anterior regions, usually dark brown and not as intensively pigmented as in mature males. Caudal fin dark brown or black throughout its length.

**Size and sexual maturity (Fig. 9F)** *Symphurus tessellatus* is one of the largest species in the genus and is the second largest species of Atlantic tonguefish after *S. jenynsi* (Ginsburg, 1951; Menezes and Benvegnú, 1976; Munroe, 1987, 1991). Size-related life history information is based on data from 385 fish. Males and females attain nearly similar sizes, but females are somewhat larger. The largest fish measured in this study was a female of 220 mm; the largest male measured 205 mm. There were 214 males (51.5–205 mm), 155 females (49.5–220 mm), and 16 immature fish (13.4–65.8 mm) of indeterminate sex among material examined. Mature females ($n$=124) ranged in size from 104 to 220 mm. Based on reproductive stages for females, sexual maturity in this species occurs at sizes of 104–120 mm, but usually larger than 115 mm. Most mature females exceeded 140 mm, with only nine smaller than 125 mm and two smaller than 110 mm among fish examined. Thirty-one females of 49.5–119 mm were immature. The smallest of these, measuring 49.5 and 62.8 mm, had scarcely elongate ovaries. Other imma-

ture females (68.6–119 mm) had only partially elongate ovaries without indications of developing ova.

**Geographic distribution (Fig. 63)** A widespread tropical species ranging from the larger Caribbean Islands such as Cuba, Hispaniola, and Puerto Rico, south to Uruguay. In the West Indies, adults and juveniles have frequently been taken in abundance at several localities but appear to be limited to soft silt and mud sediments which are more common on the larger islands with riverine and estuarine habitats. *Symphurus tessallatus* has been taken at several inshore locations in Puerto Rico, Cuba, and Haiti, and a large number of adults were collected by the RV *Oregon* on the shelf area southwest of Jamaica (Caldwell, 1966). Juveniles have been taken from several inshore areas in Jamaica as well.

Along the continental margin *S. tessellatus* has been frequently captured on muddy bottoms from Belize (17°12'N) south to Uruguay (ca. 37°S). Absence of this species in the Yucatan region may be explained by upwelling (Rivas, 1968) or by different sediments in this region. The Yucatan Shelf is a broad limestone plateau with a minimum of land-derived detrital sediments (Harding, 1964; Topp and Hoff, 1972). Sediments on the inner shelf off the Yucatan Peninsula are firm, consisting of skeletal remains of various planktonic and benthonic organisms, ooids, calcareous pellets, lithic fragments, and grapestone aggregates, instead of soft silt and mud typical of more southern locations. This dramatic change in substrates to firmer sediments in the Yucatan region may account for the absence of *S. tessellatus* in the waters off southern Mexico.

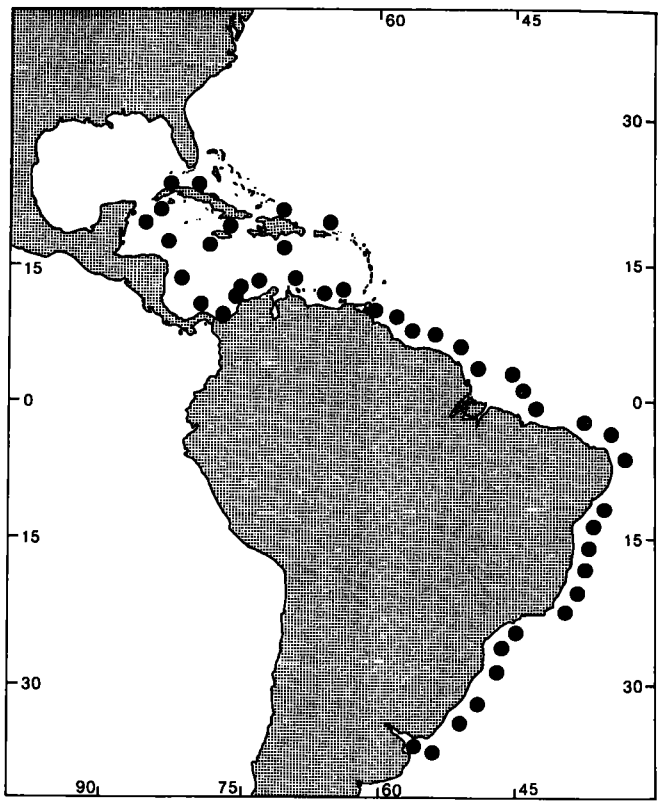


**Figure 63**

Geographic distribution of *Symphurus tessellatus* based on material examined (discussion of geographic distribution appears in species account)

*Symphurus tessellatus* is one of the most abundant and frequently collected tonguefish species, especially in trawls, from Belize and Honduras south to Venezuela and along the entire coastline of northern South America from the Guianas to about southern Brazil (Meek and Hildebrand, 1928; Cervigón, 1966; Palacio, 1974; Carvalho et al., 1968; Menezes and Benvegnú, 1976). Menezes and Benvegnú (1976) described *S. tessellatus* as the most abundant tonguefish collected along the Brazilian coast from about 26°49'S to 4°S in northern Brazil. South of 28°S, it appears to be much rarer, and all specimens I examined from Rio Grande do Sul and southwards were juveniles. This suggests that adult *S. tessellatus* are not regular components of the ichthyofauna of Uruguay and northern Argentina, but that juveniles either seasonally migrate into, or are passively transported into, the waters off Uruguay and northern coastal Argentina. Thus it appears that the region south of Rio Grande do Sul, which comes under periodic influence from the cold Falkland Current, does not harbor large populations of this essentially tropical species so common in warmer waters farther north.

The specimen from the inner continental shelf of Argentina identified by Lazzaro (1973) as *S. plagiusa* and listed in the distribution section for *S. plagusia* (=*S. tessellatus* in the present study) by Menezes and Benvegnú (1976) is probably not *S. tessellatus*. From the counts and figure provided by Lazzaro, it more closely matches *S. trewavasae* in meristic features and general body shape.

**Bathymetric distribution** Throughout its range, juvenile *S. tessellatus* are commonly taken by beach seine in nearshore habitats, and larger adults are frequently captured by trawl in deeper waters. Individuals have been collected from depths of 1 to 86 m (Table 10). There is an ontogenetic migration offshore. Juveniles occur commonly in medium- to high-salinity regions of estuaries and in high-salinity, soft-bottom habitats in nearshore mudflats. Adults generally range into deeper water, although a few large fishes that I examined were taken in relatively shallow water. Most (352/374, 94%) of the *S. tessellatus* examined in this study were collected between 1 and

70 m (Table 10), but the majority of captures, and the center of abundance for this species, occurs in depths between 1 and 50 m (82% of the individuals in this study). The deepest captures are for a single specimen taken at 86 m and 21 individuals at 73 m. The majority of shallow water captures were specimens smaller than 130 mm.

Interestingly, Menezes and Benvegnú (1976) reported that in southern Brazil, *S. tessellatus* (identified as *S. plagusia*) occurs only in shallow water (<12 m), although it is known to occur in deeper water in northern Brazil. They suggested that the presence of *S. jenynsi* off southern Brazil, which generally occurs on the continental shelf at depths greater than 12 m, somehow prevented the occurrence of *S. tessellatus* at these depths. Another explanation for the shallow depth distribution of *S. tessellatus* is that it is primarily a tropical species reaching its southern limit of distribution in southern Brazil south of Rio de Janeiro. Its bathymetric distribution in these waters may be limited not by competitive interaction from *S. jenynsi*, but rather the offshore distribution of *S. tessellatus* may be restricted by cooler water temperatures on the shelf. The appearance of *S. jenynsi*, a temperate water species (Menezes and Benvegnú, 1976), in these regions indicates that temperature may strongly influence the offshore distribution of *S. tessellatus* in southern Brazil.

Throughout its range south to at least Rio de Janeiro, juvenile *S. tessellatus* occur in similar habitats and are often collected with a complete size range of *S. plagusia*. In the Caribbean, juvenile *S. tessellatus* are also taken with a complete size range of *S. caribbeanus*. Along the northeastern coast of South America from Suriname to eastern Brazil, large adults of this species are collected in deeper areas with a wide size range of specimens of *S. oculellus* and *S. diomedeanus*.

**Geographic variation** A tropical-temperate cline was evident (Table 40) for selected meristic features examined in *S. tessellatus*. Counts of dorsal- and anal-fin rays and vertebrae generally increased in specimens collected from more southern portions of the species range. Specimens collected in various regions of the northern Caribbean had similar counts of fin rays and total vertebrae, whereas values for these features were progressively greater in specimens taken in the southern Caribbean, off northern Brazil, and especially off southern Brazil, where highest values for meristic features were recorded.

**Remarks** Comments regarding the nomenclatural history and synonymy of this species were provided in Munroe (1991:269).

**Table 40**

Geographic variation in selected meristic features of *Symphurus tessellatus*. Abbreviations: PR = Puerto Rico; CUB = Cuba; JAM = Jamaica; HAI = Haiti; BEL = Belize; HON = Honduras; PAN = Panama; COL = Colombia; VEN = Venezuela; TRI = Trinidad; GUY = Guyana; SUFG = Surinam and French Guiana; NBR = Northern Brazil; SBR = Southern Brazil; *n* = no. of specimens measured.

| Character | Area | *n* | Mean | Range | SD |
|---|---|---|---|---|---|
| Dorsal rays | PR | 28 | 96.4 | 95–99 | 1.17 |
| | CUB | 4 | 94.7 | 93–97 | 2.08 |
| | JAM | 25 | 95.9 | 93–98 | 1.41 |
| | HAI | 23 | 94.5 | 91–99 | 1.93 |
| | BEL | 13 | 91.2 | 93–98 | 1.34 |
| | HON | 27 | 95.8 | 94–97 | 1.05 |
| | PAN | 8 | 95.0 | 92–97 | 1.77 |
| | COL | 10 | 95.4 | 94–98 | 1.26 |
| | VEN | 26 | 97.8 | 96–101 | 1.07 |
| | TRI | 1 | — | 95 | — |
| | GUY | 29 | 98.6 | 95–101 | 1.47 |
| | SUFG | 13 | 99.3 | 97–101 | 1.18 |
| | NBR | 38 | 98.1 | 96–102 | 1.39 |
| | SBR | 39 | 98.4 | 95–101 | 1.59 |
| Anal rays | PR | 28 | 80.3 | 78–83 | 1.21 |
| | CUB | 4 | 79.5 | 78–81 | 1.29 |
| | JAM | 25 | 80.0 | 77–82 | 1.37 |
| | HAI | 23 | 78.4 | 77–81 | 1.47 |
| | BEL | 13 | 79.6 | 78–82 | 1.31 |
| | HON | 27 | 79.7 | 78–82 | 1.14 |
| | PAN | 8 | 79.1 | 78–80 | 0.83 |
| | COL | 10 | 79.0 | 75–81 | 1.70 |
| | VEN | 26 | 81.3 | 78–85 | 1.82 |
| | TRI | 1 | — | 79 | — |
| | GUY | 29 | 82.3 | 80–84 | 1.12 |
| | SUFG | 13 | 82.7 | 81–84 | 0.95 |
| | NBR | 38 | 82.1 | 79–84 | 1.32 |
| | SBR | 39 | 82.3 | 78–86 | 1.62 |
| Vertebrae | PR | 28 | 51.2 | 50–52 | 0.72 |
| | CUB | 4 | 50.3 | 49–51 | 0.96 |
| | JAM | 25 | 50.7 | 49–52 | 0.79 |
| | HAI | 23 | 50.4 | 48–52 | 0.89 |
| | BEL | 13 | 50.6 | 50–51 | 0.51 |
| | HON | 27 | 50.7 | 50–52 | 0.53 |
| | PAN | 8 | 50.6 | 50–51 | 0.52 |
| | COL | 10 | 50.6 | 50–52 | 0.70 |
| | VEN | 26 | 51.4 | 50–53 | 0.86 |
| | TRI | 1 | — | 50 | — |
| | GUY | 29 | 52.1 | 51–53 | 0.47 |
| | SUFG | 13 | 52.3 | 51–54 | 0.75 |
| | NBR | 38 | 51.9 | 50–53 | 0.80 |
| | SBR | 39 | 52.4 | 51–54 | 0.78 |

**Comparisons** *Symphurus tessellatus* most closely resembles and is completely sympatric throughout the Caribbean and warmer waters of the western South Atlantic with *S. oculellus*, *S. caribbeanus*, and *S. plagusia*. *Symphurus tessellatus* can readily be distinguished from these tonguefishes by features

discussed in the "Comparisons" section of accounts for these other species.

*Symphurus tessellatus* is distinct from other species including *S. ginsburgi*, *S. billykrietei*, *S. stigmosus*, *S. marginatus*, *S. diomedeanus* which is sometimes collected with *S. tessellatus*, and *S. jenynsi*, a species that sometimes co-occurs with *S. tessellatus* in the southern extent of its range. Differences between *S. tessellatus* and these others are discussed in the "Comparisons" sections of the accounts for these species, respectively.

There are nine eastern Pacific *Symphurus* with somewhat similar ID patterns, comparable fin-ray counts, or pigment patterns reminiscent of those observed in *S. tessellatus*. Of these nine, only *S. chabanaudi* and *S. elongatus* are similar to *S. tessellatus* in that they lack a pupillary operculum. Of all species in the genus, *S. tessellatus* is most similar in form, size, and pigmentation pattern to *S. chabanaudi*. However, *S. tessellatus* is distinguished from *S. chabanaudi* primarily by differences in number of dorsal- (91–102 vs. 98–109 in *S. chabanaudi*) and anal-fin rays (74–86 vs. 82–92); total vertebrae (48–54, usually 50–53 vs. 52–57, usually 53–56); and longitudinal scales (81–96 vs. 92–102 in *S. chabanaudi*). The two species also differ in relative frequencies of occurrence of particular ID patterns. In *S. chabanaudi*, 50% (49/95) of the individuals had a 1-5-3 ID pattern, whereas only 30% (28 specimens) featured a 1-4-3 pattern. In contrast, 209 of 278 (75%) *S. tessellatus* possessed a 1-4-3 ID pattern, whereas only 5% (15 specimens) had a 1-5-3 pattern.

There is some overlap in fin-ray and vertebral counts between *S. tessellatus* and *S. elongatus*; however, these counts are the only similarities between these otherwise distinctive species. *Symphurus tessellatus* has a pattern of crossbands on the body and a large, black blotch on the ocular-side opercle, whereas in *S. elongatus*, the body is uniformly pigmented without crossbands and this species lacks the prominent black blotch on the ocular-side opercle. Further differences include the small ctenoid scales on blind-side dorsal- and anal-fin rays in *S. tessellatus* (lacking in *S. elongatus*) and absence of a fleshy ridge on the ocular-side lower jaw in *S. tessellatus* (a well-developed ridge present in *S. elongatus*). *Symphurus tessellatus* also has a much larger eye (15–21 SL) compared with that of *S. elongatus* (9–15 SL).

## Discussion

### Biogeography

*Symphurus*, the only cynoglossid genus in the western Atlantic Ocean, is the most widespread tonguefish genus with members occurring worldwide in all temperate and tropical oceans. No fossils of cynoglossid fishes are known (Menon, 1977), and relative age of these flatfishes is unknown. The distribution of *Symphurus* throughout the Pacific and Atlantic oceans suggests that the genus evolved prior to the Miocene Epoch when interconnections existed between Indo-Pacific and Atlantic oceans through the Mediterranean and between the western Atlantic and eastern Pacific oceans through what is now Central America (Menon, 1977). If the species groups, as defined by ID patterns (Munroe, 1992), represent monophyletic assemblages, then not only was *Symphurus* in existence prior to closure of the seaways, but the genus had also undergone a significant level of diversification because multiple species groups are shared across what are now land barriers.

In the western Atlantic Ocean, species of *Symphurus* have an extensive distribution from Nova Scotia (ca. 45°N) to Argentina (ca. 45°S). Most species, however, are found in tropical and warm-temperate regions. All 24 western Atlantic species of *Symphurus* occur between 34°N and 25°S latitudes, with the greatest diversity in tropical and warm-temperate regions (10 and 12 species, respectively). At extremes of their geographic range in the western Atlantic, the diversity of tonguefishes is minimal (2 and 3 species, respectively) compared with that in tropical and subtropical regions. Furthermore, no species occurring beyond temperate faunal boundaries (Cape Hatteras in the north and Río de la Plata in the south) are endemic to these regions. Adults of only two species (*S. billykrietei* and *S. minor*) occur in boreal seas of the western North Atlantic, and only *S. billykrietei* is a permanent resident in this area. In the South Atlantic, the geographic limit for the genus is in the temperate seas off central Argentina (ca. 45°S), where only *S. trewavasae* is found. The geographical distribution of *Symphurus* in the eastern Atlantic Ocean (Munroe, 1990), by comparison, is far less extensive to the south (from ca. 45°N to 12°S) than that in the western Atlantic (ca. 45°N to 45°S). *Symphurus nigrescens*, the most northerly occurring of the eastern Atlantic species, extends into the Bay of Biscay (ca. 45°N) but usually is more abundant farther south, especially near the entrance to, and in, the Mediterranean Sea, and off the coast of West Africa (to ca. 7°S). This species and *S. ligulatus* are the only symphurine tonguefishes found in the Mediterranean Sea. Two other species (*S. normani* and *S. vanmelleae*) occur on the continental shelf and slope off tropical Africa (to ca. 12°S).

Geographic distributional patterns of marine organisms have been well studied in the Atlantic Ocean. In the western North Atlantic, Cape Hatteras

has been recognized as an important transitional zone where many groups of shallow-water organisms reach their geographic limits (Briggs, 1974). Cape Hatteras also delimits the geographic limits of many warm-temperate tonguefishes, especially the shallow-water species. Eight tonguefish species occur north of Cape Hatteras, or only slightly over half the diversity (14 species) recorded immediately south of the Cape. However, of these, only *S. billykrietei* is taken more frequently and in greater abundance north of the Cape, whereas the other seven species are more abundant in collections south of Cape Hatteras. Of species occurring north of Cape Hatteras, only for *S. billykrietei* and *S. minor* are adults taken as far north as the continental shelf off Nova Scotia. *Symphurus billykrietei* is the only species whose population(s) is centered north of Cape Hatteras, with all but three of the 99 specimens identified as this species collected north of this point. Adults and larvae of *S. minor* have rarely been reported from temperate waters off Nova Scotia (Ginsburg, 1951; Markle et al., 1980), but with nearly a 100-year gap between the collection of the specimens. Thus, the occurrence of *S. minor* in these northern waters is unusual and likely represents expatriate individuals transported north by the Gulf Stream. *Symphurus plagiusa* reaches its northern distributional limit in Long Island Sound off Connecticut (Ginsburg, 1951) but again is not abundant north of the Chesapeake Bay region. *Symphurus nebulosus*, a poorly known species, ranges from just south of Long Island, New York (40°48'N), to the Blake Plateau (26°28'N), but 21 of 27 known specimens were collected south of Cape Hatteras. *Symphurus pusillus* extends to off Long Island (ca. 40°N), but only nine of 29 known specimens of this poorly known species were collected north of Cape Hatteras. Although *S. marginatus* ranges into continental shelf waters off New Jersey, it is collected more frequently and in greater abundance (105 of 110 individuals) south of Cape Hatteras (Fig. 33). *Symphurus diomedeanus* (Fig. 47) and *S. civitatium* (Fig. 57) range along the inner continental shelf a relatively short distance north of Cape Hatteras, but the major populations of both species are located well south of this area.

Eleven *Symphurus* species occur in warm temperate areas of the western North Atlantic. Of these, *S. urospilus* and *S. civitatium* appear to be endemic to this region. Except for *S. nebulosus* and *S. minor*, the other species have extensive distributions throughout warm temperate regions ranging from Cape Hatteras to southern Florida and through the Gulf of Mexico. *Symphurus nebulosus* is unique in being restricted to the outer continental shelf and upper continental slope off the eastern United States. With the exception of irregularly captured individuals transported north by the Gulf Stream, *S. minor* has a somewhat restricted geographic distribution. This species occurs from about Cape Hatteras south into the eastern Gulf of Mexico off west Florida, and west to the DeSoto Submarine Canyon. It is unknown from the western Gulf of Mexico. Of other species whose center of abundance is shallower than 100 m and that are recorded from the region immediately south of Cape Hatteras, only *S. plagiusa* has a large population to the north in Chesapeake Bay. *Symphurus urospilus* and *S. parvus* have their northernmost records at Cape Hatteras, with the majority of captures of these species occurring farther south and in the Gulf of Mexico (both species), or off northern South America (*S. parvus*). Major populations of *S. plagiusa* are found in coastal waters of the southeastern United States and northern Gulf of Mexico. *Symphurus civitatium* is abundant in warm-temperate waters off the southeastern United States and through the central and western Gulf of Mexico. *Symphurus diomedeanus* is also commonly collected in this region and farther south. Most (20/29) *S. pusillus* specimens were taken in warm-temperate areas along the southeastern United States and Gulf of Mexico. *Symphurus pelicanus* has been collected in central and western areas of the Gulf, but most individuals were collected in the Caribbean. *Symphurus piger* is occasionally taken in the central and eastern Gulf of Mexico, but this species also occurs more often in the Caribbean region, including the Straits of Florida. *Symphurus marginatus* is found in the eastern and central Gulf of Mexico as far west as Louisiana (91°18'W), and throughout the Caribbean Sea. *Symphurus billykrietei* is rarely taken in the Gulf of Mexico (two specimens, one from the Tortugas area in the eastern Gulf, another off Yucatan).

Twelve species of *Symphurus* occur in tropical regions of the western Atlantic with six (*S. arawak*, *S. rhytisma*, *S. ommaspilus*, *S. caribbeanus*, *S. stigmosus*, and *S. oculellus*) endemic to this region. *Symphurus diomedeanus* has the most extensive distribution of the species occurring in tropical waters, occurring from northern warm-temperate areas to warm-temperate regions of the South Atlantic. *Symphurus marginatus* is widespread throughout the western Atlantic from warm-temperate regions of the north to comparable areas in the South Atlantic. The recent first report (Séret and Andreata, 1992) of *S. marginatus* off tropical Brazil (21°S) reflects our limited knowledge of South Atlantic environments deeper than ca. 200 m. Intensified sampling may reveal other deep-sea tonguefishes in this area.

*Symphurus piger* and *S. pelicanus* occur from southern Florida south to about Guyana and French Guiana, respectively. *Symphurus plagusia* and *S. tessellatus* range from the Caribbean region to warm-temperate areas in the South Atlantic.

Six species endemic to western Atlantic tropical regions have somewhat restricted distributions. *Symphurus arawak*, *S. rhytisma*, and *S. ommaspilus* are dwarf species occurring primarily in the Caribbean Sea on sand substrates on or near coral reefs or tropical seagrass meadows. These species have been reported from various localities in the Bahamas, West Indies, and several insular locations with coral reefs. Only *S. rhytisma* extends beyond the Caribbean into tropical seas off Brazil (ca. 20–21°S), whereas *S. arawak* has been collected once at Alligator Reef off southern Florida (Starck, 1968). *Symphurus caribbeanus* occurs in shallow water from the Greater Antilles to Colombia. *Symphurus oculellus* has a restricted distribution in tropical waters from Guyana to northeastern Brazil (2°S). *Symphurus stigmosus* is known from 12 specimens taken in deep water in the Yucatan Channel, Straits of Florida, off southern Florida, and off Dominica. Interestingly, most specimens of *S. stigmosus* were in deep waters under strong surface currents, such as those in the Yucatan Channel and beneath the Florida Current.

The fish fauna of the Argentinean Province (between 21°S and 42°S) has a relatively low level (about 10%) of endemic species (Figueiredo, 1981; Haimovici et al., 1994). Oceanographic features in this region are dynamic and characterized by temperature and salinity variations resulting from influences of seasonal shifts of the Subtropical Front and seasonal upwelling of cold waters off southeastern Brazil (Figueiredo, 1981; Matsuura, 1986). Seven species of symphurine tonguefishes reported from warm-temperate seas in the western South Atlantic are *S. plagusia*, *S. tessellatus*, *S. diomedeanus*, *S. trewavasae*, *S. kyaropterygium*, *S. jenynsi*, and *S. ginsburgi*. Of these, *S. ginsburgi*, *S. kyaropterygium*, *S. trewavasae*, and *S. jenynsi* are endemic to this region. *Symphurus plagusia* is a tropical species reaching its southern limit at ca. 23°S. *Symphurus diomedeanus* and *S. tessellatus* range to ca. 35°S, but *S. diomedeanus* is rare south of ca. 23°S, and *S. tessellatus* is also more common farther north. Most captures of *S. tessellatus* south of 28°S are juveniles presumably transported southward by the Brazil Current. All specimens of *S. kyaropterygium* were collected between ca. 24°S and 31°S. *Symphurus ginsburgi* ranges from 21° to 35°S, whereas most captures of *S. trewavasae* have been made within the warm-temperate region from 23°S to 35°S, with the southernmost record at 45°S. *Symphurus jenynsi* occurs from southern Brazil to northern Argentina (ca. 28°–35°S).

At the northeastern margin of the tropics in the western Atlantic, the warm Florida Current appears to demarcate the separation zone for tropical and temperate species of tonguefishes, especially those inhabiting shallow waters. This oceanographic feature strongly influences the distributions of many marine fishes (Robins, 1971). Few shallow-water tonguefishes regularly transcend this boundary. For example, occurrences of temperate species, such as *S. civitatium* and *S. urospilus*, in the West Indies tropical region are based on a single specimen of *S. civitatium* that had washed onto a beach at Bermuda (ANSP 137573) and a specimen of *S. urospilus* taken off Cuba (Vergara Rodriguez, 1976). Inclusion of these species among faunal lists of fishes for Bermuda and Cuba are based on these records, but it is doubtful that either is a regular component of the fish fauna of these areas. *Symphurus plagiusa*, widely distributed along the southeastern United States and northern Gulf of Mexico, has a limited West Indian distribution at Cuba (Ginsburg, 1951, this study) and the Bahamas (Böhlke and Chaplin, 1968). Of tropical species, only *S. arawak* has been collected west of the Florida Current off southern Florida (Starck, 1968). None of the other common shallow-water tropical species (i.e. *S. plagusia*, *S. tessellatus*, *S. ommaspilus*, or *S. caribbeanus*) have been reported from locations along the continental United States.

In the southern western Atlantic, the boundary between tropical and temperate regions (Briggs, 1974; Figueiredo, 1981) occurs at approximately Cabo Frio between 21°S and 23°S latitude. *Symphurus plagusia* reaches its southern limit of distribution at about 23°S latitude, whereas southern limits of *S. marginatus* and *S. rhytisma* are located slightly northward of this point (ca. 20–21°S). Although *S. diomedeanus* is also known from areas south of 23°S, the majority of captures of this species off South America are made in tropical seas off northeastern Brazil (Menezes and Benvegnú, 1976). *Symphurus tessellatus* is another species found south of 23°S, albeit primarily as juveniles presumably transported south by the Brazil current (Munroe, 1991).

## Diversity

Including two new species described in this study, 24 of 72 recognized species in *Symphurus* occur in the western Atlantic Ocean (Munroe, 1992). In terms of relative numbers of species, *Symphurus* is the most speciose of genera recognized in Cynoglossidae; approximately 49 species are assigned to *Cynoglossus* (Menon, 1977), whereas approximately five species

of *Paraplagusia* are known (Chapleau and Renaud, 1993). *Symphurus* is also the most diverse pleuronectiform taxon occurring in the western Atlantic ocean. The other speciose pleuronectiform genera in this region, the paralichthyids *Citharichthys* (with ca. seven species) and *Paralichthys* (ca. 11 nominal species), are both distinctly less speciose than the 24 species of symphurine tonguefishes.

The *Symphurus* species assemblage in the western Atlantic is diverse both in terms of numbers of species and in diversity of species groups. Five of nine species groups recognized in the genus (Munroe, 1992) have species in this region. Unique to the western Atlantic, is a group of four species with the 1-4-2 ID pattern. The majority (9/11) of species possessing a 1-4-3 ID pattern are found in the western Atlantic, with two others occurring in the eastern Pacific. Nine western Atlantic species have a 1-3-2 ID pattern. Seven other species, four in the eastern Pacific and three in the eastern Atlantic, share this ID pattern. Only *S. trewavasae* among western Atlantic tonguefishes has the 1-3-3 ID pattern, but three other species, one eastern Atlantic and two eastern Pacific, share this ID pattern. *Symphurus nebulosus* is also unusual in that it is the only western Atlantic species characterized by a 1-2-2 ID pattern. At least 14 other species in the genus possess this ID pattern, and all, except the eastern Atlantic *S. ligulatus*, are found in the Indo-Pacific. No western Atlantic tonguefishes have the 1-2-2-1-2 ID pattern limited to one eastern Atlantic and six Indo-Pacific species, the 1-2-3 pattern of three nominal Indo-Pacific species, the 1-3-4 limited to one eastern Pacific species, or the 1-5-3 ID pattern found in eight eastern Pacific species.

The diversity of symphurine tonguefish species recorded from the western Atlantic is comparable with that of the Indo-Pacific (ca. nominal 24 species), and is greater than the 17 found throughout the eastern Pacific region (Munroe, 1992; Munroe et al., 1995). There are four times as many species of *Symphurus* in the western Atlantic as in the comparatively depauperate eastern and central Atlantic regions combined, where only six species are known to occur (Munroe, 1990).

The greater diversity of symphurine flatfishes in the western compared with the eastern Atlantic reflects not only differences in composition of the species groups between these areas but also the greater diversity of habitats available to, and occupied by, tonguefishes in the western Atlantic. Members from two species groups (four species with 1-4-2 ID pattern and seven with 1-4-3 ID pattern) are especially abundant in shallow-water and neritic habitats of the western Atlantic but are entirely absent in the eastern Atlantic. Also, more western Atlantic species ($n$=8) with the 1-3-2 ID pattern are known than are found in eastern and central Atlantic areas (where only three species have this ID pattern). Other eastern Atlantic *Symphurus* are a single species each with either a 1-2-2, 1-2-2-1-2, or a 1-3-3 ID pattern, and members of these species groups typically inhabit substrates on the continental shelf and upper continental slope (Munroe, 1992). The few shallow-water representatives in these groups are found on sandy substrates in coral reef environments. The eastern Atlantic region lacks the diversity of substrates found in tropical and subtropical regions of the western Atlantic, largely as a consequence of the comparatively narrow continental shelf off tropical West Africa with its highly turbid, cool waters and lack of extensive coral reefs and associated habitats. The more diverse symphurine tonguefish fauna in the western Atlantic results from the presence of species groups (i.e. those with 1-3-2, 1-4-3, and 1-4-2 ID patterns) that successfully exploit relatively shallow-water habitats, including the extensive coral reefs and associated habitats, which are more common on the comparatively wide continental shelves in the western Atlantic.

Large differences in diversity occur in other distantly related fish groups occurring in both eastern and western regions of the Atlantic Ocean (Briggs, 1974; Collette[9]). Among these are toadfishes (*Batrachoides*), which are closely associated with the substrate, as well as fishes lacking strong substrate affinities, including needlefishes (*Strongylura*), halfbeaks (*Hyporhamphus*), and Spanish mackerels (*Scomberomorus*). Greater species diversity within these genera in western Atlantic regions, irrespective of degree of substrate association for the component taxa, indicates that factors other than substrate diversity account for the greater number of species found in the western Atlantic.

None of 24 western Atlantic species of *Symphurus* are known to occur in the Indo-Pacific, eastern Atlantic, or eastern Pacific regions. However, several hypothesized species pairs are identified among western Atlantic species, and among western Atlantic species and those from eastern Atlantic or eastern Pacific regions. Hypothesized species pairs occurring in northern (listed first) and southern regions of the western Atlantic are *S. billykrietei*: *S. ginsburgi*; *S. parvus*: *S. kyaropterygium*; and *S. civitatium*: *S. plagusia*.

*Symphurus billykrietei* and *S. ginsburgi* represent a species pair with distinct antitropical distribution.

[9] Collette, B. B. 1997. National Marine Fisheries Service Systematics Laboratory, National Museum of Natural History, Washington, D.C. 20560. Personal commun.

Antitropical species pairs are well known from many groups of marine organisms (Hubbs, 1952; Hedgpeth, 1957), and their origin has been the focus for much study and debate (White, 1985, 1986; Briggs, 1987; Stepien and Rosenblatt, 1996). Antitropical taxa originate by allopatric speciation (Mayr, 1963), wherein populations diverge owing to random genetic drift or natural selection following genetic isolation (or both), and where gene flow has been disrupted by some type of barrier to migration or by distance (Stepien and Rosenblatt, 1996). Barriers to gene flow may arise through vicariant events (White, 1985, 1986) or dispersal events (Stepien and Rosenblatt, 1996). In the eastern Pacific, antitropical distributions of several species pairs were best explained by dispersal and varying temperature tolerances by the species than by vicariance (Stepien and Rosenblatt, 1996). The tropics presented more of a barrier to some species than to others, so that genetic isolation varied among respective members of the different species pairs. Tropical Atlantic waters are an effective barrier separating antitropical species pairs of *Symphurus*. Whether these species arose owing to restricted dispersal capabilities or through vicariant events is unknown. Little is known of temperature tolerances and dispersal capabilities of *Symphurus*, especially those of deep-sea species. However, because both *S. billykrietei* (Munroe, unpubl. data) and *S. ginsburgi* (Kurtz and Matsuura, 1994) have planktonic larval stages, as do other deep-sea *Symphurus* species, climatological events occurring in surface waters could directly affect species survival and dispersal at this point in their life histories.

*Symphurus parvus* and *S. kyaropterygium* represent a north–south Atlantic species pair with members having discontinuous distributions on opposite sides of the Amazon River outflow. The Amazon River plume as a barrier to dispersal of tropical Atlantic species was shown to be incomplete for some taxa (Collette and Rützler, 1977). More detailed studies of fish communities off northeastern Brazil will augment our knowledge of fish distributions across this region.

*Symphurus plagusia* and *S. civitatium* are a species pair that occur in the Caribbean Sea and south (*S. plagusia*), and on the inner continental shelf in the Gulf of Mexico and off the southeastern United States (*S. civitatium*). The ranges of these species are separated by the Florida Current, which apparently serves as an effective barrier to dispersal.

Several species pairs with western (listed first) and eastern Atlantic components are *S. nebulosus*: *S. ligulatus*; *S. pusillus*: *S. nigrescens*; and *S. rhytisma*: *S. reticulatus*. *Symphurus nebulosus* and *S. ligulatus* occur on the outer continental shelf and upper slope, whereas *S. pusillus* and *S. nigrescens* inhabit the outer continental shelf. Formation of species pairs with discontinuous distributions on opposite sides of the Atlantic perhaps results from a distance factor where once common gene pools have now become widely separated by seafloor spreading of the Atlantic basin with subsequent separation of the respective continental shelves. The other east-west species pair, *S. rhytisma* and *S. reticulatus*, in contrast, are insular species, which probably reach island habitats by dispersal of larval stages. Usually, founder populations at remote locations comprise a small number of individuals, which if they survive to reproduce, subsequently diverge through time owing to genetic drift and isolation characteristic of small populations at remote island locations (compared with species on the continental shelf with large and contiguous populations).

Species pairs with component members distributed on either side of the Isthmus of Panama are common in a wide variety of taxa (Briggs, 1974; White, 1985, 1986; Crabtree, 1987). The emergence of the Isthmus of Panama some three million years ago separated the Atlantic Caribbean fauna from that of the eastern Pacific (Briggs, 1974). Hypothesized species pairs of New World tonguefishes with component taxa occurring in western Atlantic (listed first) and eastern Pacific areas include *S. pelicanus*: *S. gorgonae*; *S. tessellatus*: *S. chabanaudi*; *S. urospilus*: *S. fasciolaris*; and *S. marginatus*: *S. diabolicus*.

## Ecological distributional patterns

In the western Atlantic, *Symphurus* species inhabit a broad diversity of substrates located throughout a considerable range of bathymetric environments, from shallow estuarine areas only a few centimeters in depth (Reichert and Van der Veer, 1991) to demersal habitats 810 meters deep on the continental slope. Nearly equal numbers of species of western Atlantic *Symphurus* are found in shallow-water (<50 m) and deepwater (>50 m) environments. *Symphurus nebulosus*, *S. marginatus*, and *S. billykrietei* have been collected at depths ranging from 500 to 810 m, and are among the deepest dwelling of western Atlantic flatfishes. Other deep-dwelling flatfishes in this region include *Reinhardtius hippoglossoides* and *Hippoglossus hippoglossus*, reportedly from depths reaching 2,000 m (Nielsen, 1986), *Glyptocephalus cynoglossus*, collected at about 1,570 m (Scott and Scott, 1988), and *Chascanopsetta lugubris danae*, ranging from 160 to 460 m (Amaoka and Yamamoto, 1984).

Previous researchers (Ginsburg, 1951; Topp and Hoff, 1972; Menezes and Benvegnú, 1976; Munroe, 1990, 1991) noted that Atlantic tonguefish species generally inhabit rather discrete depth zones. Data

summarized herein indicate that for the majority of western Atlantic species, the center of abundance of the adult population is usually concentrated within a relatively narrow depth range. Among western Atlantic species, *S. nebulosus* is unique in that its bathymetric center of occurrence (500–810 m) is nearly completely allotopic from that of its western Atlantic congeners. Nor does any other western Atlantic *Symphurus* have as wide a bathymetric range as *S. nebulosus*. The approximately 600-m-wide depth range noted for this species is typical for most other deep-water tonguefishes with the 1-2-2 ID pattern in other geographic regions (Munroe, 1992). Presumably, in contrast to the more dynamic conditions on the inner continental shelf, environmental parameters in deep-sea environments are more uniform over a broader depth range, with this uniformity over depth reflected in the distinctively broader depth range of deepwater tonguefishes.

Topp and Hoff (1972) examined distributional patterns of 18 species of flatfishes, including those of five tonguefishes, inhabiting the inner continental shelf off west Florida. They concluded that through resource partitioning these flatfishes co-exist sympatrically without competing for resources. However, any hypothesis that invokes ecological co-existence of multiple species as resulting only from reduced competition through resource partitioning completely ignores historical information about the species, especially evolutionary information directly related to the distributional ecology of that species.

Distributional patterns of western Atlantic tonguefishes have not been examined within the context of the evolutionary history of the genus. Although this information would best be analyzed within the framework of hypothesized relationships of the species, such an hypothesis of intrageneric relationships of species of *Symphurus* is unavailable. Information (Munroe, 1992) used to define species groups within *Symphurus* provides a preliminary framework to serve as a basis for proposing testable hypotheses regarding distributional ecology of these fishes. For example, members of each species group as defined by ID pattern have a bathymetric distribution somewhat different from that of most other groups (Munroe, 1992). Species with the 1-4-3 ID pattern are primarily shallow-water inhabitants with most member species commonly inhabiting depths shallower than 100 m (*S. oculellus* to 110 m). Several species with this ID pattern, in fact, occur within estuarine and extremely shallow (<1 m) coastal environments. Species with a 1-4-2 ID pattern occur predominantly on the inner continental shelf. Western Atlantic species with the 1-3-2 ID pattern inhabit a bathymetric range from ca. 1 to 750 m, but most occur in deeper waters (between 30 and 200 m) on the continental shelf. There are two ecological groups of species with this ID pattern that have quite different bathymetric distributions. Species possessing the 1-3-2 ID pattern and a black peritoneum live on the continental shelf: *S. pelicanus* (30–150 m); *S. pusillus* (100–233 m); *S. ginsburgi* (110–300 m); *S. billykrietei* (48–650 m); *S. stigmosus* (192–373 m), *S. piger* (92–549 m), and *S. marginatus* (37–750 m). Two dwarf western Atlantic species with this ID pattern and an unpigmented peritoneum inhabit relatively shallow (1–45 m) sandy substrates adjacent to coral reefs, almost exclusively in habitats at insular locations through the Caribbean Sea. Two other dwarf species of *Symphurus* characterized by the 1-3-2 ID pattern and an unpigmented peritoneum also inhabit similar depths at central and eastern Atlantic islands (Munroe, 1990). Species with a 1-3-3 ID pattern, such as *S. trewavasae*, the only western Atlantic *Symphurus* with this ID pattern, typically are found from about 30 to 100 m. The deepest-dwelling *Symphurus* species are those with 1-2-2 ID pattern, such as *S. nebulosus*, the only western Atlantic species with this pattern. No other western Atlantic *Symphurus* occurs as deep or has as wide a bathymetric range (239–810 m) as does *S. nebulosus*.

Two other general patterns regarding the distributional ecology of Atlantic tonguefishes became apparent when data were examined within the comparative context of the species groups identified by ID patterns. First, sympatric members of a species group do not occur syntopically, especially as adults. They either inhabit different depth zones, or if they occur at similar depths within the same geographic region, they are found on different substrates. Second, allopatric members of a species group are usually found at similar depths (and possibly also on similar types of substrates). These general patterns of sympatric and allopatric distributions are exemplified within each species group occurring in the Atlantic. For example, *S. nebulosus* occurs on soft mud bottoms at 239–810 m. Its bathymetric occurrence is nearly completely allotopic in comparison with that of all other western Atlantic tonguefishes. The only other Atlantic symphurine tonguefishes inhabiting similar depths are the eastern Atlantic *S. ligulatus* and *S. vanmelleae* (Munroe, 1992), which have a 1-2-2 and 1-2-2-1-2 ID pattern, respectively. Although all three species inhabit similar depths, they are entirely allopatric geographically. *Symphurus ligulatus* occurs in the Mediterranean and off the west coast of North Africa, whereas *S. vanmelleae* occurs off the west coast of equatorial Africa (Munroe, 1990).

Nine western Atlantic species have a 1-3-2 ID pattern, three others occur in eastern and central re-

gions of the Atlantic. Several deepwater western Atlantic members of this species group inhabit similar depths but have allopatric geographic distributions (*S. pusillus*—western North Atlantic, *S. ginsburgi*—western South Atlantic, and *S. nigrescens*—eastern Atlantic; *S. billykrietei* on continental shelf off eastern United States, *S. stigmosus* and *S. piger* on continental shelf off southern Florida and Caribbean Sea). Conversely, other deepwater species in this group with sympatric geographic distributions, such as *S. pusillus* and *S. billykrietei*, and *S. piger* and *S. marginatus,* do not overlap extensively with respect to depth of occurrence. Among shallow-water members of this species group, *S. arawak* and *S. rhytisma* have sympatric distributions in the Caribbean Sea and both species occupy a similar range of depths (6–39 m, and 3–25 m, respectively). It is unknown to what degree, if any, these species occur syntopically. None of the collections I examined contained both species, nor have these species been reported to occur syntopically. *Symphurus rhytisma* is rare in collections (only nine specimens available to this study), and more specimens with associated depth-of-capture information are necessary before a detailed statement can be made regarding its ecological requirements. This species is very similar with respect to shape, meristics, size, and depth of occurrence to *S. lubbocki* and *S. reticulatus* (Ascension Island and St. Helena-Madeira, respectively; Munroe, 1990). Interestingly, and consistent with findings for other species where more information is available, all three species have allopatric distributions but apparently similar ecological requirements.

*Symphurus trewavasae*, the only western Atlantic species with the 1-3-3 ID pattern, has been collected on the inner continental shelf off Brazil to Argentina at depths of ca. 7 to 180 m. Among other Atlantic species, only *S. normani* has a 1-3-3 ID pattern (Munroe, 1990). This species occurs allopatrically off West Africa at depths (25–80 m) approximately similar to those inhabited by *S. trewavasae*.

Similar patterns of geographical and ecological occurrence are also evident for the four species with a 1-4-2 ID pattern. Three are North Atlantic species, but only two, *S. minor* and *S. parvus*, occur sympatrically. *Symphurus ommaspilus* is completely different, both in its preferred habitat and in its depth of occurrence, and is therefore completely allotopic relative to other members of this ID pattern group. It is the only species in the group that occurs on shallow (1–20 m) sandy substrates, namely those with submerged aquatic vegetation, on or adjacent to Caribbean coral reefs. Other members in this group are more similar phenotypically and inhabit substrates on the continental shelf. The geographic distribution of *S. minor* extends along the southeastern coast of the United States to the west coast of Florida, including areas extending westward into the Gulf of Mexico almost to the DeSoto Canyon. The phenetically similar *S. parvus*, occurs from North Carolina to Venezuela, and throughout its geographic range, commonly inhabits mud substrates at depths from 40 to 90 m. Although *S. parvus* occurs sympatrically with *S. minor* in the northeastern section of its geographic range, these species are nearly always completely allotopic with respect to depth of occurrence. The geographic distribution and bathymetric center of abundance (11–50 m) of *S. minor* corresponds closely with the occurrence of live-bottom areas. The abrupt change in sediments that occurs in the region of the Mississippi River outflow and which extends into the central and western areas of the Gulf may account for the absence of the species in these areas. The geographic distribution of *S. minor* off the southeastern United States closely parallels that of *S. urospilus*, another species inhabiting live-bottom substrates but belonging to the 1-4-3 ID pattern species group (see below). *Symphurus kyaropterygium*, which occurs off southern Brazil, is hypothesized to be most closely related to *S. parvus.* These two represent another example of related species with allopatric distributions that occupy nearly identical bathymetric environments (36–69 m for *S. kyaropterygium*).

The nine western Atlantic species characterized by the 1-4-3 ID pattern are the most diverse shallow-water tonguefish group in this area. Many are sympatric, or partially sympatric, with other members of the group, and several species also overlap with respect to bathymetric occurrence. These species, however, do not usually occur syntopically. Rather, adults of sympatric species are found at different depths, or if occurring at similar depths, then they inhabit different substrates. Along the southeastern coast of the United States and in the northern Gulf of Mexico, *S. plagiusa*, *S. civitatium*, *S. urospilus*, and *S. diomedeanus* co-occur sympatrically. *Symphurus plagiusa* is unique among these tonguefishes in being the only species that occurs predominantly in nearshore shallow-water and estuarine mud and silt substrates. Although larger individuals of *S. plagiusa* are occasionally found on the continental shelf to depths of 40 m and beyond, the majority of the population is found in nearshore areas and largely allopatric to populations of other tonguefishes. This species sometimes co-occurs in collections with *S. civitatium*, but the majority of the adult population of *S. civitatium* is found in deeper water on inner continental shelf terrigenous sand substrates. Adult *S. civitatium* are very abundant in collections and, although inhabiting a wide depth

range (1–73 m), are more commonly captured at 11 to 45 m where approximately 90% (200/222) of the specimens examined in this study were collected. Adult *S. civitatium* rarely occur in deeper or shallower habitats. Little is known concerning early life history stages of *S. civitatium*. Few studies have identified juveniles of this species, and those studies reporting juveniles (Allen and Baltz, 1997) indicate these were taken at inshore locations. Occurrence of early life history stages in nearshore waters suggests a life history pattern similar to that of *S. tessellatus* (Munroe, 1991), where adults occur in deeper waters on the inner continental shelf and where juveniles inhabit estuarine or nearshore nurseries.

Along the southeastern coast of the United States, *S. civitatium* occurs sympatrically with *S. urospilus* and at depths similar to those for *S. urospilus*, but these two species are completely allotopic with respect to substrate preferences. *Symphurus civitatium* is usually found on terrigenous sand substrates, whereas *S. urospilus* occurs on live-bottom substrates. In fact, differences in geographic occurrences for the species largely reflect their different substrate requirements. *Symphurus urospilus* occurs more or less continuously along the southeastern coast of the United States from about Cape Hatteras, North Carolina, south and around the Florida Peninsula, as far as approximately Apalachee Bay. It has a disjunct distribution in the western Gulf of Mexico off Galveston, Texas, and on the Yucatan Banks. Through its range, this species is found on live-bottom habitats usually between 5 and 40 m. It is generally absent from central and western regions of the Gulf of Mexico where predominant substrates are composed of mud, silt, or quartzite sands. In contrast, along the southeast coast of the United States to southern Florida, *S. civitatium* is also taken commonly on the inner continental shelf, but unlike *S. urospilus*, this species is found predominantly on terrigenous sand substrates, not live-bottom substrates. *Symphurus civitatium* is almost completely absent along live-bottom areas of the west Florida coast (only one citation for St. Joseph Bay, Ginsburg, 1951; and a few specimens from the south Florida shelf, this study). However, west of the Mississippi River to the Yucatan region, *S. civitatium* is one of the most abundant tonguefishes on the inner continental shelf (Hildebrand, 1954).

*Symphurus diomedeanus*, one of the most widely distributed species of Atlantic tonguefish, ranges from the region of Cape Hatteras, North Carolina, to Uruguay. The center of abundance for this species is north of northeastern Brazil. Throughout its range, *S. diomedeanus* is taken commonly and abundantly on diverse inner continental shelf substrates including those composed of calcareous mud, shell hash, and calcareous sands at depths ranging from 18 to 100 m, but usually deeper than 20 m. At these depths, it usually does not co-occur with *S. plagiusa*, the only other western North Atlantic *Symphurus* with the combination of 10 caudal-fin rays and a 1-4-3 ID pattern. The latter has its center of abundance occurring in nearshore embayments and estuaries and only rarely extends into deeper waters commonly inhabited by *S. diomedeanus*. In the western Gulf of Mexico, *S. diomedeanus* is taken occasionally with *S. civitatium*, whereas off Central America it co-occurs in collections with *S. tessellatus* taken on soft mud bottoms. *Symphurus diomedeanus* also occurs sympatrically with *S. urospilus* on the continental shelf off Florida, and some collections examined in this study contained both species.

Atlantic members of the *S. plagusia* complex (Munroe, 1991) are generally shallow-water species, inhabiting nearshore and coastal seas usually shallower than 80 m. Only rarely have individuals been collected deeper than 80 m, and none at depths greater than 110 m. Three of the five Atlantic species of the *S. plagusia* complex have overlapping geographic ranges, but these species do not occur syntopically at all life history stages, especially with respect to bathymetric occurrences. Three of the five Atlantic members of the *S. plagusia* complex, *S. plagusia*, *S. tessellatus*, and *S. caribbeanus*, occur syntopically at some stage in their life history in shallow waters of the Caribbean. Juveniles of all three species have been taken exclusively in beach-seine and otter-trawl collections in shallow-water (<10 m) estuarine and mudflat habitats. However, striking differences are apparent in how these species use inshore habitats. In these habitats, juvenile *S. tessellatus* are collected with all life history stages of *S. plagusia* and *S. caribbeanus*. *Symphurus tessellatus*, however, apparently undergoes an ontogenetic migration from shallow, nearshore habitats to deeper waters farther offshore (11–80 m) on the continental shelf. In contrast, although small numbers of *S. caribbeanus* and *S. plagusia* have been taken as deep as 30–50 m on the continental shelf, these were isolated captures of large adults (>110 mm SL). The majority of *S. plagusia* and *S. caribbeanus* (80% and 83%, respectively), including all juveniles examined, were collected in waters shallower than 20 m, with most taken by beach seine and small otter trawls in less than 10 m on nearshore mudflats, in mangrove habitats, and other estuarine locations.

*Symphurus oculellus*, although occurring sympatrically with *S. plagusia* and *S. tessellatus* (see Figs. 59, 61, and 63), apparently has a different life history than these other species. *Symphurus oculellus*

inhabits deeper waters than the others (Table 10), spanning an overall bathymetric range from 7 to 110 m, but is captured most frequently in waters deeper than 20 m (83% collected deeper than 20 m). *Symphurus oculellus*, including juveniles as small as 76 mm SL, have been collected in neritic waters deeper than 7 m, and none have been collected from estuarine habitats contrary to the capture depths of *S. plagusia* and *S. tessellatus*. However, estuarine environments in the geographic range of *S. oculellus* along northeastern South America have not been as thoroughly sampled as have the nearshore habitats occupied by *S. plagusia* and juvenile *S. tessellatus* in the northern Caribbean and southern Brazilian areas. *Symphurus civitatium*, the northernmost-occurring species in this group, is the only Atlantic species with a distribution that is allopatric in comparison with that of other members of this species group. Depth distribution and substrate requirements of this species were discussed above.

The majority of the *S. jenynsi* population is allopatric in comparison with populations of other tonguefishes. This species lives on mud bottoms on the inner continental shelf in the South Atlantic. The bathymetric distribution spans depths ranging from about 17 m to 190 m (Menezes and Benvegnú, 1976), but most specimens have been collected between 12 and 25 m. In this region, *S. jenynsi* is sometimes collected with juvenile *S. tessellatus*.

Factors influencing ecological distributions observed for western Atlantic tonguefishes are rather complex. On a geographic scale, the species' range corresponds mostly with the limits of previously identified faunal regions. The ecological, or local, distribution of a species is reflected in the spatial and bathymetric distribution of particular substrates (Topp and Hoff, 1972) within the broader geographic range. Association of most flatfishes with sediments rather than hard substrata indicates that the structure of the sea bed is an important factor controlling their distribution (Gibson, 1994, and references therein). Topp and Hoff (1972) suggested that strong interrelationships between apparent substrate requirements of individual species of flatfish could possibly explain patterns of geographical and bathymetric distributions observed for these fishes. Other studies (Pearcy, 1978) cautioned that direct examination only of substrate types without examination of depth of occurrence may be incomplete because influences of depth and sediments on the distribution of benthic organisms are usually closely correlated and are difficult to separate. Sediment texture generally decreases with increasing depth of water, with small particles usually transported from regions of high energy waves and currents into deep, low-energy sedimentary environments, and coarse sediments, such as sands, generally are deposited in shallow water close to their continental source. According to Thorson (1957), physical and chemical compositions of sediments may be the main factor in determining the general patterns of distributions of infaunal and epifaunal invertebrates on the level sea floor. Faunal changes in both benthic invertebrates and vertebrates on the continental shelf and slope have also been thought to result from depth-related changes in physicochemical properties (Sanders and Hessler 1969; Haedrich et al., 1975). However, the emerging paradigm is that the relations between organism distributions and the dynamic sedimentary and hydrodynamic environment are complex (Snelgrove and Butman, 1994), especially when considering that grain size covaries with other factors including sedimentary organic matter content, pore-water chemistry, and microbial abundance and composition, all of which are influenced by near-bed flow regime.

Ecological distributional patterns observed for western Atlantic tonguefishes may result directly through an active process in which tonguefishes select particular substrates based on physical characteristics of the substrate (i.e. particle size and composition of the sediments, ease of burying, coloration of the sediments). Conversely, tonguefishes may indirectly occupy particular substrates because the suite of physicochemical characteristics (temperature regime, current strength, water depth, salinity, oxygen concentration, ambient light levels, etc.) required by that species may occur coincident with depositional environments for particular sediment types. Reichert and Van der Veer (1991) provided descriptive information regarding substrate preference of settling *S. plagiusa* juveniles, but no experimental work on substrate selection or preference has been done for any species of western Atlantic tonguefish, and hypotheses concerning active selection of substrates by tonguefishes remain untested.

Yet another factor potentially contributing to substrate selection, and indirectly to the ecological distributional patterns observed for tonguefishes, may be related to substrate selection by biotic associates of tonguefishes. Diet studies (Mahadeva, 1956; Austin and Austin, 1971; Topp and Hoff, 1972; Stickney, 1976; Kawakami, 1976; MacPherson, 1978; Toepfer and Fleeger, 1995) indicate strong preferences by symphurine tonguefishes for small epibenthic and infaunal invertebrates as food sources. Morphological characteristics of tonguefishes, such as the relatively small size of the mouth and reduced or absent dentition on ocular-side jaws in many shallow-water species, may also reflect adaptations (or constraints) for specialized feeding that would determine the size

spectrum and variety of organisms that these fishes include in their diets (Stickney, 1976). Some invertebrates exhibit strong substrate preferences and are differentially distributed with respect to substrate types (Hedgpeth, 1953; 1954; Williams, 1958; Butman, 1987). Hence, substrate selectivity (either by passive or active means) exhibited by invertebrates that are preferred food sources of tonguefishes would in turn be mirrored by tonguefishes through their selective foraging activities. This hypothesis is also untested, because, beyond descriptive studies for those few species where diets have been examined, virtually nothing is known concerning the relative degree (if any, see Toepfer and Fleeger, 1995) of dietary selection or preference exercised by these flatfishes.

## Size-related life history information

Adult western Atlantic symphurine tonguefishes span a size continuum from ca. 25 to 320 mm SL, encompassing the entire size range within the genus. In these waters, both the largest (*S. jenynsi*, attaining maximum sizes ca. 320 mm and maturing at sizes of ca. 120 mm or more) and smallest (*S. arawak*, maximum sizes ca. 50 mm and maturing at sizes as small as 25 mm) members of the genus occur. Most western Atlantic tonguefishes, however, are intermediate in size, usually reaching maximum sizes smaller than 200 mm (usually between 80–180 mm) and maturing at sizes between 50 and 110 mm. Although no western Atlantic tonguefish attains sizes large enough to support directed commercial fisheries, several species have been used when taken in industrial fisheries (Roithmayr, 1965).

Species of *Symphurus* are the smallest members of the Cynoglossidae. For example, adults of five species of *Paraplagusia* range in size from 184 to 334 mm SL (Chapleau and Renaud, 1993), whereas adult sizes of 49 species of *Cynoglossus* range between 99 and 530 mm SL (Menon, 1977).

Despite superficial similarities in overall external morphology and general body plan, western Atlantic *Symphurus* display striking differences in body sizes and the relative sizes at which maturity is attained in individual species (Figs. 6–9). Although species of western Atlantic *Symphurus* more or less form a continuum along a size gradient, marked differences in size-related features between species are apparent when overall maximum sizes (based on the largest specimen observed for the species) and minimum sizes at sexual maturity (based only on females) are compared (Figs. 6–9). Based on these parameters, species were assigned to one of four size categories.

Dwarf tonguefishes are those with adult sizes ranging up to ca. 80 mm and attaining sexual maturity at sizes usually of 40 mm or less. Six western Atlantic tonguefishes categorized as dwarf species are (in order of increasing maximum size) *S. rhytisma* (ca. 45 mm), *S. arawak* (ca. 50 mm), *S. ommaspilus* (60 mm), *S. pelicanus* (70 mm), *S. pusillus* (77 mm), and *S. minor* (78 mm). *Symphurus arawak*, which matures at sizes as small as 25–30 mm, is one of the smallest tonguefish species. Only a small number of the *S. minor* studied actually exceeded 70 mm (most in fact were smaller than 65 mm), and maturity in this species is reached at sizes (29–40 mm) comparable to those noted for other dwarf tonguefishes.

Several species of dwarf tonguefishes, such as *S. arawak*, *S. ommaspilus*, and *S. rhytisma*, which attain lengths of only 35–60 mm and mature at sizes as small as 25–30 mm, are among the smallest of pleuronectiform fishes. The small adult sizes in these species are comparable with those of *S. lubbocki* (Munroe, 1990), known only from two mature females of ca. 28 mm collected at Ascension Island. Among other western Atlantic flatfishes, only the bothid *Citharichthys gymnorhinos*, from the Gulf of Mexico, approaches such small sizes, attaining maximum lengths usually less than 55 mm and reaching sexual maturity at ca. 30 mm (Topp and Hoff, 1972). Other small species of flatfishes, such as members of the bothid genus *Etropus* (Leslie and Stewart, 1986), the paralichthyid *Tarphops* (Hoshino[10]) and perhaps some freshwater achirid soles (*Achirus* spp.), mature at sizes ca. 50–60 mm, and reach maximum lengths only slightly greater than this.

Three diminutive tonguefishes are species reaching maximum sizes from ca. 80 to 100 mm and maturing at sizes greater than 40 mm, but usually less than 70 mm. Smallest of species in this category is *S. parvus* (maximum lengths ca. 88 mm, maturity at 40–45 mm). The other species in this category (*S. ginsburgi* and *S. nebulosus*) attain similar maximum sizes (ca. 90 mm) but mature at somewhat larger sizes (50 and 60–65 mm) than *S. parvus*. Diminutive tonguefishes inhabit a variety of substrates in relatively deepwater habitats on the middle and outer continental shelf (*S. ginsburgi* and *S. parvus*), or outer continental shelf and upper continental slope (*S. nebulosus*).

Medium-size species reach maximum sizes of ca. 110 to 150 mm and mature at ca. 70 to 90 mm. Medium-size western Atlantic species are *S. marginatus* (ca. 146 mm, matures at ca. 79–90 mm), *S. billykrietei* (ca. 113 mm, matures at ca. 80 mm), *S. stigmosus* (ca. 127 mm, matures at ca. 80 mm), *S. piger* (ca.

[10] Hoshino, K. 1996. Laboratory of Marine Zoology, Faculty of Fisheries, Hokaido Univ., 3-1-1 Minato-cho, Hakodate, Hokaido 041, Japan. Personal commun.

130 mm, matures at 70 mm), *S. kyaropterygium* (ca. 120 mm, matures at ca. 74–85 mm), *S. plagusia* (ca. 130 mm, matures at ca. 85 mm), *S. caribbeanus* (ca. 130 mm, matures at 70–80 mm), and *S. trewavasae* (ca. 139 mm, matures at ca. 70–80 mm).

Large species of *Symphurus* are those ranging in size from ca. 150 to 320 mm and maturing at sizes usually greater than 90 mm. As a group, large-size western Atlantic tonguefishes are also those species that reach maturity at the largest sizes observed for any tonguefish in the other size categories. The largest western Atlantic tonguefishes are (in order of increasing maximum sizes) *S. civitatium* (ca. 152 mm, matures at sizes slightly greater than 90 mm), *S. urospilus* (ca. 166 mm, matures at ca. 100 mm), *S. plagiusa* (ca. 175 mm, matures at 85–95 mm), *S. diomedeanus* (207 mm, matures at 90–120 mm), *S. oculellus* (190 mm, matures at ca. 110 mm), *S. tessellatus* (ca. 220 mm, matures at 104 to 120 mm), and *S. jenynsi*, the largest species in the genus (maximum sizes of ca. 320 mm, matures ca. 115 mm).

Because body size is considered to be among the most important determinants of organismal function and ecological role (Peters, 1983; LaBarbera, 1986; Hanken and Wake, 1993), comparison of size-related features among the species studied could reveal interesting patterns among the species groups. The smallest tonguefishes are those (*S. arawak*, *S. rhytisma*, *S. ommaspilus*) inhabiting sandy substrates on and adjacent to coral reefs. In fact, a total of five Atlantic species of dwarf tonguefishes (three western Atlantic species and *S. lubbocki* and *S. reticulatus* from central and eastern Atlantic localities) occur on sand substrates in tropical seagrass beds, or on sand habitats on or adjacent to coral reefs. Other dwarf species (*S. minor*, *S. pelicanus*, and *S. pusillus*) that inhabit a variety of substrates on the inner continental shelf (*S. minor* on live-bottom substrates, *S. pelicanus* and *S. pusillus* on soft mud substrates) attain somewhat larger sizes than the dwarf species occurring in coral reef environments. Among western Atlantic dwarf tonguefishes, *S. pusillus* is quite unusual in being the only one occurring in relatively deep waters (100–230 m) and frequently found beyond tropical and warm-temperate regions (Fig. 29). Eight Atlantic species of dwarf tonguefishes belong to two of nine species groups recognized by Munroe (1992). Six are members of the species group characterized by the 1-3-2 ID pattern. Two others (*S. ommaspilus* and *S. minor*) possess a 1-4-2 ID pattern. No western Atlantic dwarf tonguefishes are known from other ID pattern species groups. Species with different ID patterns may reflect divergent lineages within the genus, indicating that small body size has evolved in at least two different lineages within the genus.

Many specialized niches or habitats demand tiny body size (Hanken and Wake, 1993). Because many dwarf tonguefishes inhabit shallow-water, sandy habitats on or adjacent to coral reefs and tropical seagrass beds, it would appear that small size is favorable for survival in these habitats. Robins and Randall (1965) suggested that, for fishes living on exposed sandy substrates near coral reefs, small body size may reflect a generalized adaptational response to the extreme predation pressure exerted by the high concentration of predators generally associated with the coral reef environment. Evidence they used to support this hypothesis is that dwarf species are known for tonguefishes and also for unrelated taxa such as cuskeels (*Ophidion*), which inhabit areas with similar types of substrates.

Information based on recent collections on vertical faces of Caribbean coral reefs (Hensley)[11] where sizeable numbers of dwarf tonguefishes have been captured from extremely small (<1 m), isolated sand patches located in small depressions on the reef provides alternative hypotheses that may explain the successful exploitation of these habitats by dwarf tonguefishes. Given the limited size of the sand patches (<1 m in area) where dwarf tonguefishes have been taken, small body size may reflect morphological specialization to the limiting physical size of suitable substrates available in these isolated sand patches. Alternatively, small size in tonguefishes may reflect morphological specialization to potentially limiting trophic resources, i.e. the reduced abundance of benthic organisms, that would be available as prey items for tonguefishes in these small, specialized habitats. Hypotheses regarding ecological success of dwarf tonguefishes inhabiting coral reef areas are untested, however, because nothing is known regarding predation rates on these or other dwarf fishes in this region. Nor is there any information available concerning movements and patterns of substrate use, diet composition, or relative degree of food selection (if any) exhibited by tonguefishes within these specialized habitats.

More than one species group is represented among the species comprising the other size categories of tonguefishes. Three species, from three different species groups, are categorized as diminutive tonguefishes (*S. nebulosus*, 1-2-2 group; *S. ginsburgi*, 1-3-2 group; and *S. parvus*, 1-4-2 group). Four species groups are represented among those categorized as medium-size tonguefishes. Deepwater medium-size species inhabiting the outer continental shelf and upper continental slope include *S. marginatus*, *S.*

[11] Hensley, D. A. 1990. Department of Marine Sciences, Univ. Puerto Rico, Mayagez, Puerto Rico 00708. Personal commun.

*piger*, *S. billykrietei*, and *S. stigmosus*, all of which share the 1-3-2 ID pattern. *Symphurus marginatus* is the largest western Atlantic species possessing the 1-3-2 ID pattern (ca. 146 mm, matures at ca. 79–90 mm). The only western Atlantic species characterized by a 1-3-3 ID pattern, *S. trewavasae*, is also included in this size range, as is *S. kyaropterygium*, the largest member of the 1-4-2 species group. Both species occur at similar depths on the inner continental shelf off Brazil. In this size range are *S. plagusia* and *S. caribbeanus*, the smallest of five Atlantic species in the *S. plagusia* species complex (Munroe, 1991), featuring a 1-4-3 ID pattern. Unlike other tonguefishes in this size category, these two inhabit shallow estuaries and nearshore coastal habitats throughout the tropical western Atlantic.

All large-size western Atlantic tonguefishes possess the same ID pattern (1-4-3). Interestingly, these species, together with *S. chabanaudi* and *S. elongatus*, eastern Pacific species that have a 1-5-3 ID pattern, are the largest species of symphurine tonguefishes. These are the predominant tonguefishes collected in abundance in shallow-water environments located in both north and south warm-temperate and tropical regions throughout the western Atlantic and eastern Pacific oceans, the only areas worldwide where such diversity and abundance of shallow-water species of *Symphurus* is found. Of special note is the fact that only in the New World do large-size *Symphurus* occur, and this interestingly is the only tropical, shallow-water, region of continental seas where large-size tonguefishes of other cynoglossid genera (*Cynoglossus* and *Paraplagusia*) are absent.

More complete analysis of geographical distributions and patterns of historical ecology for western Atlantic tonguefishes must await further resolution of monophyletic groups within the genus. Such resolution and testing of hypotheses put forth in this work can only be made with a more detailed osteological study of the entire genus and suitable outgroups, an analysis beyond the scope of this investigation.

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# Appendix

## Western Atlantic material examined

***Symphurus nebulosus*** 27 specimens (36.4–86.2 mm SL)

**Counted and measured (24 specimens, 45.0–86.2 mm SL).** NORTHWEST ATLANTIC: EASTERN UNITED STATES: UMO 311.8; (76.7); 40°48'N, 66°36–38'W; 524 m; 19 Jun 1974. USNM 152842; (45.0); 39°55'31"N, 70°39'W; 355 m; 4 Oct 1882. VIMS 5577; 2(64.3–66.5); 36°00.5'N, 74°45'W; 400 m; 12 Nov 1974. UNC 4951; 8(67.7–86.2); 33°48–52'N, 76°12–05.30'W; 495 m; 29 Jul 1970. USNM 285758; 2(81.1–84.2; cleared and stained); 33°48'18"–52'30"N, 76°12–05'30"W; 495 m; 29 Jul 1970 (Formerly UNC 4951). MCZ 27966; holotype; (76.6); 32°07'N, 78°37'30"W; 421 m, 12 Jul 1880. USNM 291326; 2(69.5–69.6); 31°43'N, 79°21'W; 239 m; 21 Jan 1972. MCZ 39480; (67.0); 30°58'N, 79°34'W; 511 m; 24 Feb 1940. USNM 291327; (67.7); 30°54'N, 79°40'W; 488 m; 21 Jan 1972. USNM 265179; (63.8); 29°29'N, 79°53'W; 686 m; 19 Nov 1965. VIMS 8833; (77.7); 29°O8–12'N, 78°56.00–07'W; 800 m; 22 Sep 1980. UMML 20746; 2(67.9–68.1); 28°09–10'N, 79°02–00'W; 810 m; 18 Jul 1965. UMML 27439; (54.9); 26°28–27'N, 78°40–43'W; 658 m; 21 Jul 1965.

**Counted (3 specimens, 3 lots).** NORTHWEST ATLANTIC: EASTERN UNITED STATES: MCZ 97453; (36.4); 39°40'N, 70°58'W; 450 m; 29 Jun 1981. USNM 291330; (57.1); (locality information approximate); 39°09.1'N, 72°32.8'W; 384 m; 4 Feb 1975. USNM 84490; (76.0); 29°41'N, 79°55'W; 0–683 m; 4 May 1886.

***Symphurus arawak*** 47 specimens (11.7–49.3 mm SL)

**Counted and measured (42 specimens, 11.7–49.3 mm SL).** FLORIDA: UMML 19274; (28.0); Alligator Reef; 15 m; 16 Jul 1965. CARIBBEAN SEA: BAHAMAS: AMNH 27327; (18.0); Mayaguana; 9 m; 19 Mar 1966. AMNH 27706; (24.4); Acklins; 20 m; 9 Mar 1966. AMNH 29214; (35.4); Mayaguana; 15 m; 19 Mar 1966. AMNH 34603; (25.2); Eleuthera; 11 m; 2 Feb 1968. ANSP 111924; 3(23.1–27.1); Eleuthera; 11 m; 2 Feb 1968. AMNH 33161; (13.9); Little Inagua; 25 m; 21 Jan 1968. ANSP 147929; (17.8); Cat Island; 28 m; 31 Jan 1968. UF 13380; (11.7); Little San Salvador; 31 m; 9 Sep 1966. UF 13455; 2(29.2–34.7); Green Cay (about 17 miles east of Andros Island, 24°03'N, 77°10'W); 20 m; 21 Aug 1966. UF 17054; (31.6); Green Cay; 18 m; 22 Aug 1966. GREATER ANTILLES: GRAND CAYMAN: UF 12269; paratype; (29.8); Paradise Rocks; 15 m; 22 Oct 1964. JAMAICA: UMML 31430; (30.6); Discovery Bay; 25 m; 24 Jun 1972. UMML 34385; 2(38.5–49.3); 11 m; 17 Jun 1970. UMML 34386; (37.7); unknown locality; summer, 1972. HAITI: ANSP 111378; (26.6); Gulf of Gonave, St. Marc Channel off Mount Rouis; 39 m; 16 Sep 1967. ANSP 119056; (27.7); Gulf of Gonave, south of St. Marc Point; 29 m; 14 Sep 1967. ANSP 119057; (41.3); Port Au Prince Bay; Pelican Cays; 22 m; 13 Sep 1967. UMML 21421; (27.3); St. Marc Bay; 6 m; 22 Dec 1959. UMML 15492; paratypes; 2(28.8–38.3); St. Marc Bay; 6 m; 22 Dec 1959. PUERTO RICO: ANSP 144354; 2(13.2–24.3); 6 mi south of La Parguara; 9 m; 12 Nov 1976. LESSER ANTILLES: DOMINICA: USNM 265177; 2(26.7–41.0); 8 m; 10 Nov 1964. USNM 265178; (20.4); 8 m; 14 Nov 1964. USNM 265182; 2(18.6–20.8); 12 m; 15 Nov 1964. CURAÇAO: ANSP 101985; holotype; (33.1); Lagoen; 14 m; 25 Nov 1962. UMML 15491; paratypes; 2(26.3–36.3); 14 m; 25 Nov 1962. USNM 198200; paratypes; 2(29.4–30.3); Lagoen; 14 m; 25 Nov 1962. UNKNOWN: UMML uncat; (34.9); no data. BELIZE: FMNH 94817; (32.5); Glovers Reef, near top of dropoff at NE Cay; 25 m; 28 Jun 1979. USNM 267784; (29.3); 16°48'N, 88°04'W; 24 m; 2 Apr 1983. COLOMBIA: PROVIDENCIA: UF 25721; (30.3); 34 m; 14 Aug 1969. UF 25876; (22.0); 18 m; 11 Aug 1969.

**Counted (4 specimens, 4 lots).** CARIBBEAN SEA: BELIZE: FMNH 97497; (14.8); west side of Lighthouse Reef; 1 Aug 1973. HONDURAS: FMNH 97496; (23.3); Roatan, Port Royal, 0.5 mi off Port Royal/Roatan Lodge; 12 Jun 1983. FMNH 97498; (21.0); Roatan, off Caw and Calf Cay; 18 Feb 1984. FMNH 97499 (34.0); Mary's Place, reef 1.5 mi west of French Harbor; 20 Feb 1984.

**Other material examined** (1 specimen, 1 lot). COLOMBIA: UMML 29971; (17.5); Isla de Tierra Bomba, 10°23'N, 75°35'W; 15 m; 1 Sep 1971.

***Symphurus rhytisma*** 9 specimens (21.7–45.1 mm SL).

**Counted and measured (6 specimens, 21.7–45.1 mm SL).** CARIBBEAN SEA: BAHAMAS: ANSP 93812; holotype; (25.6); Little Bahama Bank, West of Wood Cay, off Grand Bahama Island (ca. 26°44'15"N, 79°02'37"W); 16 m; 19 Jul 1959. ANSP 124854; 2(36.6–45.1); Samana Cay (Atwood Cay), middle of west half of south side of island; 6 m; 27 Jan 1968. UF 13456; (34.3); High Cay; 3 m; 19 Aug 1966. BELIZE: FMNH 94821; (21.7); Glovers Reef, dropoff off Long Cay; 25 m; 1 Jul 1979. LESSER ANTILLES: USNM 324677; (25.7); 15°42'N, 63°38'W (near Isla de Aves); 12 Aug 1972.

**Counted (3 specimens, 3 lots).** CARIBBEAN SEA: CURAÇAO: UMML 14379; (32.7); Lagoen; 14 m; 25 Nov 1962. SOUTHWEST ATLANTIC: BRAZIL: USU 1079; (26.7); 20°21'S, 36°59'07"W; 97.5 m; 14 May 1987. USU 1054; (27.0); 21°37'S, 40°19'W; 37 m; 11 May 1987.

***Symphurus ginsburgi*** 62 specimens (30.8–90.4 mm SL).

**Counted and measured (55 specimens, 30.8–90.4 mm SL).** SOUTHWEST ATLANTIC: BRAZIL: MZUSP 12339; holotype; (61.5); Rio Grande do Sul; 31°31'S, 49°52'W; 200 m; 11 Apr 1972. PARATYPES: MNHN 1975-270; 3(87.2–0.4); 23°08'S, 42°30'W; 103 m; 2 Dec 1961. MZUSP 12314–15; 2(59.3–60.2); 23°15'S, 42°24'W; 111 m; 8 Aug 1970. MZUSP 12370; (35.4); 29°53'S, 48°19'W; 194 m; 3 Aug 1972. MZUSP 12327; (58.0); 30°26'S, 48°50'W; 150 m; 7 Apr 1972. MZUSP 12899–901; 3(33.8–51.1); 30°26'S, 48°50'W; 150 m; 7 Apr 1972. MZUSP 12328–33; 6(32.0–51.9); 30°36'S, 49°25'W; 145 m; 9 Apr 1972. MZUSP 12335; (43.9); 31°02'S, 49°52'W; 135 m; 4 Oct 1972. MZUSP 12902–03; 2(30.9–31.1); 31°02'S, 49°52'W; 135 m; 10 Apr 1972. MZUSP 12340–48; 9(31.6–60.7); 31°31'S, 49°52'W; 200 m; 11 Apr 1972. MZUSP 12391–93; 3(31.8–60.2); 32°21'S, 50°13'W; 180 m; 21 Aug 1972. MZUSP 12320; (54.0); 32°46'S, 50°25'W; 200 m; 21 Jan 1972. MZUSP 12316–19; 4(47.7–62.8); 34°06'S, 51°33'W; 180 m; 18 Jan 1972. MZUSP 12385–89; 5(39.1–62.6); 34°27'S, 51°50'W; 175 m; 15 Aug 1972. MZUSP 12371–75; 5(30.8–61.8); 34°42'S, 49°03'W; 192 m; 6 Aug

1972. MZUSP 12377–84; 8(33.2–81.0); 34°45'S, 52°05'W; 179 m; 15 Aug 1972.

**Counted (7 specimens, 5 lots).** SOUTHWEST ATLANTIC: BRAZIL: USU 1372; (57.4); 21°31'S, 40°08'W; 298 m; 31 May 1987. USU 1389; (60.0); 21°35'S, 40°06'W; 262 m; 10 May 1987. USU 1086; (54.5); 23°36'S, 42°01'W; 208 m; 1 Jun 1987. MNHN 1989-420; (57.2); 23°36'40"S, 42°01'67"W; 208 m; 1 Jun 1987. MZUSP 12336–38; paratypes 3(34.6–42.8); 31°31'S, 49°52'W; 200 m; 11 Apr 1972.

***Symphurus billykrietei*** 103 specimens (49.6–119.0 mm SL).

**Counted and measured (70 specimens, 49.6–112.2 mm SL).** NORTHWEST ATLANTIC: USNM 326637; holotype, (112.2); off Virginia, 36°41.4'–41.8'N, 74°40.1–39.7'W; 275 m; 17 Sep 1975. PARATYPES: CANADIAN ATLANTIC: ARC 8703371; (80.1); 42°58'N, 60°40'W; oblique trawl between 2,100 meters and surface (not used for depth information); 29 Aug 1986. ARC 8705134; (91.2); 42°49'N, 63°29'W; 212 m; 14 Oct 1985. EASTERN UNITED STATES: USNM 291328; (74.6); 39°59'N, 70°46'W; 292 m; 8 Mar 1976. MCZ 91580; (108.1); 39°32'N, 72°25'W; 292 m; 22 Sep 1987. MCZ 64849; 6(58.7–74.6); off southern New England. USNM 291329; (85.0); 38°50'N, 72°55'W; 264 m; 20 May 1975. VIMS 5581; (59.8); 37°04'N, 74°38'W; 252 m; 12 Jun 1973. VIMS 3073; (105.6); 37°00.7'N, 74°36'W; 292 m; 12 Jun 1973. VIMS 4891; (105.5); 37°00'N, 74°37'W; 340 m; 30 Jan 1976. USNM 326634; 3(63.4–94.4); 36°41'18"–43'42"N, 74°38'48"–37'36"W; 366 m; 20 Nov 1974. VIMS 9191; 6(54.0–103.6); 36°43'N, 74°38'W; 269 m; 16 Nov 1974. VIMS 5572; 6(49.6–105.5); collected with holotype.

**Nontype specimens counted and measured:** CANADIAN ATLANTIC: NMC 82-0332; (95.5); 43°26'N, 60°29'W; 183 m; 20 Nov 1978. ARC 8705132; 2(88.4–108.4); 43°16'N, 61°12'W; 174 m; 19 Nov 1978. ARC 8705136; (71.3); 42°48'N, 63°04'W; 205 m; 8 Oct 1986. ARC 8600284; (93.6); 42°46'N, 63°59'W; 264 m; 23 Feb 1982. EASTERN UNITED STATES: MCZ 94336; (62.6); 41°37'N, 65°51'W; 247 m; 17 Oct 1987. MCZ 91589; 4(60.4–74.1); 40°21'N, 67°44'W; 232 m; 7 Oct 1987. VIMS 1905; 4(51.8–93.8); 40°00'N, 69°11'W; 231 m; 25 Oct 1970. AMNH 40834; (80.9); 39°13'N, 72°26'W; 297 m; 26 Sep 74. USNM 327179; 2(66.1–101.0); 39°04'N, 72°44'W; 221 m; 28 Sep 1983. VIMS 1600; 3(52.1–56.7); 38°25'N, 73°24'W; 247 m; 10 Aug 1969. VIMS 1601; (64.8); 38°20'N, 73°40'W; 117 m; 10 Aug 1969. VIMS 5574; (70.0); 37°04'N, 74°36'W; 238 m; 30 Jan 1976. VIMS 5564; 2(62.8–77.1); 37°01'N, 74°37'W; 292 m; 12 Jun 1973. VIMS 9189; (82.7); 36°43'N, 74°38'W; 260 m; 18 Nov 1974. VIMS 5569; 2(57.8–83.3); 36°37.5'N, 74°43'W; 301 m; 9 Jun 1973. VIMS 3072; (68.3); 36°37.6'N, 74°41.2'W; 256 m; 8 Jun 1973. MCZ 76387; (50.1); 36°36.5'N, 74°41.5'W; 155 m; 15 Mar 1972. VIMS 3070; 2(68.4–97.1); 36°35'N, 74°42'W; 317 m; 8 Jun 1973. VIMS 5570; 3(61.6–68.9); 36°32'N, 74°42'W; 330 m; 20 Sep 1975. USNM 327177; 3(65.1–83.9); 36°08'N, 74°43'W; 320 m; 2 Oct 1973. USNM 327180; (64.4); 34°46'N, 75°27'W; 352 m; 4 Mar 1984. STRAITS OF FLORIDA: USNM 158310; (81.6); off Dry Tortugas, 24°20'N, 83°20'W; 348 m; 13 Apr 1954. SOUTH-CENTRAL GULF OF MEXICO: FMNH 88819; (107.0); north of Yucatan Peninsula, 23°51'N, 87°49'W; 183 m; 9 Dec 1963.

**Counted (8 paratypes, 3 lots).** NORTHWEST ATLANTIC: EASTERN UNITED STATES: MCZ 99447; 4(88.2–101.4); 38°22'N, 73°35'W; 304 m; 10 Sep 1991. VIMS 4891; (67.8); 37°00'N, 74°37'W; 340 m; 30 Jan 1976. VIMS 5511; 3(86.7–91.3); 36°44'N, 75°38'W; 304 m; 17 Sep 1975.

**Counted (14 non-type specimens, 8 lots).** NORTHWEST ATLANTIC: CANADIAN ATLANTIC: ARC 8705135; 2(95–97.8); 43°11'N, 61°23'W; 206 m; 19 Jun 1979. ARC 8705133; (95.0); 43°03'N, 61°32'W; 397 m; 13 Oct 1985. EASTERN UNITED STATES: VIMS 1900 (cleared and stained); 5(59.4–99.8); 40°02'N, 70°19'W; 222 m; 24 Jul 1969. VIMS 9190; (83.0); 36°42'48"N, 74°36'36"W; 650 m; 16 Nov 1974. VIMS 5579; 2(68.2–76.3); 36°38'N, 74°41'W; 255 m; 8 Jun 1973. VIMS 5575; (109.8); 36°37'N, 74°42'W; 316 m; 9 Jun 1973. VIMS 3071; (77.8); 36°35'N, 74°42'W; 317 m; 8 Jun 1973. USNM 327178; (107.5); 35°57'N, 74°49'W; 245 m; 11 Mar 1982.

**Other material examined (11 nontype specimens, 8 lots).** NORTHWEST ATLANTIC: EASTERN UNITED STATES. MCZ 150775; (119.0); 40°38'N, 72°18'W; 48 m; 19 Feb 1997. MCZ 135301; (55.7); 40°13'N, 68°33'W; 257 m; 4 Oct 1991. MCZ 150774; (52.2); 39°59'N, 69°46'W; 137 m; 20 Feb 1997. MCZ 91643; (62.2); 37°59'N, 73°55'W; 344 m; 9 Mar 1990. MCZ 91581; (72.9); 36°38'N, 74°42'W; 206 m; 10 Mar 1990. MCZ 135302; (60.4); 37°41'N, 74°13'W; 222 m; 8 Mar 1995. Uncatalogued; (70.6); specific locality information and capture date unknown. STRAITS OF FLORIDA: UMML 27173 (tentatively identified as this species, see comments in the "Remarks" section above); 4(68.4–77.2); southeast of Dry Tortugas, 24°18'N, 82°33'W; 2 Feb 1968.

***Symphurus stigmosus*** 12 specimens (54.4–126.2 mm SL).

**Counted and measured:** CARIBBEAN SEA: MEXICO: USNM 326635; holotype, (126.2); off Yucatan Peninsula, 21°04'N, 86°19'W; 352 m; 10 Sep 1967. PARATYPES: BAHAMAS: MCZ 39205; 2(73.1–77.5); in NW Providence Channel, 26°08'N, 79°02'W; 284 m; 3 Feb 1938. USNM 328062; (91.6); off east side of Andros Island, 25°29'N, 79°19'W; 366 m; 9 Nov 1960. MEXICO: off Yucatan Peninsula, USNM 326636; (96.0); collected with holotype. UMML 35291; (98.8); collected with holotype. UMML 35290; (54.4); 21°10'N, 86°21'W; 281 m; 10 Sep 1967.

**Nontype specimens counted and measured.** STRAITS OF FLORIDA: UMML 35289; (59.6); Gulf Stream off Miami, ca. 7 mi east of Govt. Cut, ca. 25°45'N, 79°59'W; 201 m; 29 Mar 1965. UMML 13917; (66.1); 24°32–29'N, 80°54–53'W; 192 m; 21 Jun 1963. UMML 16314; (85.4); off Tortugas, 24°17'N, 82°15'W; 373 m; 28 Nov 1964. CARIBBEAN SEA: DOMINICA: MCZ 27968; (77.8); 15°16'50" N, 61°23'30" W; 202 m; 29 Jan 1879. NICARAGUA: USNM 327176; (85.7); east of Puerto Cabezas and off Serrana Bank, Colombia, 14°14'12"N, 80°28'30"W; 287 m; 5 May 1964.

**Questionable identification (nontypes, not included in data summaries):** STRAITS OF FLORIDA: UMML 15642; 5(53.7–89.5); 24°40–42'N, 80°23–20'W; 258 m; 23 Jun 1963.

***Symphurus pusillus*** 29 specimens (35.2–76.9 mm SL).

**Counted and measured (18 specimens, 35.2–62.7 mm SL).** NORTHWEST ATLANTIC: EASTERN UNITED STATES. USNM 28730; paralectotype; (53.5); 40°07'48"N, 70°43'54"W; 123 m; 16 Jul 1881. USNM 28778; lectotype; (54.5); 40°01'N,

69°56'W; 139 m; 4 Aug 1881. USNM 325958; paralectotype; (58.4); 40°01'N, 69°56'W; 139 m; 4 Aug 1881. VIMS 9116; (43.0); 40°00'N, 69°11'W; 233 m; 25 Oct 1970. VIMS 5573; 2(46.1–48.2); 37°02'N, 74°39'W; 183 m; 1 Aug 1975. VIMS 5571; 2(45.6–54.2); 36°37'N, 74°02'W; 200 m; 17 Sep 1975. VIMS 1129; 2(50.5–62.7); 34°37'N, 75°41'W; 230 m; 18 Apr 1971. UNC 12180; (40.0); 32°49'N, 77°56'W; 229 m; 19 Apr 1957. UMML 17387; (62.1); 24°39'N, 80°47'W; 134 m; 23 Jan 1965. UF 82430; (50.2); 24°24'30"N, 81°55'54"W; 104 m. UMML 35228; 2(41.6–52.1); 24°18'N, 82°20'W; 167 m; 26 Apr 1969. USNM 153089; (48.9); Palm Beach (ca. 26°N); February, 1950. GULF OF MEXICO: USA 4822; (38.5); 26°25'N, 84°15'W; 183 m; 21 Aug 1977. UF 72139; (35.2); 29°17'N, 87°55'W; 11 Oct 1970.

**Counted (11 specimens, 6 lots).** NORTHWEST ATLANTIC: EASTERN UNITED STATES: AMNH 19426; (38.6); off southern Florida. GULF OF MEXICO: FLORIDA: USNM 153099; (55.3); off Sombrero Light; 102 m; 6 Jun 1950. UF 29778; (50.4); 29°36'N, 87°27'W; 112 m; 8 Apr 1977. ALABAMA: UF 70885; 2(45.8–76.9); 29°24'N, 87°34'W; 187 m; 11 Oct 1970. MISSISSIPPI: TCWC 6819.14; 3(47.6–68.2); 29°05'11"N, 88°49'94"W; 115 m; 4 Oct 1987. UNSPECIFIED LOCATION: UMML uncatalogued lot; 3(62.1–68.0); RV *Gillis* Cruise 10.

***Symphurus pelicanus*** 66 specimens (27.2–69.2 mm SL).

**Counted and measured (19 specimens, 27.2–69.2 mm SL).** NORTHWEST ATLANTIC: SARGASSO SEA: UMML 1328; (44.1); 29°55'W, 70°20'W; captured at surface; 25 Oct 1956. GULF OF MEXICO: LOUISIANA: FMNH 103611; (62.1); 28°55'N, 89°15'W; 60 m; 23 Oct 1953. FMNH 94460; (57.3); 28°52'N, 89°42'W; 64 m; 28 Mar 1962. FMNH 88821; (43.8); 28°40'N, 89°42'W; 110 m; 28 Mar 1962. TEXAS: USNM 155234; holotype; (50.2); 26°43'N, 96°32'W; 46 m; 4 Feb 1939. USNM 155235; paratype; (58.8); 26°34'N, 96°32'W; 82 m; 5 Feb 1939. MEXICO: TCWC 6248.2; 3(51.6–59.2); 25°09'N, 97°03'W; 52 m; 18 Nov 1975. FMNH 46372; (43.0); Campeche Bay, 19°16'N, 92°14'W; 40 m; 23 Aug 1951. CARIBBEAN SEA: HONDURAS: UF 15662; (44.8); 15°46'N, 88°10'W; 111 m. PANAMA: UMML 34371; (54.9); 9°18'N, 80°03'W; 24 m; 20 Jul 1966. COLOMBIA: UMML 30181; 3(65.4–69.2, cleared and stained); 11°08–07.6'N, 74°18.1–19.3'W; 133 m; 31 Jul 1968. UMML 30081; 2(27.2–42.1); 8°58'N, 76°31'W; 60 m; 12 Jul 1966. TRINIDAD AND TOBAGO: USNM 74331; paratype; (60.7); 10°37'N, 61°42'W; 57 m; 3 Feb 1884. USNM 113252; (54.4); 10°37'N, 61°42'W; 57 m; 3 Feb 1884.

**Counted (42 specimens, 16 lots).** CARIBBEAN SEA: HONDURAS: UMML 35279; 5(38.6–44.6); 15°46'N, 88°01'W; 113 m; 19 Mar 1967. PANAMA: UMML 26762; (37.3); 9°43.7'N, 79°22.2'W; 46 m; 20 Jul 1966. USNM 324675; (42.0); 9°38.9–40.2'N, 79°17.4'W; 67 m; 19 Jul 1966. UMML 26616; 4(51.0–54.2); 9°31.0–31.9'N, 79°59.5–56.0'W; 35 m; 13 Jul 1966. USNM 324676; (43.8); 9°14.6–13.5'N, 80°21.8–22.8'W; 48 m; 20 Jul 1966. UMML 26544; 2(37.2–40.4); 9°00.1–8°59.7'N, 80°45.8–46.7; 55 m; 20 Jul 1966. COLOMBIA: UMML 30132; 4(39.9–48.8); 10°20.8–18.4'N, 75°39.1–38.1'W; 63 m; 1 Aug 1968. UMML 35276; 3(40.9–49.3); 9°40'N, 76°03'W; 49 m; 13 Jul 1966. UMML 26780; (46.3); 9°31.3–32.5'N, 76°17'W; 57 m; 13 Jul 1966. UMML 35275; (41.0); 8°50'N, 77°02'W; 72 m; 17 Jul 1966. UMML 22282; (45.3); 8°48.7–47.6'N, 77°12.7–14.2'W; 99 m; 17 Jul 1966. VENEZUELA: UMML 35277; 10(34.6–54.2); 10°44'N, 64°16'W; 65 m; 21 Jul 1968. UMML uncatalogued lot (specimen dried up); (45.4); 10°21'N, 65°41'W; 59 m; 22 Jul 1968. UMML 35278; 5(39.5–59.3); 9°58'N, 60°46'W; 57 m; 30 Jun 1969. GUYANA: UMML 35274 (58.9); 8°36'N, 58°53'W; 57 m; 16 Jul 1968. LESSER ANTILLES: UMML uncatalogued lot; (26.5); RV *Gilliss* sta. 53, 15°42'N, 63°38'W; 9 m; 12 Aug 1972.

**Other material examined (5 specimens, two lots).** STRAITS OF FLORIDA: UF 32430; 1 specimen; 24°23.36'N, 81°55.54'W; 119 m; 31 May 1981. GULF OF MEXICO: LOUISIANA: UF 103521; 4(52.9–62.9); 15 miles east of Mississippi Delta; 60 m; 6 Nov 1991.

***Symphurus marginatus*** 110 specimens (56.9–146.1 mm SL).

**Counted and measured (30 specimens, 56.9–146.1 mm SL).** NORTHWEST ATLANTIC: SOUTHEASTERN UNITED STATES: VIRGINIA: VIMS 4302; (130.5); 36°40.4'N, 74°40'W; 335 m; 8 Jun 1973. VIMS 5510; (123.2); 36°37.5'N, 74°42.7'W; 301 m; 9 Jun 1973. FLORIDA: UMML 10519; (84.9); 29°44'N, 80°11'W; 329 m; 19 Jun 1958. USNM 291315; 2(111.6–112.9); 29°39'N, 80°11'W; 348 m; 10 Feb 1965. UMML 10590; 2(78.6–80.5); 29°30'N, 80°09'W; 348 m; 18 Aug 1957. UMML 35232; (114.7); 29°20'N, 80°07'W; 379 m; 16 Nov 1964. UMML 35241; 2(110.2–111.0); 29°16'N, 80°06'W; 390 m; 16 Nov 1964. UMML 35234; 2(112.4–113.0); 29°14'N, 80°05'W; 375 m; 15 Nov 1964. UMML 35242; (105.0); 28°21'N, 79°51'W; 329 m; 26 Jan 1962. GULF OF MEXICO: UNSPECIFIED LOCATION: FMNH 47908; (95.2); 750 m; 1952. FLORIDA: USA 4665; (96.8); 24°17.5'N, 82°57.5'W; 458 m; 22 Apr 1974. UF 72224; (56.9); 29°27'N, 87°21'W; 405 m; 9 Apr 1971. ALABAMA: FMNH 88818; (104.5); 29°14'N, 87°46'W; 406 m; 28 Oct 1962. FMNH 88815; 2(91.0–99.0); 29°10'N, 87°56'W; 668 m; 26 Jul 1962. FMNH 88817; (114.2); 29°10'N, 88°10'W; 366 m; 7 Aug 1962. USNM 186042; 2(116.3–118.6); 29°05'N, 88°22'W; 458 m; 12 Jun 1959. LOUISIANA: MCZ 27967; holotype; (90.1); 28°42'N, 88°40'W; 593 m. CARIBBEAN SEA: COLOMBIA: UMML 23248; (97.6); 9°28'N, 76°27'W; 531 m; 16 Jul 1966. UMML 35240; (99.5); 11°09'N, 74°26'W; 289 m; 19 May 1965. USNM 291314; (114.5); 12°30'N, 72°08'W; 470 m; 10 Oct 1965. TRINIDAD AND TOBAGO: UMML 35239; (123.8); 11°30'N, 60°46'W; 403 m; 22 Sep 1964. SURINAME: FMNH 90539; (146.1); 7°34'N, 54°50'W; 366 m; 6 Nov 1957. FRENCH GUIANA: USNM 159236; (107.7); 7°12'N, 53°11'W; 329 m; 9 Nov 1957. FMNH 86396; (135.5); 7°10'N, 53°10'W; 366 m; 9 Nov 1951.

**Counted (74 specimens, 51 lots).** NORTHWEST ATLANTIC: EASTERN UNITED STATES: NEW JERSEY: MCZ 151172; (136.6); 39°55'N, 70°35'W; 439–915 m; Nov 1994. GEORGIA: UNC 12175; (120.1); 31°58'N, 79°08'W; 366 m. FLORIDA: UMML 35231; (90.7); 29°57'N, 80°10'W; 293 m; 22 Feb 1962. UMML 10589; (101.1); 29°48'N, 80°12'W; 384 m; 14 Aug 1957. USNM 236609; 2(106.8–114.7); 29°39'N, 80°11'W; 348 m; 10 Feb 1965. UMML 35230; (108.6); 29°31'N, 80°09'W; 348 m; 14 Nov 1964. UMML 35243; 2(105.8–109.2; cleared and stained); 29°31'N, 80°09'W; 384 m; 14 Nov 1964. UMML 35236; (112.9); 29°21'N, 80°06'W;

379 m; 14 Nov 1964. UMML 35233; 6(105.9–116.2); 29°21'N, 80°06'W; 390 m; 17 Nov 1964. UF 41164; (127.2); 29°20'N, 80°05.9'W; 320 m; 30 May 1984. UF 44394; (116.8); 29°19.39'N, 80°29.71'W; 549 m; 26 Mar 1985. UMML 35235; (105.9); 29°17'N, 80°04'W; 403 m; 24 Aug 1962. UMML 10569; (97.1); 29°15'N, 80°05'W; 384 m; 31 May 1957. USNM 236603; (107.4); 29°14'N, 80°05'W; 357 m; 29 Nov 1965. UMML 35238; (96.4); 29°06'N, 80°00'W; 360 m; 26 Jan 1960. USNM 291287; (100.4); 29°03'N, 80°00'W; 348 m; 10 Feb 1965. UMML 10587; (72.1); 28°36'N, 79°54'W; 403 m; 30 Jul 1957. UF 33889; 2(91.1–93.6); 28°23'N, 79°49'W; 342 m; 13 Jun 1961. UMML 35242; 4(92.7–102.2); 28°21'N, 79°51'W; 329 m; 26 Jan 1962. UNC 12179; (126.1); 28°02'N, 79°50'W; 329 m; 31 Jan 1957. UMML 20569; (80.1); 27°18'N, 79°49'W; 324 m; 16 Jul 1965. UMML 20536; (58.7); 27°02'N, 79°49'W; 501 m; 16 Jul 1965. UMML 17440; (104.1); 24°50'N, 80°37'W; 37 m; 14 Apr 1965. BAHAMAS: UMML 10565; (101.4); 27°29'N, 78°58'W; 366 m; 2 Feb 1957. GULF OF MEXICO: FLORIDA: TU 11024; (97.2); 24°19'N, 83°20'W; 329 m; 14 Apr 1954. USNM 291036; 2(77.5–90.7); 24°27'N, 83°32'W; 512 m; 26 Nov 1965. FMNH 86366; (107.1); 24°26'N, 83°24'W; 388 m; 14 Oct 1959. FDNR 6751; (80.5); 28°14'N, 85°49'W; 476 m; 9 Sep 1968. ALABAMA: UMML 35229; (109.1); 29°12'N, 87°52'W; 531 m; 25 Jul 1962. FMNH 94486; (102.7); 29°11'N, 88°05'W; 476 m; 26 Aug 1962. UF 44377; 2(121.2–132.9); 29°09.20'N, 88°09.80'W; 467 m; 13 Nov 1984. USNM 131634; paratype; (104.7); 29°03'15"N, 88°16'W; 593 m; 11 Feb 1885. USNM 158981; (120.9); 29°06'N, 88°19'W; 476 m; 13 Mar 1955. MISSISSIPPI: FMNH 88820; (113.7); 29°00'N, 88°35'W; 403 m; 24 Aug 1962. LOUISIANA: MCZ 51900; (95.9); 27°45'N, 91°18'30"W; 549 m; 23 Feb 1964. CARIBBEAN SEA: PUERTO RICO: USNM 108416; (71.5); 18°32'N, 66°21'W; 476 m; 4 Feb 1933. HONDURAS: FMNH 94462; (102.1); 16°43'N, 82°44'W; 470 m; 16 Sep 1957. FMNH 94468; 6(77.4–95.1); 16°42'N, 82°40'W; 549 m; 16 Sep 1957. FMNH 90533; (92.8); 16°42'N, 82°30'W; 549 m; 19 Sep 1957. FMNH 90534; (90.6); 16°42'N, 82°36'W; 549 m; 16 Sep 1946. COLOMBIA: UMML 30106; 3(76.4–108.5); 10°32'N, 75°35'W; 45 m; 1 Aug 1968. UMML 35240; (107.9); 11°09'N, 74°26'W; 289 m; 19 May 1965. UF 33894; (92.7); 11°26'N, 73°41'W; 403 m; 10 Nov 1970. VENEZUELA: MCZ 58657; (91.0); 11°36'N, 62°40'W; 72 m; 19 Apr 1960. TRINIDAD AND TOBAGO: UMML 35237; (117.2); 11°09'N, 60°55'W; 66 m; 22 Sep 1964. FMNH 88847; (97.8); 11°31'N, 60°51'W; 448 m; 22 Sep 1964. SURINAME: USNM 159607; (122.8); 7°36'N, 54°42'W; 412 m; 7 Nov 1957. SOUTHWEST ATLANTIC: BRAZIL: MNHN 1989-421; 2(79.7–84.7); 19°36.03'S, 38°53.27'W; 640 m; 30 May 1987. USU 1371; 3(78.4–85.1); 19°36'S, 38°53'W; 713 m; 30 May 1987. USU 1393; (87.0); 21°34'S, 40°08'W; 600 m; 31 May 1987. WESTERN ATLANTIC: AMNH 40249; (1); unspecified location.

**Other material examined (seven specimens, five lots).** NORTHWEST ATLANTIC: NEW JERSEY: USNM 315614; (126.1); 39°11'N, 72°27'W; 330 m; 19 Aug 1974. GULF OF MEXICO: FLORIDA: TCWC 3956.1; 2(87.5–95.7); 29°27'N, 86°45'W; 384 m; 4 Aug 1968. ALABAMA: TCWC 6187.7; (118.4); 29°07'N, 88°18'W; 476 m; 15 Oct 1969. TCWC 6187.8; (118.0); 29°07'N, 88°18'W; 476 m; 15 Oct 1969. CARIBBEAN SEA: SURINAME: UMML 11177; 2(121.6–139.0); 7°34'N, 54°50'W; 370 m; 6 Nov 1957.

***Symphurus piger*** 184 specimens (27.3–127.1 mm SL).

**Counted and measured (33 specimens, 58.6–120.5 mm SL).** NORTHWEST ATLANTIC: STRAITS OF FLORIDA: UMML 17635; 7(58.6-90.1); 25°49–51'N, 79°19'W; 225 m; 29 Jun 1965. CARIBBEAN SEA: BAHAMAS: ANSP 144936; (78.2); 22°55'N, 78°36'W; 274 m; 7 Nov 1961. UF 15637; 3(71.4–82.0); 22°55'N, 78°36'W; 274 m; 7 Nov 1961. GREATER ANTILLES: PUERTO RICO: FMNH 90536; (112.4); 18°26'N, 67°11'W; 229 m; 6 Oct 1959. FMNH 91116; 10(84.7–120.5); 18°26'N, 67°10.5'W; 274 m; 6 Oct 1959. LESSER ANTILLES: VIRGIN ISLANDS: FMNH 94463; (92.7); 18°37.5'N, 64°57'W; 403 m; 26 Sep 1959. SAINT KITTS ISLAND: MCZ 27965; holotype; (84.6); ca. 17°N, 62°W; 458 m. NETHERLANDS ANTILLES: FMNH 90538; 2(72.6–94.1); 17°38.5'N, 63°27'W; 348 m; 30 Sep 1959. HONDURAS: FMNH 94469; (76.5); 15°15'N, 81°19'W; 265 m; 25 Aug 1957. COLOMBIA: UMML 30166; 5(67.0–95.5); 11°20–22'N, 73°48.51–44'W; 158 m; 21 Jul 1968. GUYANA: FMNH 86414; (92.1); 9°36'N, 59°44'W; 146 m; 4 Nov 1957.

**Counted (113 specimens, 26 lots).** NORTHWEST ATLANTIC: SOUTHEASTERN UNITED STATES: FLORIDA: UMML 35251; 2(100.5–103.1); 29°57'N, 80°10'W; 293 m; 22 Feb 1962. GULF OF MEXICO: FLORIDA: FDNR 12566; 2(103.7–106.9); 24°20.5'N, 82°41.6'W; 105 m; 22 Aug 1981. LOUISIANA: TCWC 6819.60; 2(61.7–62.7); 29°05'11"N, 88°49'94"W; 115 m; 4 Oct 1987. MEXICO: TCWC 4468.11; 9(87.6–122.3); 18°50.8'N, 93°38'W; 146 m; 12 Nov 1975. TCWC 6097.14; 11(57.9–123.2); 18°50'N, 93°39'W; 166 m; 12 Nov 1975. CARIBBEAN SEA: BAHAMAS: UMML 14146; (51.2); 27°25'N, 78°41–37.5'W; 302 m; 5 Feb 1964. UMML 35250; 2(51.6–64.4); 25°50'N, 78°22'W; 251 m; 11 Dec 1971. UF 33888; 11(30.5–85.9); 23°34'N, 79°05'W; 274 m; 11 Jun 1960. USNM 285197; 6(68.9–75.1); 23°34'N, 79°05'W; 274 m; 6 Nov 1960. GREATER ANTILLES: PUERTO RICO: FMNH 86398; 4(79.1–91.4); 18°12'N, 67°18'W; 6 Oct 1959. FMNH 90540; (104.0); 18°13'N, 67°14.5'W; 229 m; 6 Oct 1959. LESSER ANTILLES: VIRGIN ISLANDS: USNM 285198; 3(83.0–99.7); 18°12'N, 64°18'W; 274 m; 6 Oct 1959. ANGUILLA ISLAND: USNM 285195; 3(93.0–98.6); 18°11'N, 63°15'W; 296 m; 25 Feb 1966. NETHERLANDS ANTILLES: UMML 35255; 3(73.6–87.4); 17°34'N, 63°30'W; 92 m; 30 Sep 1959. MEXICO: TCWC 6207.17; (92.9); 20°26.3–51.5'N, 87°14.7–19.0'W; 265 m; 11 Apr 1976. BELIZE: UMML 35245; 7(82.7–104.7); 17°17'N, 87°59'W; 229 m; 10 Jun 1962. HONDURAS: FMNH 94465; (79.1); 16°38'N, 82°34'W; 384 m; 21 Aug 1957. PANAMA: UMML 35247; (78.1); 9°18'N, 80°25'W; 137 m; 29 May 1962. COLOMBIA: UMML 35244; 3(94.1–104.0); 11°08.51–07.6'N, 74°18.1–19.3'W; 133 m; 31 Jul 1968. TRINIDAD AND TOBAGO: UMML 35252; (75.9); 11°21.2'N, 60°38.7'W; 174 m; 20 Sep 1964. GUYANA: UMML 11175; (97.3); 9°39'N, 59°47'W; 183 m; 4 Nov 1957. USNM 159609; 7(83.4–106.1); 9°39'N, 59°47'W; 183 m; 11 Apr 1957. USNM 159605; 2(94.7–98.2); 9°36'N, 59°44'W; 146 m; 11 Apr 1957. SURINAME: FMNH 94461; 5(96.1–114.6); 7°30'N, 55°00'W; 183 m; 24 Mar 1963. GCRL 3817; (112.5); 7°27'N, 54°30'W; 201 m; 16 May 1969. FRENCH GUIANA: USNM 159211; 23(89.3–122.0); 7°18'N, 53°32'W; 183 m; 8 Nov 1957.

**Other material examined (38 specimens, 20 lots).** NORTHWEST ATLANTIC: STRAITS OF FLORIDA: UMML 27458; (75.6); 24°00'N, 79°47'W; 300 m; 31 Aug 1967. GULF OF MEXICO: FLORIDA: TORTUGAS AREA: USNM 117176; (103.4); no station data. USNM 117287; 3(101.8–113.2); no station data. MISSISSIPPI: UF 44356; (127.1); 29°12.30'N, 88°25.10'W; 165 m; 3 Apr 1985. CARIBBEAN SEA: BAHAMAS: UMML 35253; (85.7); 27°08'N, 77°52'W; 289 m; 25 Oct 1961. UMML 35249; 5(72.7–75.9); 24°25'N, 79°13'W; 229 m; 7 Nov 1960. UMML 35254; 2(79.5–81.4); 23°52'N, 79°11'W; 375 m; 6 Nov 1960. UMML 35246; 2(69.9–79.4); 23°05'N, 78°49'W; 434 m; 7 Nov 1961. UMML 17958; (87.5); 25°28'N, 78°07'W; 458 m; 24 Apr 1965. UMML 35256; (66.6); 25°13'N, 79°13'W; 366 m; 8 Nov 1960. FMNH 94458; 2(61.3–75.3); 24°25'N, 79°13'W; 229 m; 7 Nov 1960. FMNH 94459; (71.1); 24°40'N, 79°16'W; 366 m; 7 Nov 1960. MCZ 39395; (27.3); 22°34'N, 78°15'W; 329 m; 28 Apr 1939. GREATER ANTILLES: CUBA: MCZ 39218; 3(65.1–72.3); 22°34'30"N, 78°16W; 333 m; 28 Apr 1939. JAMAICA: UMML 35285; 3(38.5–105.8); 17°56'N, 78°60'W; 238 m; 7 Jul 1970. PUERTO RICO: UMML 7124; 4(83.6–117.8); 18°18'N, 67°18.5'W; 549 m; 6 Oct 1959. FMNH 91116; 2(80.5–98.1); 18°26'N, 67°10.5'W; 274 m; 6 Oct 1959. HONDURAS: FMNH 86416; 2(85.4–91.7); 16°39'N, 81°43'W; 229 m; 22 Aug 1957. FMNH 94466; (66.5); 16°38'N, 82°43'W; 256 m; 21 Aug 1957. USNM 285196; (77.2); 16°35.4'N, 80°47.2'W; 259 m; 11 Mar 1960.

***Symphurus trewavasae*** 90 specimens (41.0–131.0 mm SL).

**Counted and measured (24 specimens, 59.5–131.0 mm SL).** BRAZIL: BMNH 1913.12.4:264; holotype; (117.0); Cabo Frio (ca. 23°53'S); 73 m. BMNH 1913.12.4:265–273; paratypes; 9(59.5–112.1); Cabo Frio (ca. 23°53'S); 73 m. MNHN 50–69; paratype; (105.5); Cabo Frio (ca. 23°53'S); 73 m. MNHN 1975-271; 6(78.3–131.0); 24°18'S, 45°22'W; 66 m; 11 Dec 1961. URUGUAY: MZUSP 12498–500; 3(113.6–124.7); 35°11'S, 52°47'W; 97 m; 30 Oct 1972. ARGENTINA: MNHN 1975-272; 4(101.8–124.1); 37°00'S, 55°21'W; 69 m; 29 Dec 1961.

**Counted (55 specimens, 12 lots).** BRAZIL: BMNH 1913.12.4:265–273; paratypes; 6(59.5–112.1); Cabo Frio (ca. 23°53'S); 73 m. MNHN 1989-486; (95.5); 22°58'S, 42°06'W; 50 m. USU 954; 4(32.9–48.6); 22°58'S, 42°06'W; 50 m; 1 Jun 1987. USU 1106; 9(26.2–45.8); 22°58'S, 42°06'W; 50 m; 1 Jun 1987. USU 984; 2(104.5–112.5); 23°07'S, 42°03'W; 100 m; 1 Jun 1987. MNHN 1989-487; 2(117.5–123.3); 23°07'S, 42°03'W; 100 m; 1 Jun 1987. MZUSP 12476–77; 2(123.8–125.1); 29°33'S, 48°57'W; 96 m; 6 Apr 1972. MZUSP 12829; 8(54.8–119.1); 31°12'S, 50°35'W; 26 Jan 1972. USNM 314774; 2(93.8–94.6); 32°09'S, 51°55'W; 14 m; 1 Sep 1982. MZUSP 12485–89; 3(66.7–112.8); 33°50'S, 51°51'W'; 65 m; 19 Apr 1972. USNM 290668; 2(110.7–113.1); 33°50'S, 51°51'W'; 65 m; 19 Apr 1972. MNHN 1992-1411; (77.2); (location approximate) 35°00'S, 55°00'W; 7 m. URUGUAY: MZUSP 12457–68; 12(52.5–119.1); 34°11'S, 52°19'W; 58 m; 16 Jan 1972.

**Other material examined (11 specimens, 6 lots).** ARGENTINA: INIDEP 479; 2(68–98); 34°28'S, 53°42'W; 27 m; 10 Jul 1992. INIDEP 480; 2(51–59); 34°45'S, 54°18'W; 28 m; Feb 1992. INIDEP 478; (63); 34°57'S, 54°47'W; 19 m; 12 Jul 1993. INIDEP 481; (78); 38°32'S, 58°10'W; 27 m; 22 Jul 1993. INIDEP 482; 2(41–60); 38°32'S, 58°10'W; 27 m; 22 Jul 1993. INIDEP 477; 2(53–107); 41°S, 64°40'W; 70 m; Dec 1992. INIDEP 476; (79); 45°S, 65°10'W; 1991.

***Symphurus kyaropterygium*** 14 specimens (31.9–120 mm SL).

**Counted and measured (12 specimens, 31.9–120 mm SL).** BRAZIL: MZUSP 12425; holotype; (119); 26°34'S, 48°10'W; 52 m; 14 May 1975. PARATYPES: MZUSP 12783; (31.9); Baia de Ilha Grande, May, 1966. MZUSP 12784; (85.9), Ilha de São Sebastiao; October, 1925. MZUSP 12913; (92.7); 24°57'S, 45°32'W; 61 m; 26 Feb 1975. MZUSP 12914–15; 2(86.3–94.7); 25°33'S, 46°42'W; 55 m; 17 May 1975. MNHN 1975-264; 2(74.1–106); 23°26'S, 44°36'W; 36 m; 9 Dec 1961. MNHN 1975-266; (96.5); 24°34'S, 46°31'W; 45 m; 14 Dec 1961. MNHN 1975-267; (117); 31°24'S, 50°36'W; 66 m; 17 Dec 1961. MNHN 1975-268; 2(106–110); 31°24'S, 50°36'W; 69 m; 29 Dec 1961.

**Counted (2 paratypes, one lot).** BRAZIL: MNHN 1975-265; 2(96.0–116); 24°18'S, 45°22'W; 66 m; 11 Dec 1961.

***Symphurus minor*** 83 specimens (7.3–70.6 mm SL).

**Counted and measured (31 specimens, 22.6–70.6 mm SL).** CANADA: NOVA SCOTIA: USNM 92614; paratypes; 3(22.6–47.3); 44°23'30"N, 61°44'15"W; 170 m; 7 Jul 1885. EASTERN UNITED STATES: NORTH CAROLINA: USNM 134272; paratype; (26.3); 34°26'N, 76°12'W; 40 m; 19 Oct 1885. UF 24577; (48.4); 34°23'N, 76°14'W; 26 m; 23 Aug 1977. SOUTH CAROLINA: USNM 155232; paratype; (64.5); 32°34.5'N, 79°19.5'W; 31 m; 9 Mar 1940. GCRL 17370; (69.1); 32°05'N, 79°38'W; 39 m; 17 Feb 1977. GEORGIA: USNM 155230; paratype; (70.6); 31°40'N, 80°24.5'W; 22 m; 14 Mar 1940. UF 33893; 2(55.4–61.7); 30°48'N, 75°51'W; 33 m; 30 Jul 1969. GMBL 79-106; 2(63.0–63.1); 30°44.2'N, 80°13.9'W; 45 m; 1 May 1979. GULF OF MEXICO. FLORIDA: UMML 35248; (62.4); 24°47'N, 82°58'W; 44 m; 7 Mar 1970. USNM 131643; holotype; (36.2); 28°46'N, 84°49'W; 48 m; 15 Mar 1885. USNM 152734; paratypes; 2(23.9–33.6); 28°46'N, 84°49'W; 48 m; 15 Mar 1885. UWF 2964; (35.6); 28°36'N, 84°15'W; 37 m; 29 Jun 1977. USNM 131293; paratype; (33.1); 29°15'30"N, 82°29'30'W; 50 m; 17 Feb 1885. USNM 131591; paratypes; 3(27.2–56.7); 29°11'30"N, 85°29'W; 48 m; 7 Feb 1885. USA 2185; (54.4); 29°04'N, 85°14'W; 38 m; 25 Jun 1975. USA 3733; 2(34.7–70.2); 30°07'N, 86°45'30"W; 46 m; 8 Mar 1977. USA 1907; (55.4); 29°30'N, 86°53'W; 20 m. USA 1786; (52.3); 30°00'N, 87°12'30"W; 29 m; 22 Apr 1975. GCRL 14893; 3(51.8–59.5); 16 mi off Perdido Bay; 22 m; 14 Sep 1975. ALABAMA: USA 1864; 2(47.3–49.9); 30°05'N, 87°34'W; 26 m; 21 Apr 1975.

**Counted (48 specimens, 31 lots).** EASTERN UNITED STATES: SOUTH CAROLINA: USNM 155231; paratype; (44.9); 32°52'N, 79°04'W; 20 m; 12 Feb 1940. UNC 3913; (42.5); 33°42.2'N, 76°41.9'W; 27 Apr 1965. MCZ 58655; 2(43.2–46.2); 32°44.5'N, 79°00.2'W; 24 m; 24 Mar 1972. GEORGIA: USNM 155233; paratype; (63.3); 31°46.4'N, 79°47.5'W; 44 m; 13 Mar 1940. FLORIDA: GMBL 76-279; (42.3); 29°59'N, 80°39'W; 35 m; 17 Sep 1976. UMML 35259; (47.8); 29°58'N, 80°33.5'W; 40 m; 8 Jul 1961. UMML 35258; 2(41.4–48.0);

29°53.5'N, 80°24.5'W; 46 m; 8 Jul 1961. UF 33928; (42.2); 28°40'N, 80°16'W; 35 m; 5 Apr 1977. GULF OF MEXICO. FLORIDA: USA 2989; 3(47.4–55.7); 30°10'N, 87°05'W; 28 m; 14 Sep 1975. UF 71511; 3(53.7–61.5); 30°10'N, 86°41.5'W; 36 m; 21 Jul 1973. USA 3727; (37.5); 30°06'N, 86°44'30"W; 62 m; 8 Mar 1977. UF 70904; 2(54.1–68.1); 30°06'N, 86°25'W; 40 m; 25 Jan 1971. USA 2140; (35.3); 29°50'N, 86°06.5'W; 42 m; 20 Jul 1975. UWF 1468; (38.1); 29°49.9'N, 86°05.1'W; 37 m; 19 Oct 1975. UWF 3714; (34.1); 29°45'N, 86°00'W; 42 m; 4 Jun 1978. UF 70937; (48.2); 29°41.5'N, 86°06'W; 49 m; 9 Jul 1971. UF 70442; 2(54.6–58.8); 29°31'N, 85°55'W; ca. 40 m; 27 Nov 1969. UF 70918; 4(46.1–64.2); 29°28'N, 85°09'W; 20 m; 6 Apr 1971. USNM 131590; paratype; (29.2); 29°11'30"N, 85°29'W; 48 m; 7 Feb 1885. UF 71385; 2(47.2–47.8); 29°00'N,; 86°38'W; 34 m; 3 Oct 1970. UF 71419; 2(50.5–64.4); 28°33'N, 84°40'W; 61 m; 1 Dec 1970. UF 70707 (two specimens cleared and stained); 28°32.5'N, 84°37'W; 55 m; 2 Apr 1971. FDNR 6542; (40.1); 27°37'N, 83°28'W; 37 m; 20 May 1967. FDNR 5144; 2(26.6–39.3); 27°37'N, 83°07'W; 18 m; 2 Nov 1967. UF 21066; (57.1); 26°58.5'N, 83°24.5'W; 49 m. UWF 1321; (26.8); 26°25.5'N, 82°59.5'W; 37 m; 22 Oct 1975. FDNR 6536; (31.6); 26°24'N, 82°38'W; 48 m; 5 Mar 1981. FDNR 6540; (44.8); 26°24'N, 82°38'W; 37 m; 7 Apr 1967. FDNR 18025; 2(56.6–56.7); 25°45.7'N, 83°11.07'W; 54 m; 2 Dec 1982. UMML 35257; 2(49.6–69.5); 24°24'N, 82°43'W; 51 m; 27 Apr 1969. FDNR 2977; (44.7); West Egmont Key; 25 m; 17 Dec 1964.

**Other material examined (4 specimens, 3 lots).** CANADIAN ATLANTIC: ARC H2774; (7.3 mm larva); Scotian shelf. 42°21'N, 65°01'W; surface; 14 Aug 1977. SOUTHEASTERN UNITED STATES: FLORIDA: UF 33928; (41.5); 28°40'N, 80°16'W; 35 m; 5 Apr 1977. GULF OF MEXICO: FLORIDA: MCZ 49374; 2(23.2–25.8); 18 miles south by west, Destin, Okaloosa County; October 1941.

***Symphurus parvus*** 121 specimens (21.8–88.2 mm SL).

**Counted and measured (33 specimens, 33.8–88.2 mm SL).** EASTERN UNITED STATES: NORTH CAROLINA: VIMS 8832; (88.2); 34°23'N, 75°58'W; 80 m; 12 Mar 1982. FLORIDA: USNM 153097; paratype; (42.2); off Palm Beach; 73 m. USNM 153088; paratype; (38.2); off Palm Beach; 46 m; April 1950. USNM 153087; (50.2); off Palm Beach; 1950. USNM 161351; (33.8); off Palm Beach; 64 m; January 1951. AMNH 18887; 2(45.4–47.1); southeast of Pompano Beach; 101 m; 1 Aug 1949. UMML 15589; (43.6); 25°38–47'N, 80°05'W; 79 m; 1 Apr 1964. UMML 20911; (62.0); 24°49'N, 80°38'W; 48 m; 15 Sep 1965. UMML 3680; (43.2); southeast Ship Channel out of Key West; 52 m; 30 Dec 1958. GULF OF MEXICO: FLORIDA: USNM 153090; paratype; (55.5); off Sombrero Light; 101 m; 6 Jun 1950. MCZ 50863; (55.3); 7 mi east of Sombrero Light; 70 m. UMML 10737; (43.3); off Sombrero Key; 146 m; July 1949. UF 70586; 3(47.5–62.4); 28°44'N, 85°06'W; 18 Apr 1970. UF 70769; 2(47.7–58.8); 28°33'N, 84°39'W; 55 m; 17 Jul 1971. USNM 84491; holotype; (64.0); off Boca Chica, 24°45'45"N, 81°46'W; 82 m; 15 Jan 1885. USNM 74330; nontype (50.5); off Boca Chica, 24°25'45'N, 81°46'W; 82 m; 15 Jan 1885. USNM 152733; paratype; (69.0); off Boca Chica, 24°25'45"N, 81°46'W; 82 m; 15 Jan 1885. USNM 74330; paratypes; 3(45.9–55.1); off Boca Chica, 24°25'45'N, 81°46'W; 82 m; 15 Jan 1885. UF 21834; (58.5); 24°25'35"N, 81°52'30"W; 64 m; 29 Apr 1976. ALABAMA: USA 6361; (84.7); 29°23'N, 87°48'30"W; 90 m; 15 Mar 1978. MEXICO: FMNH 46371; (46.8); Bahía de Campeche, 21°38'N, 92°10.5'W; 54 m; 17 Aug 1951. CARIBBEAN SEA: NICARAGUA: FMNH 88816; 2(52.8–59.3); 12°16'N, 82°53'W; 55 m; 2 Jun 1962. COLOMBIA: UMML 30114; (56.9); 10°56–56.9'N, 75°26–26.9'W; 43 m; 1 Aug 1968. UMML 30123; (46.5); 10°40'N, 75°31'W; 27 m; 1 Aug 1968. UMML 29281; (63.1); 9°37.9'–37.6'N, 75°50.4–51.5'W; 37 m; 13 Jul 1966. UMML 26769; (71.3); 9°31.3–32.5'N, 76°15.4–17'W; 57 m; 13 Jul 1966.

**Counted (49 specimens, 31 lots).** EASTERN UNITED STATES: SOUTH CAROLINA: GMBL 78-159 (61.3); 33°06'N, 77°47.3'W; 67 m; 29 Sep 1978. FLORIDA: UMML 35263; (54.0); 29°17'N, 80°05'W; 383 m; 15 Nov 1964. USNM 153098; (31.1); off Palm Beach; 74 m. WEST INDIES (doubtful location): USNM 47657; (one specimen, ca. 56.8, broken into two pieces); uncertain locality, listed as probably West Indies, collected by the *Blake* between 1877 and 1880; jar label reads *Blake* XXV (see Eschmeyer, 1965, regarding discrepancies in *Blake* station data reported in USNM ledgers). GULF OF MEXICO: FLORIDA: UF 71280; (41.5); 28°56'N, 85°20'W; 1 Nov 1970. UF 71301; (53.5); 28°32.5'N, 84°39'W; 55 m; 2 Apr 1971. USA 4906; 2(47.4–70.3); 27°50'N, 84°31'W; 102 m; 24 Aug 1977. USA 4915; (80.6); 27°50'N, 84°31'W; 102 m; 24 Aug 1977. FDNR 6543; (30.8); 27°37'N, 83°28'W; 36 m; 11 Aug 1967. FDNR 6615; (55.3); 27°37'N, 83°58'W; 55 m; 12 May 1967. FDNR 6537; (49.1); 27°36'N, 84°13'W; 73 m; 3 Jul 1966. FDNR 18026; (42.4); 26°45.86'N, 83°21.44'W; 50 m; 29 Oct 1980. FDNR 18028–29; 5(44.1–67.3); 26°45.70'N, 84°00.13'W; 90 m; 31 Jan 1982. UWF 2670; (48.2); 26°24'N, 83°49'W; 92 m; 15 Jul 1976. FDNR 18027; 2(63.7–65.5); 26°16.72'N, 83°12.81'W; 48 m; 5 Mar 1981. UMML 17406; (58.3); 24°21'N, 82°37–34'W; 59 m; 13 Apr 1965. ALABAMA: UWF 1484; (26.6); 29°45.4'N, 87°46.4'W; 40 m; 18 Oct 1975. TEXAS: TCWC 3406.2; 6(62.4–68.8); 28°18.2'N, 94°04'W; 55 m; 18 Jul 1970. TCWC 3321.1; (78.0); 28°04'N, 95°19'30"W; 55 m; 3 Dec 1980. MEXICO: TCWC 6193.15; (57.7); 21°10.0–09.5'N, 92°17.1–15.0'W; 64 m; 15 Apr 1976. TCWC 6191.7; 2(59.2–65.3); 21°09.3–09.0'N, 92°14.5–13.0'W; 15 Apr 1976. CARIBBEAN SEA: NICARAGUA: UMML 35260; (41.6); 12°42'N, 82°47'W; 42 m; 29 Jan 1971. FMNH 88816; 3(39.8–46.8); 12°16'N, 82°53'W; 55 m; 2 Jun 1962. PANAMA: USNM 323887; (45.5); 9°43'N, 79°20'W; 95 m; 19 Oct 1965. UMML 26744; (40.1); 9°38.9–40.2'N, 79°15.3–17.4'W; 67 m; 19 Jul 1966. UMML 26658; (37.0); 9°14.6–13.5'N, 80°21.8–22.8'W; 48 m; 20 Jul 1966. COLOMBIA: UMML 35261; 5(45.7–58.2); 9°40'N, 76°03'W; 49 m; 13 Jul 1966. UMML 35288; 2(54.1–56.6); 8°57.5–9°00.3'N, 76°33.6–30.5'W; 59 m; 12 Jul 1966. VENEZUELA: USNM 323888; (43.5); 12°16'N, 71°08'W; 20 m; 8 Oct 1965. UMML 35262; (59.8); 10°44'N, 64°16'W; 65 m; 21 Jul 1968.

**Other material examined (39 specimens, 15 lots).** GULF OF MEXICO: FLORIDA: UF 36456; 3(21.8–50.4); 24°24.34'N, 81°58.26'W; 64 m; 4 Jun 1980. CARIBBEAN SEA: HONDURAS: UMML 26640; 2(48.8–58.8); 16°00'N, 86°08–07'W; 49 m; 21 Mar 1968. UMML 31661; (56.6); 15°59.5'N, 86°05.5–04'W; 42 m; 21 Mar 1968. NICARAGUA: UMML

35269; (71.2); 11°37'N, 83°33'W; 31 m; 28 Jan 1971. PANAMA: USNM 324966; (39.3); 9°37'N, 78°53'W; 95 m; 8 Jul 1968. UMML 26837; (45.8); 9°33–32.8'N, 78°49–49.9'W; 57 m; 8 Jul 1966. UMML 23919; 5(33.4–70.7); 9°20.5–19.6'N, 80°13.5–15.5'W; 66 m; 20 Jul 1966. UMML 26554; 16(46.2–63.0); 9°07'N, 80°40.3'W; 57 m; 20 Jul 1966. UMML 26547; (55.5); 9°00.1–8°59.7'N, 80°45.8–46.7'W; 55 m; 20 Jul 1966. VENEZUELA: USNM 324962; 2(40.7–48.9); 11°58'N, 66°50'W; 65 m; 24 Jul 1968. USNM 324961; (61.8); 11°52'N, 70°23'W; 35 m; 27 Jul 1968. USNM 324963; 2(46.2–51.3); 10°45'N, 68°08'W; 45 m; 26 Jul 1968. USNM 324965; (60.0); 10°44'N, 66°07'W; 66 m; 22 Jul 1968. USNM 324678; (61.5); 10°36'N, 68°12'W; 24 m; 25 Jul 1968. TRINIDAD: USNM 324964; (73.1); 11°22'N, 62°22'W; 78 m; 19 Jul 1968.

***Symphurus ommaspilus*** 28 specimens (14.4–56.4 mm SL).

**Counted and measured (28 specimens, 14.4–56.4 mm SL).** BAHAMAS: ANSP 93810; holotype; (40.9); Great Bahama Bank, Andros Island, west side of the southern of two Long Bay Cays; 1 m; 12 Jul 1957. ANSP 93811; paratype; (36.4); north of eastern end of Green Cay (25°07'N, 77°11'15"W); 11 m; 16 May 1956. AMNH 26260; (56.4); Cat Island, 11 Oct 1965. AMNH 29196; 5(14.4–42.7); Hogsty Atoll; 10 m; 13 Mar 1966. AMNH 30969; 2(27.7–32.0); Ragged Island, Nurse Cay; 2 m; 12 Jan 1968. ANSP 143267; (18.3); South of Nassau, ca. 0.25 miles north of eastern half of Green Cay; to 15 m; 27 Aug 1969. UMML 12813; (33.4); eastern shore Oyster Cay; 20 Aug 1963. UMML 34387; (55.0); Gum Key; 6 Jun 1948. PUERTO RICO: UPRM 2660; 7(20.7–48.1); Aguadilla; 12 m. VIRGIN ISLANDS: ZMUC 8652; (42.7); Crux Bay, Saint James; 27 m; 9 Mar 1906. SAINT CROIX: uncatalogued; 3(32.6–41.0); Tague Bay; 1 m; 16 Apr 1978. SAINT BARTHELEMY: ANSP 103419; (20.1); French West Indies, Port de Gustavia, southeastern channel midway between Les Saintes and Fort Karl; 8 m; 14 Jul 1965. SINT EUSTATIUS: ZMA 119.422; (23.6); 1904–1905. CURACAO: ZMA 116.187; (32.0); 9 m; November, 1975. BELIZE: FMNH 94820; (53.6); Glovers Reef; 13 m; 24 Jun 1980.

***Symphurus diomedeanus*** 353 specimens (33.8–183 mm SL).

**Counted and measured (41 specimens, 88.8–175 mm SL).** SOUTHEASTERN UNITED STATES: NORTH CAROLINA: VIMS 1137; 6(97.1–175); 34°28'N, 76°15.3'W; 35 m; 21 Nov 1971. SOUTH CAROLINA: UMML 10580; (164); 32°27'N, 78°54'W; 51 m; 24 Jun 1957. GEORGIA: UMML 10552; (166); 31°49'N, 79°31'W; 82 m; 8 Oct 1957. UMML 10551; (164); 31°38'N, 79°40'W; 79 m; 8 Oct 1957. FLORIDA: UNC 1565; (173); 30°32'N, 80°19'W; 42 m; 10 Jan 1957. UNC 1563; 3(137.0–162); 29°40'N, 80°17'W; 73 m; 3 Sep 1956. GULF OF MEXICO: FLORIDA: USNM 37347; holotype; (137.9); 25°04'30"N, 82°59'15"W; 48 m; 19 Mar 1885. UMML 34374; 5(106.2–151); 24°47'N, 82°58'W; 44 m; 27 Mar 1970. UMML 34380; (97.5); 24°34'N, 81°06'W; 63 m; 26 Feb 1969. USA 5959; 3(88.8–139.6); 28°29'N, 84°21'W; 40 m; 5 Feb 1978. LOUISIANA: USNM 158306; 2(121.1–143.2); 21°09'N, 91°41'W; 51 m; 13 May 1954. TEXAS: TU 10594; 2(136.1–137.2); 26°10'N, 96°54'W; 33 m; 3 Jun 1954. UMML 11160; (136.6); 28°07'N, 95°53'W; 37 m; 26 Jan 1958. CARIBBEAN SEA: VENEZUELA: MCZ 40943; 2(148.6–156); 11°32'N, 71°44'W. SOUTH ATLANTIC: BRAZIL: MNHN 1975-269; 9(91.7–163); 18°18'S, 38°53'W; 38 m; 29 Nov 1961. BMNH 1923.7.30:345; holotype of *S. sumptuosus* (111.5); São Francisco (do Sul?). URUGUAY: USNM 87770; holotype of *S. pterospilotus* (115.2); Isla de Flores; 1925.

**Counted (176 specimens, 79 lots).** SOUTHEASTERN UNITED STATES: NORTH CAROLINA: UNC 4031; (151); 34°48'N, 75°31'W; 119 m; 13 Mar 1961. UMML 34381; (110.4); 34°30'N, 76°12'W; 37 m; 12 Mar 1961. VIMS 2503; 13(93.3–169); 34°27'N, 76°16'W; 33 m; 30 Apr 1973. VIMS 1599; (92.0); 34°15'N, 76°04'W; 70 m; 10 Nov 1969. Uncatalogued; (149.0); 33°56'N, 76°46'W; 40 m; 16 Mar 1982. SOUTH CAROLINA: UMML 34382; (143.9); 32°27'N, 78°32'W; 123 m; 9 Aug 1961. UNC 1552; 3(159–178); 32°22'N, 79°06'W; 46 m; 1 Nov 1956. UNC 14920; 2(141.5–165); 32°12'N, 78°12'W; 31 m; 26 Jun 1978. UMML 34376; 2(145.5–150); 32°11'N, 79°08'W; 90 m; 18 May 1964. GEORGIA: UMML 34375; 2(153–155); 31°59'N, 79°24'W; 79 m; 14 Dec 1961. FLORIDA: UMML 34384; 3(130.8–152); 28°22'N, 80°05'W; 60 m; 14 Mar 1965. USNM 291319; (148); 28°12'N, 80°05'W; 60 m; 14 Mar 1965. UMML 17441; 2(66.8–74.2); 24°50'N, 80°37'W; 37 m; 14 Apr 1965. UMML 20932; (112.9); 24°50'N, 80°38'W; 44 m; 15 Sep 1965. UMML 34378; (152); 24°42'N, 80°46'W; 82 m; 26 Oct 1960. UMML 34379; 2(128.8–138.5); 24°32'N, 81°17'W; 73 m; 27 Oct 1960. GULF OF MEXICO: FLORIDA: ANSP 101294; 2(128.6–134.5); 24°32'N, 81°17'W; 73 m; 27 Oct 1960. UF 35415; 2(100.6–102.5); 24°47'N, 81°41'W; 38 m; 19 May 1978. MCZ 58654; 24(123.3–159); 24°36'N, 83°10'W; 55 m; 18 Oct 1966. USA 5748; 6(144.5–177); 27°40'N, 84°11'W; 79 m; 3 Feb 1978. UWF 3230; 2(127.1–144.9); 28°56'N, 85°20'W; 1 Dec 1970. UF 71434; (164); 29°43'N, 86°00'W; 18 Jan 1971. TU 83888; (166); 29°50'N, 86°05'W; 40 m; 5 Jun 1973. TU 82989; (156); 29°52'N, 86°16'W; 64 m; 5 Apr 1973. FMNH 61301; 3(144.7–156); 29°50'N, 86°30'W; 42 m; 21 Mar 1954. TU 82932; (161); 29°58'N, 86°31'W; 79 m; 5 Apr 1973. USA 3563; 6(119.3–145.5); 30°04'N, 86°48'W; 91 m; 29 Aug 1976. USNM 133935; (151); 22°08'N, 86°51'W; 46 m; 30 Jan 1885. FMNH 45428; (150); 30°04'N, 86°57'W; 92 m; 14 Nov 1952. ALA 5871.21; 3(141.1–152); 29°54'N, 87°12'W; 10 Aug 1979. LOUISIANA: USNM 157692; (115.5); 20°05'N, 91°28'W; 31 m; 26 Aug 1951. FMNH 88848; (126.1); 28°45'N, 92°17'W; 51 m; 13 Sep 1962. TEXAS: TU 12956; (86.2); 26°10'N, 97°00'W; 20 m; 3 Jun 1954. MEXICO: UF 12785; (141.3); 21°14'N, 98°28'W; 46 m; 13 May 1959. UF 30333; (146.6); 21°11'N, 91°49'W; 48 m; 28 Aug 1980. UF 17018; (142.5); 21°09'N, 91°41'W; 51 m; 13 May 1954. FMNH 45429; 6(118.8–143.8); 20°18'N, 91°48'W; 42 m; 7 Dec 1952. UMML 34383; 3(130.7–138.9); 20°18'N, 91°48'W; 37 m; 7 Dec 1952. UMML 11226; (149.3); 20°06'N, 91°47'W; 42 m; 3 May 1958. FMNH 46370; 6(116.1–132.0); 19°48'N, 91°20'W; 25 Aug 1951. IMS 548; 4(102–119); Campeche; 26 m. CARIBBEAN SEA: GREATER ANTILLES:. JAMAICA: LACM 6216; 6(104.4–108.8); 17°47'N, 77°40'W; 41 m; 15 May 1962. LACM 6214; 2(105.1–111.7); 17°54'N, 77°51'W; 43 m; 15 May 1962. LACM 45537-1; (113.8); 17°52'N, 77°53'W; 41 m; 15 May 1962. LESSER ANTILLES: VIRGIN ISLANDS: FMNH 97487 (97.3); 18°35'N, 64°42'W; 50 m; 27 Sep 1959. UMML

7746; (91.5); 18°35'N, 64°42'W; 50 m; 27 Sep 1959. PANAMA: UMML 23893; (103.5); 8°49'N, 81°22'W; 31 m; 21 Jun 1966. COLOMBIA: USNM 291323; (83.9); 12°13'N, 72°25'W; 68 m; 12 Oct 1965. USNM 291322; (133); 12°07'N, 72°13'W; 48 m; 12 Oct 1965. USNM 291321; (137); 11°58'N, 72°29'W; 35 m; 12 Oct 1965. UMML 34377; (92.9); 11°08'N, 74°23'48"W; 183 m; 19 May 1964. UMML 35216; (104.7); 10°57'36"N, 75°10'W; 27 m; 23 May 1964. UMML 35217; 2(102.4–112.4); 10°53'N, 75°22'W; 42 m; 23 May 1964. UMML 26697; (107.3); 9°45'N, 76°09'W; 76 m; 16 Jun 1966. VENEZUELA: USNM 291324; 2(113–119); 12°14.5'N, 70°20'W; 73 m; 10 Nov 1958. UMML 30188; (98.3); 11°52'N, 70°22'W; 35 m; 27 Jun 1968. USNM 291052; (166); 11°24'N, 63°52'W; 49 m; 24 Sep 1965. GUYANA: FMNH 86413; (121.3); 8°32'N, 58°42'W; 86 m; 29 Aug 1958. FMNH 86363; (131.8); 7°40'N, 57°34'W; 51 m; 31 Aug 1958. SURINAME: FMNH 90541; (113.0); 7°20'N, 56°49'W; 60 m; 1 Sep 1958. FMNH 86415; (146.6); 7°12'N, 56°47'W; 49 m; 1 Sep 1958. FMNH 90942; 3(81.1–111.1); 6°40'N, 54°25'W; 48 m; 15 Sep 1958. FRENCH GUIANA: UMML 11153; (125.4); 6°13'N, 52°53'W; 55 m; 11 Nov 1957. FMNH 90083; (126.4); 6°03'N, 52°22'W; 66 m; 13 Sep 1958. USNM 159610; (133.2); 5°52'N, 52°03'W; 73 m; 12 Nov 1957. USNM 159619; 2(135.0–150); 5°46'N, 52°02'W; 70 m; 12 Nov 1957. USNM 274483; 4(132.1–148.4); 5°46'N, 52°02'W; 68 m; 12 Nov 1957. FMNH 103609; (129.2); 5°46'N, 52°02'W; 70 m; 12 Nov 1957. USNM 159617; 2(124.4–134.1); 5°35'N, 51°50'W; 66 m; 12 Nov 1957. BRAZIL: FMNH 94464; (94.6); 4°02'N, 50°33'W; 70 m; 12 Nov 1957. FMNH 91115; (120.1); 4°05'N, 50°27'W; 92 m; 13 Nov 1957. FMNH 90537 (106.5); Para, 1°57'N, 48°12'W; 56 m; 17 Nov 1957. FMNH 90535 (121.1); Para; 2°00'N, 48°19'W, 46 m; 16 Nov 1957. FMNH 90084 (151); Para; 2°00'N, 48°19'W; 46 m; 16 Nov 1957. SOUTH ATLANTIC: BRAZIL: FMNH 103610; (126.5); 2°09'S, 42°44'W; 59 m; 10 Mar 1963. MCZ 11377; 2(60.2–81.7); Vitoria (ca. 19.7°S); (1862 or 1865). MCZ 39982; 5(115.5–131.5); Rio de Janeiro (ca. 21°S); (1862 or 1865). MNHN B.570; (145.7); unspecified location.

**Other material examined (136 specimens, 66 lots).** MID-ATLANTIC BIGHT: MCZ 135329 (123.8); 35°23'N, 74°55'W; 87 m; 13 Sep 1992. SOUTHEASTERN UNITED STATES: SOUTH CAROLINA: UMML 10553; (167); 32°32'N, 79°01'W; 64 m; 25 Jun 1957. FLORIDA: UMML 1846; (148); 30°14'N, 80°16'W; 24 m; 9 Mar 1956. UMML 34391; (166); 29°35'N, 80°19'W; 48 m; 2 May 1964. UMML 34389; (153); 29°30'N, 80°19'W; 49 m; 19 Jan 1960. UMML 10554; (148); 29°26'N, 80°16'W; 70 m; 2 Jun 1957. UMML 35203; (151); 29°24'N, 80°25'W; 39 m; 19 Jan 1960. UMML 10539; (148); 29°19'N, 80°15'W; 64 m; 1 Jun 1957. FMNH 94457; (174); 29°17'N, 80°19'W; 44 m; 5 Feb 1961. UMML 11205; 2(128–136); 29°10'N, 80°19'W; 46 m; 1 Jun 1957. UMML 10555; (154); 29°03'N, 80°13'W; 51 m; 1 Jun 1957. UMML 10546; 3(147–157); 28°58'N, 80°13'W; 55 m; 1 Jun 1957. UMML 35201; (150); 28°40.5'N, 80°11'W; 48 m; 29 Sep 1963. UMML 35202; 4(138–155); 28°40'N, 80°11'W; 48 m; 29 Sep 1963. UMML 35214; (153); 28°33.5'N, 80°15.5'W; 35 m; 9 Jul 1961. UMML 35200; (165); 28°33.5'N, 80°09.5'W; 51 m; 9 Jul 1961. UMML 34373; 2(171–180); 28°31'N, 80°14'W; 42 m; 24 Jun 1964. UMML 35207; (153); 27°55'N, 80°07'W; 37 m; 26 Sep 1963. UMML 34372; (154); 27°54'N, 80°08'W; 37 m; 25 Jan 1962. UMML 35211; 2(136–136); 27°52.5'N, 80°08.5'W; 38 m; 28 Sep 1963. UMML 34388; (156); 27°50.5'N, 80°07'W; 37 m; 12 Jul 1961. UMML 35215; 2(171–183); 27°49'N, 80°09'W; 27 m; 25 Jan 1962. UMML 35204; (132); 27°47.5'N, 80°13.5'W; 37 m; 28 Sep 1963. UMML 35212; 3(134–163); 27°43'N, 80°07'W; 37 m; 28 Sep 1963. TU 75908; (132); 27°35'N, 80°04'W; 38 m; 5 Sep 1965. TU 79168; 14(119–148); 27°35'N, 80°04'W; 38 m; 5 Sep 1965. UMML 34390; (126); 27°19'N, 79°59'W; 41 m; 21 May 1968. USNM 236120; 9(134–157); 27°16'30"N, 80°01'W; 53 m; 15 Mar 1965. UMML 35219; 2(112–134); 27°13'N, 79°54'W; 61 m; 20 May 1968. UMML 35206; (105); Key Biscayne; 6 m; 13 Oct 1967. UMML 20993; (156); 25°13'N, 80°10'W; 98 m; 26 Jan 1966. UMML 20997; (162); 25°13'N, 80°10'W; 98 m; 26 Jan 1966. UMML 20972; (142); 25°11'N, 80°10'W; 112 m; 26 Jan 1966. UMML 35213; (107); 24°43'N, 80°43'W; 88 m; 26 Oct 1960. UMML 35210; (110); 24°34'N, 81°06'W; 51 m; 27 Apr 1969. GULF OF MEXICO: FLORIDA: USNM 129945; (136); 24°25'30"N, 81°47'45"W; 92 m; 15 Jan 1885. UMML 3088; 2(87.4–124); 24°45'N, 82°10'W; 24 m; 26 May 1957. UF 35442; 3(116–161); 25°17.5'N, 82°32'W; 33 m; 21 May 1978. UF 35409; (104); 24°44'N, 82°42'W; 32 m; 24 Apr 1981. FDNR 18022; (150); 26°16.82'N, 82°44.02'W; 35 m; 19 Jul 1981. UMML 35208; (127); 24°53'N, 82°56'W; 44 m; 7 Mar 1970. UMML 17395; (123); 24°25'N, 82°56'W; 64 m; 12 Jun 1965. UMML 17431; 3(118–127); 24°23'N, 82°57'W; 90 m; 13 Apr 1965. UMML 35205; 3(123–130); 24°46'N, 82°57'W; 44 m; 7 Mar 1970. UMML 35218; (101); 24°48'N, 82°58'W; 44 m; 7 Mar 1970. FDNR 12562; 2(140–150); 24°27'N, 82°58'W; 78 m; 24–25 Aug 1981. USNM 73261; (57.9); St. Martin's Key (28°26'30"N, 83°08'W); 18 m; 15 Jan 1902. FDNR 18023; (136); 26°24'N, 83°22'W; 55 m; 6 Feb 1982. UF 11650; (118); 20 mi northeast of Dry Tortugas; 146 m; May, 1962. UMML 35209; (134); 20 mi northeast of Dry Tortugas; March, 1950. FDNR 18024; (127); 26°16'N, 84°05'W; 145 m; 6 Feb 1982. UF 3633; 2 specimens, not measured; 29°50'N, 86°30'W; 92 m; 21 Mar 1954. USA 4952; 3(120–132); northwest of Tampa; 32 m; 26 Aug 1977. UWF 3684; (62.9); unspecified locality, Gulf of Mexico; 20 Jan 1974. MISSISSIPPI: ALA 3617.12; 8(103–134); south southeast of Horn Island; 8 Jul 1969. MEXICO: 2493; (176); 21°51.6–49.6'N, 86°48.3'–48.4'W; 33 m; 25 Apr 1985. IBUNAM-P 2513; (180); 21°55.6–54.3'N, 86°45.7–47.4'W; 43 m; 26 Apr 1985. CARIBBEAN SEA: NICARAGUA: USNM 324977; (110.4); 11°37'N, 83°33'W; 31 m; 28 Jan 1971. UMML 35268; 3(33.8–100.5); 12°29'N, 83°05'W; 27 m; 28 Jan 1971. VENEZUELA: UMML 35272; 11(44.2–92.0); 11°09'N, 63°17'W; 25 m; 19 Jul 1968. UMML 35270; (135); 10°49'N, 63°13'W; 48 m; 19 Jul 1968. UMML 35267; 3 specimens; 9°30'N, 60°15'W; 64 m; 16 Jul 1968. SOUTH ATLANTIC: GUYANA: UMML 35271; 2(120–121); 8°08'N, 58°34'W; 37 m; 16 Jul 1968. UMML 35266; 1 specimen; 7°42'N, 57°32'W; 27 m; 15 Jul 1968. SURINAME: UMML 35265; 3 specimens; 6°41'N, 55°17'W; 33 m; 10 Jul 1968. BRAZIL: UMML 35264; 2 specimens; 5°26'N, 52°12'W; 42 m; 8 Jul 1968. NMW 43974; (123.8); Rio de Janeiro; 1857–59.

***Symphurus jenynsi*** 106 specimens (18.8–319 mm SL).

**Counted and measured (37 specimens, 60.6–319 mm SL).** BRAZIL: MCN 2399; paratype of *S. meridionalis*;

(172); Praia do Farol da Conceicao (São Jose do Norte), Rio Grande do Sul. USNM 316768; 6(135.6–200); 32°09'S, 51°55'W; 14 m; 1 Sep 1982. MCN 2401; holotype of *S. meridionalis*; (173); Praia de Cassino, Rio Grande do Sul; 50 m. USNM 316772; 7(117.8–231); 32°23'S, 52°43'W; 44 m; 3 Sep 1983. FURG 3040; (250); 32°35'S, 52°13'W; 17 m; 3 Sep 1982. USNM 316769; 9(105.9–147.5); 32°47'S, 52°22'W; 11 m; 23 Jan 1983. MCN 2400; paratype of *S. meridionalis*; (138.8); Praia em frente ao Alfred Hotel em Torres, RS, Brazil; 50 m. USNM 316770; 4(60.6–163); Costa Mar, Brazil; 28 Oct 1980. URUGUAY: USNM 76852; holotype of *S. bergi* (177); Montevideo. USNM 86170; 3(116.5–135.0); Montevideo; 1913. USNM 86683; (131.2); Montevideo; 9 Dec 1922. USNM 87771; (319); Montevideo. ARGENTINA: USNM 55573; holotype of *S. jenynsi* (173); market at Buenos Aires.

**Counted (58 specimens, 17 lots).** BRAZIL: MNHN 1975-262; (106.8); 23°05'S, 44°217'W, 50 m. MCP 8009; (169); Porto Belo, SC (ca. 27°S). MZUSP 12849; 11(18.8–75.8); 30°49'S, 50°28'W; 10 Apr 1972. MZUSP 12558–60; 3(32.2–150); 31°27'S, 51°05'W; 17 m; 12 Apr 1972. USNM 309821; 3(70.1–146.4); 31°27'S, 51°05'W; 17 m; 12 Apr 1972 (formerly MZUSP 12555–57). MZUSP 12843; 10(30.3–93.0); 31°28'S, 52°15'W; 20 Jan 1972. MZUSP 12886; 3(157–164); 33°47'S, 53°16'W; 1 Nov 1972. URUGUAY: USNM 76892; paratypes of *S. bergi* 9(116.7–181); Montevideo. CAS-SU 22725; paratypes of *S. bergi* 13(91.1–154); Montevideo. MCZ 11384; 2(110–144); Montevideo; 1872. ARGENTINA: UMMZ 95496; (224); Argentina. BMNH 1933.2.28:4; (164); Patagonia.

**Other material examined (11 specimens, 5 lots).** BRAZIL: MNHN 1975-262; 2(123.6-218); 23°05'S, 44°27'W, 50 m. URUGUAY: USNM 327832; (232); 34°55'S, 54°44'W; 19 Sep 1993. USNM 327835; 2(168–208); 34°55'S, 54°44'W; 19 Sep 1993. USNM 327836; (220); 34°55'S, 54°44'W; 19 Sep 1993. MNHN 1975-263; 5(112.5–216); (location approximate) 35°00'S, 55°00'W; 7 m.

***Symphurus plagiusa*** 983 specimens (15.0–171 mm SL).

**Counted and measured (31 specimens, 64.7–171 mm SL).** SOUTHEASTERN UNITED STATES: VIRGINIA: VIMS 1315; 26(64.7–143.3); lower James River; 9 m; 22 Apr 1971. NORTH CAROLINA: VIMS 1598; 3(156–171); 34°26'N, 76°17'W; 35 m; 22 Apr 1971. SOUTH CAROLINA: LS 124 (ca. 122.1), holotype skin; South Carolina; ca. 1761. GULF OF MEXICO: FLORIDA: UF 35425; (124.1); 24°40'N, 81°53'W; 10 m; 20 May 1978.

**Counted (120 specimens, 36 lots).** EASTERN UNITED STATES: DELAWARE: USNM 187151; (125); Delaware River; 1951–1952. USNM 187180; 2(44–46); White Creek, Indian River; 3 Sep 1957. NORTH CAROLINA: USNM 316749; (147); 35°13'N, 75°25'W; 21 m; 17 Mar 1982. USNM 316786; (133); 35°11'N, 75°38'W; 14 m; 15 Mar 1983. USNM 316787; (111.5); 34°59'N, 76°05'W; 12 m; 17 Mar 1982. USNM 316755; 7(102–106); 34°39'N, 76°37'W; 14 m; 16 Mar 1982. MCZ 60988; (123.9); 34°37.2'N, 76°38.8'W; 15 m. USNM 316758; 8(99.7–126); 34°35'N, 76°35'W; 17 m; 16 Mar 1982. USNM 316756; 5(107–120); 34°34'N, 76°33'W; 14 m; 16 Mar 1982. USNM 316784; 2(108–111); 34°33'N, 76°47'W; 19 m; 14 Mar 1983. FLORIDA: USNM 291336; (151); 28°13.5'N, 80°21'W; 21 m; 14 Nov 1963. UMML 35223; (128); 7 mi south of Bear Cut Bridge, Key Biscayne; 6 m; 13 Oct 1967. UMML 31721; (116); 24°50'N, 80°37.5–35.5'W; 39 m; 26 Feb 1969. BAHAMAS: ANSP 101977; (132); Hatchett Bay, Eleuthera Island; 6–13 Feb 1960. ANSP 111567; 3(120–126); 3 mi offshore Great Bahama Bank, Eleuthera Island; 9 m; 20 Apr–3 May 1960. USNM 265181; (131); 20°54'N, 73°33'W; 183 m; 26 May 1965. GREATER ANTILLES: CUBA: USNM 107365 (61.5); Siguanea Bay; 6 m; 12 Apr 1937. GULF OF MEXICO: FLORIDA: FDNR 5197; (138); 26°24'N, 82°06'W; 7 Apr 1967. UF 35435; (124); 24°43.5'N, 82°09'W; 20 m; 20 May 1978. FDNR 10772; (147); 6.5 mi north-northeast of South Shoal Light, Key West, FL; 15 m; 8 Apr 1978. UMML 5217; (110); 3 mi north of Smith Shoal Light, Key West; 16 m; 1 Jun 1959. UMML 20825; 6(111–143); 5 mi northwest of Smith Shoal Light, Key West; 6 m; Dec–Jan 1963–1964. FDNR 18030; 2(108–123); 24°48'N, 82°13'W; 24 m; 19 Nov 1980. ALABAMA: USNM 158222; 3(109–130); Dauphin Island; 16 m; 6 May 1954. USNM 325135; (35.2); Old Shell Landing, Bayou Graveline; 17 Aug 1965. LOUISIANA: USNM 316739; 23(47.7–107); Calcasieu Lake; 1982. TEXAS: TCWC 547.4; 5(72.6–102); 29°15'15"N, 94°55'06"W; 1 m; 29 Jul 1975. TCWC 4160.10; (92.8); 29°23'N, 94°29'W; 15 m; 27 Oct 1973. TCWC 461.3; 2(95.4–107); Galveston; 28 Jul 1975. TCWC 528.1; 2(53.9–76.4); Galveston; 1 m; 31 Jul 1975. MEXICO: USNM 274481; 4(114–129); ca. 24°30'N; 12 m; 17 Mar 1947. USNM 274482; 3(121–141); ca. 24°30'N; 12 m; 17 Mar 1947. IMS 554; 10(113–144); 30 mi northwest of Campeche; 16 m; 6–7 Feb 1951. IMS 555; 6(125–147); west of Campeche; 26 m; 27–29 Jul 1951. IMS 553; 8(113–144); Punta Morros, ca. 19°41'N, 90°41'W; 14 m; 16 Feb 1951. UMML 35221; 2(133–150); 20°05'36"N, 91°13'W; 22 m; 8 Dec 1952.

**Other material examined (832 specimens, 147 lots).** FMNH 55920; (124); unknown locality. EASTERN UNITED STATES: CONNECTICUT: USNM 59056; 5(34.0–47.2); Long Island Sound; 24 m; 17 Sep 1892. VIRGINIA: USNM 73260; (50.2); 37°54'N; 11 m; 13 Feb 1902. USNM 302382; 3(150–159); 37°48'N, 75°26–27'W; 9 m; 21 Sep 1988. USNM 302380; 2(146–148); 37°17'N, 75°34'W; 16 m; 20 Sep 1988. USNM 316737; 28(34–67); York River, below Coleman Bridge; 12 Apr 1985. VIMS 1314; 3(76–122); York River; 3 Dec 1951. USNM 43207; 2(75–76); Cape Charles; 15–30 Sep 1890. USNM 316745; 6(96–113); James River; 12 Aug 1983. NORTH CAROLINA: USNM 302381; (157); 36°06–07'N, 75°36–38'W; 16 m; 18 Sep 1988. USNM 316765; (158); 35°30'N, 75°13'W; 33 m; 21 Sep 1983. USNM 316766; 12(98–162); 35°12'N, 75°38'W; 12 m; 8 Mar 1984. USNM 316763; 12(116–149); 35°07'N, 75°51'W; 14 m; 7 Mar 1984. USNM 316742; (147); 35°05'N, 75°57'W; 12 m; 17 Mar 1982. USNM 316764; 7(127–151); 35°04'N, 75°56'W; 13 m; 7 Mar 1984. USNM 154964; 5(92.4–130.7); 35°02'30"N, 76°00'W; 13 m; 1 Mar 1940. USNM 316740; (137); 35°01'N, 76°05'W; 119 m; 22 Mar 1983. UMML 10541; 3(156–157); 35°00'N, 75°30'W; 46 m; 17 Jun 1957. USNM 316762; 9(106–148); 35°00'N, 76°03'W; 12 m; 7 Mar 1984. USNM 316767; 9(64–138); 3 mi south of Cape Hatteras Inlet; 21 Feb 1983. UMML 10578; (158); 34°59'N, 75°20'W; 64 m; 17 Jun 1957. USNM 316744; 6(77–148); 34°58'N, 76°04'W; 10 m; 15 Sep 1983. UMML 10543; (161); 34°58'N, 75°32'W;

55 m; 17 Jun 1957. USNM 316741; 3(124–137); 34°57'N, 76°08'W; 11 m; 7 Mar 1984. UMML 35225; (144); 34°41'N, 76°50'W; 11 m; 20 Sep 1959. MCZ 58653; 5(119–133); 34°37.2'N, 76°38.8'W; 15 m, 29 Mar 1972. USNM 316760; 2(133–149); 34°35'N, 76°34'W; 11 m; 16 Sep 1983. USNM 316757; (132); 34°35'N, 77°00'W; 15 m; 6 Mar 1984. USNM 316756; 3(100–124); 34°34'N, 76°33'W; 14 m; 16 Mar 1982. USNM 316738; (107); 33°51'N, 78°06'W; 13 m; 18 Sep 1983. USNM 316750; (120); 33°48'N, 78°02'W; 12 m; 18 Sep 1983. USNM 316743; (158); 33°43'N, 78°11'W; 17 m; 14 Mar 1982. AMNH 11899; (53.2); Cape Lookout (ca. 34°40'N). USNM 15017; 4(52–110); Beaufort Harbor; 11 Dec 1885. USNM 51884; 2(78–90); Beaufort; 3–20 Jun 1904. USNM 58976; 10(32–110); Beaufort. UF 38895; (121); Core Creek, Newport River; 16 Apr 1973. USNM 105956; (51); Beaufort, Newport River; 1 Feb 1926. USNM 106352; 5(27–62); Beaufort, Fish Creek; 4 Apr 1929. USNM 340444; 196 specimens; Lower Cape Fear River near Southport, intake screens Carolina Power and Light Generating Station; 10 Apr 1991. USNM 340445; 14 specimens; Lower Cape Fear River, marshes behind Baldhead Island; 3–4 Oct 1990. USNM 340446; 8(46.0–81.1); Lower Cape Fear River near Southport, intake screens Carolina Power and Light Generating Station; 15–16 Jan 1991. USNM 341615; 29 specimens; Masonboro Sound; 20 Jul 1995. USNM 341612; 25 specimens; Zekes Island; 6 Oct 1992. Uncatalogued material (North Carolina National Estuarine Research Reserve Reference Collection; 21 lots; 135 specimens from Walden Creek, Masonboro Sound, Masonboro Island Creek, Hewletts Creek, Zeke's Island and Lower Cape Fear River Estuary near Southport, in vicinity of Carolina Power and Light, Brunswick Steam Electric Plant). South Carolina: USNM 91436; 2(107–116); 33°13'22"N, 79°11'7"W; 9 m; 10 Jul 1915. USNM 59068; 4(51–80); Cooper River; 5 m; 16 Jun 1891. USNM 59018; 3(108–135); Cooper River; 9 m; 16 Jan 1891. USNM 59041; (82); junction of May River and Skull Creek; 1891. USNM 59044; (94.4); Cat Island Creek; 1891. USNM 59059; (67); Jericho Creek; 1891. USNM 26317; (80); Charleston Harbor. USNM 30725; (144); Charleston Harbor. FMNH 38320–23; 4(27.3–42.7); Charleston Harbor; 9 Jun 1939. Georgia: USNM 131254; 2(134–155); off Sea Island; 3 m; 17 Mar 1945. USNM 154957; 2(116–143); 31°35'30"N, 81°01'W; 9 m; 14 Mar 1940. USNM 154963; 4(114–139); Barbers Bank; 4 m; 19 Apr 1940. USNM 154969; (138); Umbrella Creek; 10 Aug 1937. USNM 316751; 21(15–30); Wassaw Sound; 15 Sep 1980. USNM 316753; 8(15–30); Wassaw Sound; 12 Sep 1980. USNM 316754; 23(19–25); Wassaw Sound; 15 Oct 1980. USNM 316752; 3(17–19); Wassaw Sound; 12 Dec 1980. Florida: UMML 2916; (130); between Jacksonville and Brunswick, GA; 68 m; Jan 1956. UMML 35227; 18(118–152); 30°31'N, 81°22'W; 13 m; 5 Oct 1961. UF 35471; (151); 29°58.4'N, 81°17.1'W; 14 m; 15 May 1981. UF 35486; 29°58.1'N, 81°16.9'W; 14 m; 15 May 1981. USNM 154958; (145); 29°35'30"N, 80°59'30"W; 18 m; 28 Mar 1940. USNM 154956; (134); 29°27'N, 81°05'30"W; 16 m; 6 Apr 1940. UMML 11198; (141); 29°26'N, 84°54'W; 18 m; 25 Jul 1958. USNM 154968; (154); 28°24'N, 80°24'30'W; 17 m; 29 Mar 1940. USNM 154959; (158); 28°21'30"N, 80°21'30"W; 18 m; 4 Apr 1940. USNM 291017; (154); 28°20'N, 80°32'W; 12 m; 24 Apr 1953. USNM 291337; (161); 28°19'N, 80°34'W; 13 m; 1 Dec 1965. UMML 35226; (37.5); Vero Beach (ca. 27°40'N); December, 1950. UMML 35222; (96.5); Bear Cut, Key Biscayne, 25°43.7'N, 80°09.3'W; 1 m; 26 Oct 1967. UMML 14210; (146); Biscayne Bay; 28 May 1963. USNM 265180; 2(20.0–38.7); 2.8 mi south of Lower Matecumbe Key; 1 m; 9 Feb 1961. Gulf of Mexico: Florida: UMML 6204; 4(56.7–99.5); Florida Bay, Coot Bay Canal; 13 Apr 1959. ANSP 94304; (22.2); Marquesas Key; 1 m; 18 Mar 1954. USNM 107320; 3(94–103); W. Channel Entrance, Key West; 14 m; 13 Feb 1902. USNM 107321; 3(62–103); west of Channel Entrance, Key West; 14 m; 13 Feb 1902. USNM 134303; 4(62–108); off Key West; 13 m; 13 Feb 1902. UMML 35224; 3(109–143); 24°50.5'N, 82°12'W; 26 m; 14 Dec 1962. UF 26740; (135); 24°45'N, 82°07'W; 20 May 1970. UMML 5193; (108); 24°45–50'N, 82°10–30'W; July, 1956. USNM 39365; (66); 28°50'N, 83°00'W; 1887. UF 10295; 5(142–149); 9 mi west of Boca Grande Sea Buoy; 15 m; 22–23 Jun 1960. UMML 5723; (163); off Boca Grande (ca. 26°50'N); 12 m; 24 May 1959. USNM 112524; (41); Sarasota Bay (ca. 27°28'N); 1 Mar 1951. USNM 43871; 2(58–126); Tampa Bay (ca. 27°40'N). USNM 157589; (61.5); Tampa Bay. USNM 67679; 2(85–98); Port Tampa; 19 Jan 1898. USNM 160461; 11(52–135); Cedar Key Channel, south of Seahorse Island; 5 m; 10 Dec 1950. VIMS 7315; 16(52.9–83.4); Pinellas County; 1 m; 4 Jun 1977. USNM 157391; 4(84–92); Pilot Cove; 24 Jun 1932. USNM 159616; 13(108–129); 29°04'N, 85°49'W; 187 m; 22 Aug 1957. Mississippi: FMNH 88735; 4(104–124); 30°09'N, 88°41'W; 16 m; 22 Jun 1963. GCRL V76:15111; 4(26.3–30.4); 1 mi east of Ocean Springs; 1 m; 9 Jun 1950. USNM 72334; (91); Mississippi Sound, off 9 mi Bayou; 23 Feb 1898. USNM 147779; 2(108–112); Gulf Coast; 1948. USNM 157389; 4(74–78); Cat Island; 16 Nov 1931. Alabama: ALA 2385.29; 4(60.5–87.6); Mobile Bay. VIMS 3852; (118); Tidepool, Dauphin Island; 26 Aug 1974. Louisiana: USNM 155228; (118); 28°48'30"N, 90°34'W; 18 m; 10 Jul 1938. UMML 35220; (135); 28°56'N, 91°27'W; 6 m; 11 Apr 1962. IOH 1311; (142); 27.5–28.5°N, 91–93'W; Jun 1970. ANSP 8684; (114); Mississippi Sound. USNM 157386; 12(106–129); Bastian Island; 3 Jul 1930. USNM 154970; (149); unspecified locality. Texas: ANSP 144732; 2(73.1–75.3); Port Isabel Ship Channel; 16 Apr 1948. ANSP 144935; 2(48.8–61.0); Port Isabel Ship Channel; 30 Nov 1947. ANSP 144937; (81); Port Isabel Ship Channel; 26 Mar 1948. TCWC 461.3; 8(42.2–53.3); Galveston; 28 Jul 1975. TCWC 528.1; 7(43.4–51.0); Galveston; 1 m; 31 Jul 1975. USNM 86136; 2(108–127); Galveston; 10 m; 26–27 Feb 1917. USNM 93584; 2(116–124); off Corpus Christi. USNM 157376; 2(44–57); Harbor Island; 11 Oct 1926. USNM 157378; 2(57–80); Harbor Island; 1 Dec 1926. Mexico: IBUNAM-P 2830; (28.4); Laguna de Sontecomapan, Veracruz; 13 Jun 1985. Cuba: IOH 1310; (117); ca. 23°00'N, 83°00'W. IOH 1849; (102); G. Batabanó; 31 May 1983. IOH 1316; 2(103–107); G. Batabanó, 5 mi del Surgidero de Batabanó; 3–4 Sep 1960. IOH 1314; (110); G. Batabanó, 21°46'N, 82°30'W. IOH 789; (67); G. Batabanó; 23 Oct 1960.

***Symphurus urospilus*** 132 specimens (25.0–166 mm SL).

**Counted and measured (55 specimens, 41.3–166 mm SL).** Southeastern United States: South Carolina:

UF 28318; (141.0); 33°28'N, 78°07'W; 26 m; 22 Jun 1978. GMBL 76-266; (98.9); 32°57'N, 79°09'W; 14 m; 6 Sep 1976. GMBL 74-183; (136.9); 32°41'N, 79°38'W; 11 m; 25 Oct 1974. UF 13238; (146.3); 32°26'N, 79°03'W; 42 m; 1 Nov 1956. GEORGIA: GMBL 74-11; (142.3); 32°02'N, 79°25'W; 14 Aug 1974. USNM 155225; holotype; (123.9); off Savannah, 32°01'N, 80°11'30"W; 22 m; 3 Feb 1940. GMBL 76-273; (124.2); 31°07'N, 80°56'W; 15 m; 13 Sep 1976. MCZ 58651; 2(124.8–140.6); 30°50.4-51.8'N, 80°55.5–56.3'W; 20 m; 17–22 Mar 1971. FLORIDA: MCZ 58652; (132.3); 30°42'N, 81°04'W; 14 m; 17 Mar 1981. USNM 267315; 5(128.8–145.5); 30°37'N, 80°59'W; 28 m; 26 Aug 1965. TU 14789; 2(142.3–166); 29°03'N, 79°59'W; 324 m; 13 Jun 1956. GMBL 75-154; (125.1); 23°30'–29°12'N, 80°51–55'W; 17 m; 12 Sep 1975. GULF OF MEXICO: FLORIDA: FDNR 1595; (114.0); 24°42'N, 82°16'W; 29 m; Nov 1959. USNM 158315; 2(140.7–149.2); 25°50'N, 82°30'W; 28 m; 8 Apr 1954. UF 35443; (142.0); 25°17.5'N, 82°32'W; 33 m; 21 May 1978. UWF 2406; (111.3); 24°48'N, 82°32'W; 31 m; 12 Dec 1976. UWF 2323; 8(100.6–125.5); 24°45'N, 82°33'W; 31 m; 11 Dec 1976. FDNR 800; (88.8); 24°41'N, 82°35'W; 26 m; 26 Aug 1958. UWF 2356; (111.2); 24°47'N, 82°39'W; 33 m; 11 Dec 1976. USNM 73259; (41.3); 29°39'30"N, 83°53'10"W; 28 m; 7 Nov 1901. USNM 73262; paratype; (37.1); Pepperfish Key; 29°32'N, 83°58'30"W; 19 m; 7 Nov 1901. FDNR 2144; (103.8); northwest of Marquesas Key; 18 m; 1 May 1962. FDNR 9857; (132.5); 18 mi northwest of Smith Shoal Light; 23 m; 7 Nov 1977. FDNR 10155; (90.4); 8 mi west of Boca Grande; 15 m; 30 Nov 1977. GCRL 76-14878; (144.1); 16 mi off Perdido Bay; 22 m; 14 Sep 1975. TEXAS: TCWC 3307.1; (94.3); 28°20'N, 95°08'W; 36 m; 1 Dec 1978. TCWC 3303.1; 2(98.7–99.7); 28°36–14'N, 95°12–07'W; 37 m; 3–4 Dec 1980. MEXICO: IMS 559; 3(104.0–105.2); Punta Morros, ca. 19°41'N, 90°41'W; 14 m; 16 Feb 1951. IMS 560; 9(103.4–111.5); west of Campeche; 27 m; 27–29 Jul 1951. UF 30363; (141.1); 20°54'N, 91°30'W; 34 m; 29 Aug 1980.

**Counted (60 specimens, 22 lots).** SOUTHEASTERN UNITED STATES: FLORIDA: UMML 2914; (127.6); between Jacksonville and Brunswick, GA; 64 m; Jan 1956. FDNR 12849; (145.7); 30°40'N, 80°47'W; 28 m. FDNR 11533; (115.3); 29°07'N, 80°44'W; 18 m; 20 Sep 1973. USNM 156068; (56.8); 28°21'30"N, 78°49'W; 18 m; 7 Dec 1962. GULF OF MEXICO: FLORIDA: UF 21903; 10(91.9–100.9); 25°41'N, 81°40'W; 5 m; 1 Nov 1975. FDNR 2460; (140.8); 60 mi west of Tarpon Springs; 20 Jun 1964. FDNR 18031; 2(26.2–46.7); 25°17.34'N, 82°10'W; 23 m; 12 Feb 1982. UMML 3083; 13(101.3–128.2); 24°45'N, 82°20'W; 24 m; 26 May 1957. UMML 4699; 3(113.2–120.5); 24°45'N, 82°20'W; 18 m; 10–12 Mar 1958. UF 43331; (98.1); 24°51'N, 82°23'W; 4 May 1961. FDNR 4448; 2(107.8–135.5); 26°24'N, 82°28'W; 18 m; 3 Sep 1965. FDNR 5059; 4(134.0–157); 26°24'N, 82°28'W; 18 m; 21 Jul 1966. FDNR 4995; (133.2); 26°24'N, 82°28'W; 18 m; 14 Feb 1966. FDNR 14632; (53.5); 26°24'N, 82°28'W; 18 m; 21 Jul 1966. FDNR 14670; (109.7); 26°24'N, 82°28'W; 18 m; 21 Jul 1966. FDNR 4880; 2(115–122); 27°37'N, 83°07'W; 18 m; 1 Dec 1966. UMML 1787; (112.1); 45 mi northwest of Key West; 26 m; 15 Jun 1953. FDNR 10206; (127.0); 20 mi north of New Grounds Shoal Light; 31 m; 2 Dec 1977. FDNR 10231; (112.4); 14 mi northeast of Pulaski Shoal Light; 31 m; 2–3 Dec 1977. FDNR 10771; 2(128.1–135.1); 6.5 mi north-northeast of Smith Shoal Light; 15 m; 8 May 1978. FDNR 10932; (101.7); Cedar Keys; 9 m; 8 Jun 1978. MEXICO: FMNH 45430; 9(114.8–136.9); 20°05'N, 91°13'W; 22 m; 8 Dec 1952.

**Other material examined (17 specimens, 7 lots).** SOUTHEASTERN UNITED STATES: FLORIDA: UF 44364; 4(122.7–135.2); 30°43'N, 80°30'W; 38 m; 11 Jun 1985. GULF OF MEXICO: FLORIDA: FDNR 6544; (25.0); 27°37'N, 83°07'W; 18 m; 2 Nov 1967. UMML 20824; 2(105–119); 5 mi northwest of Smith Shoal Light, Key West; Dec–Jan 1963–1964. LOUISIANA: TCWC 3460.3; (91.8); 29°07.8'N, 93°19.8'W; 11 Jul 1971. TEXAS: TCWC 5157.1; 7(95.7–111.5); 28°50'N, 94°24'W; 21 m; 30 Nov 1978. TCWC 4145.1; (92.9); 28°36.09'N–28°14.80'N, 95°12.30–95°07.80'W; 37 m; 6 May 1981. TCWC 3317.1; (80.2); 28°44.59'N, 95°14.21'W; 22 m; 11 Feb 1980.

***Symphurus caribbeanus*** 114 specimens (24.4–130 mm SL).

**Counted and measured (21 specimens, 40.1–121.9 mm SL).** PUERTO RICO: USNM 313487; holotype (100.5); Mayaguez Bay; 1966. UPRM 740; paratypes 2(119.6–121.9); Río Anasco; 1–2 Jul 1953. UPRM 1588; paratype (98.0); Mayaguez; March, 1962. UPRM 2926; paratypes 8(58.1–97.9); Guayanilla; 23 Jul 1968. ANSP 118553; paratype (69.8); Puerto Rico; 25 Jan 1971. HAITI: FMNH 61574; paratype (40.7); Port-au-Prince Bay; 12 Sep 1953. COLOMBIA: UMML 30087; paratypes 6(88.7–98.1); 8°44.5–45.6'N, 76°52.71'W; 4 m; 12 Jul 1966. NETHERLANDS ANTILLES: UMML 5297; paratype (40.1); St. Martin; 1 m; 2 Jul 1959.

**Counted (64 specimens, 13 lots).** CUBA: MCZ 11200; (71.8); 1851. MNHN 1887-505; (63.9); Havana. HAITI: UF 83998; 10(80.7–95.4); 2 km northwest of Port Salut; sandy beach near eelgrass bed; 1 m; 7 Apr 1979. PUERTO RICO: ANSP 115601; 7(43.3–82.5); Puerto Yabucoa; 12–13 Jul 1969. FMNH 52071; (98.5); Palo Seco; 1899. UPRM 736; (95.8); Río Anasco; 17 Aug 1951. UPRM 740; 8(90.0–121.9); Río Anasco; 1–2 Jul 1953. NICARAGUA: UMML 34338; 2(79.1–94.3); 12°16'N, 83°31'W; 12 m; 28 Jan 1971. UMML 34337; 3(95.8–109.8); 11°24'N, 83°42'W; 26 m; 28 Jan 1971. PANAMA: UMML 34339; (115.1); 8°49'N, 81°13'W; 18 m; 21 Jul 1966. UMML 34340; 26(24.4–116.7); 9°48'N, 82°50'W; 19 m; 26 Jan 1971. USNM 313514; (46.2); Colon; 5 Jan 1911. COLOMBIA: USNM 313513; paratypes 2(102.8–116.7); Bajo-Sabanilla, off Barranquilla; 8 Sep 1969.

**Other nontype material examined (29 specimens, 9 lots).** CUBA: IOH 1317; (95); Rada de Playa Viriato, 82°28'02"N, 23°05'36"W; 9 Dec 1969. MCZ 25982; (108.7). PUERTO RICO: LACM 4472; 2(119-130); Tres Hermanas; 22 Mar 1962. LACM 4480; 4(93.6–117.8); mouth of Anasco River; 1–2 Jul 1953. COSTA RICA: UMML 34341; 16(52.9–116.7); 10°40'N, 83°29'W; 29 m; 27 Jan 1971. LACM 30726-5; (110); Cahuita Bay. PANAMA: UMML 35281; 1 specimen; 9°19'N, 79°55'W; 3 m; 23 Jul 1966. LACM 20309; 2(87.7–121.8); Caledonia Bay; 4 Apr 1939. ?COLOMBIA: UF 25915; (26.0); Providencia Island, north end of island in mangrove area; 1 m; 11 Aug 1969.

***Symphurus civitatium*** 427 specimens (22.0–152 mm SL).

**Counted and measured (30 specimens, 48.8–149.3 mm SL).** SOUTHEASTERN UNITED STATES: NORTH CAROLINA:

USNM 157403; paratype (109.0); 35°21'10" 75°22'40"; 26 m; 19 Oct 1884. FLORIDA: TU 75907; 3(131.3–135.7); 27°35'04"N, 80°04'04"W; 26 m; 5 Sep 1965. UF 13062; (130.2); 28°35.5'N, 80°08'W; 62 m; 21 Feb 1965. USNM 154946; paratype (139.4); Cape Canaveral; 18 m; 4 Apr 1940. GULF OF MEXICO: ALABAMA: ALA 3015; 3(75.5–85.2); to 30 m; 1968. MISSISSIPPI: ALA 606.29; (94.4); Horn Island; Jul–Aug 1958. FMNH 45979; (110.0); 29°22'N, 88°40'W; 51 m; 22 Oct 1953. LOUISIANA: USNM 155227; holotype (110.3); 29°06'30"N, 89°40'W; 17 m; 8 Jul 1938. USNM 313647; 2(48.8–72.2); Calcasieu Lake (ca. 30°N, 93°W); February, 1982. TEXAS: FMNH 45109; 3(138.1–149.3); 27°43'N, 96°51'W; 27 m; 26 Sep 1950. USNM 313646; 9(88.6–108.2); 3 mi offshore, Port Aransas (ca. 28°N, 97°W); 15 m; 16 Sep 1982. MEXICO: IMS 544; 3(120.7–139.7); west of Campeche; 27 m; 22–29 Jul 1951. UMML 34365; (130.0); 20°12'N, 91°40'W; 37 m; 11 Dec 1952.

**Counted (149 specimens, 42 lots).** PARATYPES. GULF OF MEXICO: FLORIDA: USNM 86153; (119.8); St. Joseph's Bay; 27 Jan 1917. ALABAMA: USNM 157402; (116.9); Mobile; 13 m; 7 Feb 1917. LOUISIANA: USNM 86140; (120.5); off Calcasieu Pass; 9 m; 15 Feb 1917. USNM 154945; 3(122.3–129.6); 28°54'N, 91°41.5'W; 18 m; 11 Jul 1938. USNM 154947; 5(110.2–122.6); 28°55.5'N, 91°46'W; 18 m; 11 Jul 1938. USNM 154948; 2(119.7–123.7); 28°58'N, 91°40.5'W; 16 m; 12 Nov 1938. USNM 154949; 2(105.2–128.8); 28°41.5'N, 91°10'W; 15 m; 11 Nov 1938. USNM 154950; 2(121.5–124.0); 28°47'N, 91°21.5'W; 11 Jul 1938. USNM 154951; (125.7); 29°12'N, 89°50.5'W; 13 m; 8 Jul 1938. USNM 154952; (117.0); 28°43'N, 91°13'W; 15 m; 11 Jul 1938. USNM 154953; 2(102.4–104.6); 29°12.5'N, 89°57'W; 7 m; 10 Jul 1938. USNM 154954; 3(114.0–118.3); 28°35.5'N, 91°01.5'W; 22 m; 13 Jul 1938. USNM 155226; (114.1); 28°45'N, 91°17.5'W; 16 m; 11 Jul 1938. USNM 157399; 3(108.6–120.8); Grand Terre; 2 Jul 1930. USNM 157400; 3(99.7–117.7); Grand Terre; 27 Jun 1930. TEXAS: USNM 86139; 2(117.7–125.5); Aransas Pass; 15 m; 5 Mar 1917. USNM 120081; (110.8); Galveston; 1941. USNM 120082; (81.5); Aransas Pass; 7 Aug 1941. USNM 157401; (117.3); Galveston; 10 m; 26–27 Feb 1917.

**Counted (nontype material).** BERMUDA: ANSP 137573; (79.3); washed onto shore. SOUTHEASTERN UNITED STATES: FLORIDA: UMML 34342; 3(135.8–140.3); 28°34'N, 80°15'W; 42 m; 19 Nov 1964. USNM 274484; (116.9); 28°13.5'N, 80°21'W; 22 m; 14 Nov 1963. USNM 291316; (131.8); 28°13'N, 80°21'W; 22 m; 14 Nov 1963. USNM 291317; 13(114.2–142.0); 28°13'N, 80°21'W; 22 m; 14 Nov 1963. UMML 34343; (130.7); 28°12'N, 80°05'W; 60 m; 14 Mar 1965. UMML 34344; (118.5); 27°57'N, 80°03'W; 55 m; 28 Sep 1963. GULF OF MEXICO: ALABAMA: ALA 301.17; 2(85.4–94.3); Dauphin Island; 28 Sep 1952. ALA 353.05; (108.0); Mobile Ship Channel; 6 Sep 1951. ALA 2385; 13(85.8–102.6); Dauphin Island; 15 Jul–20 Aug 1966. TEXAS: TCWC 4187.4; (100.4); 29°10'N, 94°30'W; 14 m; 28 Sep 1973. TCWC 4189.21; 18(97.8–124.0); 28°26'N,; 95°23'W; 28 m; 29 Sep 1973. TCWC 4195.31; 9(118.8–133.3); 28°25'N, 95°18'W; 35 m; 31 Oct 1973. UMML 34345; (127.6); 28°07'N, 95°53'W; 37 m; 26 Jan 1958. MEXICO: FMNH 45427; 7(125.7–139.5); 20°18'N, 91°48'W; 42 m; 7 Dec 1952. UMML 34366; (130.1); 20°12'N, 91°40'W; 37 m; 11 Dec 1952. USNM 157693; 5(116.8–125.6); 20°05'N, 91°28'W; 31 m; 26 Aug 1951. USNM 157694; 3(128.3–132.5); 20°05'N; 91°28'W; 31 m; 26 Aug 1951. USNM 291318; (127.1); Campeche, Yucatan (20°05'N, 91°28'W); 31 m; 26 Aug 1951. FMNH 46369; 11(114.6–137.8); 19°48'N, 91°20'W; 25 Aug 1951. GCRL 16383; 2(76.0–86.5); Lagunas de Terminos, Punta Zachtal, Campeche; 17 Nov 1970. IMS 543; 16(126.5–142.1); Pta Frontera; 31 m; 29 Jul–6 Aug 1951. USNM 274485; (132.0); north of Soto La Marina; 15 Mar 1947.

**Other material examined (248 specimens, 26 lots).** SOUTHEASTERN UNITED STATES: NORTH CAROLINA: 3(22–24); Cape Fear River; August, 1981; (uncatalogued reference specimens, Carolina Power & Light Biology Laboratory, Southport, NC, 28461). USNM 340449; (66.2); Lower Cape Fear River near Southport, Carolina Power & Light Generating Station, impingement screens; 15–16 Jan 1991. USNM 341611; (61.1); New Hanover County, Zeke's Island; 6 Oct 1992. USNM 341614; 3(56.0–64.4); New Hanover County, Masonboro Sound; 20 Jul 1995. USNM 341616; (23.1); Lower Cape Fear River, Walden Creek; 1 Sep 1991. FLORIDA: UF 35486; (125.2); 29°58.1'N, 81°16.9'W; 14 m. TU 92501; 25(82.0–120.0); 29°11'05"N, 80°53'05"W; 12 m; 24 Feb 1970. UMML 34346; 3(118.5–134.0); 28°22'N, 80°05'W; 60 m; 14 Mar 1965. GULF OF MEXICO: FLORIDA: ANSP 94305; (25); Key West; 1 m; 21 Mar 1958. MISSISSIPPI: FMNH 45980; 2(110.4–119.8); 28°45'N, 89°15'W; 60 m; 23 Oct 1953. FMNH 86369; (112.9); 29°42'N, 88°29'W; 37 m; 10 Aug 1951. TU 5374; 18(113.2–136.8); 29°14.4'N, 88°52.4'W; 32 m; 11 Aug 1952. TCWC 2251.1; (125.8); 29°09'N, 88°52'W; 73 m; 10–16 Dec 1963. ALABAMA: FMNH 89568; 2(119.1–121.1); 29°42'N, 88°29'W; 37 m; 10 Aug 1951. ALA 798.14; 2(107.7–110.1); Gulf Shores, Breton Island; 3 Aug 1959. UF 70946; (115.0); 29°41'N, 88°14.5'W; 45 m; 22 Jul 1971. USA 1905; 25(91.9–122.1); 29°57'N, 87°54'W; 26 m; 20 Apr 1975. LOUISIANA: ANSP 55825; (124.9); Breton Island; November, 1930. BMNH 1931.11.5:75; reversed specimen; Breton Island. FMNH 45981; 2(108.8–118.8); 28°56'N, 89°09'W; 59 m; 25 Oct 1953. Uncatalogued specimens; 1 lot with 123 specimens; Barataria Bay; 6 Jan 1993. TEXAS: CAS-SU 40556; (133.4); Freeport; 28 Apr 1940. FMNH 79851; 3(138.8–152); 27°43'N, 96°53'W; 26 m; 14 Dec 1950. UMMZ 199071; 5(46.0–57.3); 8–9 Apr 1939. USA 4070; 20(111.1–127.8); 10 mi south-southeast of Port Aransas; 3 Dec 1975. MEXICO: GCRL 16384; (32.7); Laguna el Carmen, Tabasco; 2 Mar 1978.

***Symphurus plagusia*** 48 specimens (19.5–130.3 mm SL).

**Counted and measured (15 specimens, 57.4–130.3 mm SL).** PUERTO RICO: ANSP 132030; neotype; (102.9); Puerto Yabucoa, one-half mile east of Playa de Guayanes, Municipio de Yabucoa; 24–27 Jul 1973. FMNH 3286; (83.1); Mayaguez; 20 Jan 1899. FMNH 61572; (117.0); Allasco Bay; 10 Jan 1954. UF 12059; (127.1); beach at Mani, just north of Mayaguez; 16 Apr 1964. COSTA RICA: UF 10762; (79.6); Tortuguero Lagoon, Limon Province; Aug 1963. PANAMA: GCRL 15694; (57.4); Canal Zone; 8 Feb 1977. TRINIDAD: UPRM 1828; (89.4); Icacos Bay; 4 May 1964. BRAZIL: FMNH 88853; 2(120.0–130.3); 2°09'S, 42°44'W; 40

m; 10 Mar 1963. UFPB 884; (101.4); Praiade Jacare; 13 Nov 1981. UFPB 896; 3(79.3–87.5); Rio Paraiba estuary, near Joao Pessoa (ca. 7°S, 37°W); 30 Jul 1981. ANSP 121326; 2(112.9–118.3); Atafona (23°02'S, 44°01'W); Jul–Aug 1963.

**Counted (29 specimens, 19 lots).** PUERTO RICO: ANSP 118542; (47.4); Puerto Yabucoa; 25 Jan 1971. ANSP 129952; (112.7); Puerto Yabucoa; 21 Jul 1973. ANSP 129985; (98.2); Puerto Yabucoa; 25 Jul 1973. USNM 50178; 4(61.9-83.1); Ponce; 31 Jan 1899. HAITI: UF 33896; 5(82.8–90.8); 2 km northwest of Port Salut; sandy beach near eelgrass bed; 7 Apr 1979. MNHN 1992-1412; (82.4); Baie de Saint Marc; 8 m. BELIZE: FMNH 97492; (49.3); Belizean Beach 4.5 mi on Western Highway; 16 Apr 1973. FMNH 97493; 2(52.1–68.2); Belizean Beach 4.5 mi on Western Highway; 16 Apr 1973. FMNH 97494; (25.1); Belize City, St. John's College Beach; 16 Apr 1973. FMNH 97495; (36.4); Belize City, St. John's College Beach, mangroves and beach; 3 Aug 1973. HONDURAS: FMNH 94818; (54.3); Brus Lagoon; 1 m; 10 May 1975. FMNH 94822; (34.8); Roatan; 1 m; 1 May 1975. FMNH 97490; 3(19.5–61.3); Stann Creek District along Pelican Beach, 17–33 m north of Pelican Beach Motel; 30 Mar 1973. FMNH 97491; (40.0); Stann Creek District along Pelican Beach, 17–33 m north of Pelican Beach Motel; 15 Apr 1973. COSTA RICA: LACM 30729-3; (100); Puerto Limon to San Juan del Norte, Nicaragua. PANAMA: USNM 81654; (54.9); Colon; 5 Jan 1911. GUYANA: UMML 34347; (121.5); 7°42'N, 57°32'W; 27 m; 15 Jul 1968. FRENCH GUIANA: USNM 236252; (110.5); 6°34'N, 54°28'W; 37 m; 28 Jun 1972. USNM 291331; (79.4); 5°30'N, 52°10'W; 51 m; 12 Sep 1958.

**Other material examined (4 specimens, 2 lots).** CUBA: USNM 37570; (104); unspecified locality, Cuba; 1885. TOBAGO: USNM 313648; 3(19.5–20.3); Bloody Bay, 11°18'14"N, 60°37'46"W; 3 m; 13 Sep 1990.

*Symphurus oculellus* 88 specimens (75.8–189 mm SL).

**Counted and measured (14 specimens, 75.8–164 mm SL).** GUYANA: BMNH 1950.5.15:51; paratype (138.7); off Georgetown. FMNH 86365; paratype (148.4); 7°05'N, 57°12'W; 33 m; 1 Sep 1958. FMNH 88846; paratype (131.5); 6°54'N, 57°47'W; 18 m; 25 Mar 1963. SURINAME: USNM 159606; holotype, (144.1); 6°24'N, 55°00'W; 27 m; 11 May 1957. USNM 159559; paratype (75.8); 6°04'N, 54°51'W; 70 m; 13 May 1951. ZMA 111.212; paratype (158); 5°15'N, 55°15'W; 12 m; 13 Oct 1969. FRENCH GUIANA: UMML 12254; paratype (140.9); 6°17'N, 53°35'W; 40 m; 21 Feb 1963. USNM 313518; paratypes 2(143.1–151); 6°12'N, 53°23'W; 46 m; 1 Jul 1972. UMML 11549; paratype (156); 5°57'N, 52°18'W; 70 m; 22 Feb 1963. UMML 12262; paratype (148.4); 5°24'N, 51°34'W; 64 m; 23 Feb 1963. ZMA 111.234; paratype (140.4); 3°45'N, 51°45'W; 40 m; 16 Nov 1969. BRAZIL: FMNH 86362; paratype (155); 1°57'N, 48°15'W; 48 m; 17 Nov 1957. FMNH 100385; paratype (164); 1°57'N, 48°12'W; 55 m; 14 Nov 1957.

**Counted (30 paratypes, 14 lots).** GUYANA: BMNH 1961.9.4:117–118; (163–189); 8°30'N, 59°03'W; 40 m; 25 Feb 1959. UMML 34335; (136.5); 7°42'N, 57°32'W; 27 m; 15 Jul 1968. SURINAME: GCRL 3836; 5(130.0–165); 6°56'N, 54°05'W; 2 May 1969. UMML 12249; (143.3); 6°18'N, 55°11'W; 18 m; 20 Feb 1963. ZMA 111.228; 1; 5°15'N, 55°15'W; 12 m; 10 Oct 1969. FMNH 90552; 2(142.5-147.3); Suriname; 18 m; 1957. FMNH 90553; (144.1); Suriname; 110 m; 3 May 1957. FMNH 91368; (141.4); Suriname; 1957. FRENCH GUIANA: FMNH 100386; 7(154–180); 6°03'N, 52°22'W; 65 m; 13 Sep 1958. FMNH 90085; 5(163–180); 5°46'N, 52°02'W; 70 m; 12 Nov 1957. FMNH 86397; (130.5); 5°05'N, 52°14.5'W; 20 m; 23 May 1957. BRAZIL: FMNH 100387; 2(140.5–155); 2°29'N, 48°54'W; 86 m; 15 Nov 1957. USNM 159541; (150); 2°29'N, 48,55'W; 42 m; 15 Nov 1957.

**Nontype material counted (21 specimens, 8 lots).** SURINAME: USNM 159602; 2(82.2–94.8); 6°23'N, 55°05.5'W; 27 m; 11 May 1957. USNM 159604; (131.3); 6°21'N, 55°00'W; 26 m; 12 May 1957. USNM 313517; 2(152–174); 6°21'N, 54°28'W; 28 m; 29 Jun 1972. USNM 316780; (142.7); 6°41'N, 54°17'W; 46 m; 14 Jun 1957. FRENCH GUIANA: USNM 316779; 2(152–157); 6°06'N, 52°52'W; 65 m; 2 Jul 1972. USNM 159615; 2(158–188); 5°39'N, 51°56'W; 68 m; 12 Nov 1957. USNM 316773; 10(136.3–147.9); 4°52'N, 51°49'W; 37 m; 5 May 1975. USNM 316778; (145.9); 4°42'N, 51°28'W; 19 m; 6 May 1975.

**Other nontype material examined (23 specimens, 13 lots).** GUYANA: UMML 34364; (152); 7°00'N, 57°08'W; 26 m; 15 Jul 1968. SURINAME: UMML 12498; (158); 7°01'N, 54°21'W; 64 m; 21 Feb 1963. FMNH 90223; (135.0); 6°54'N, 54°47'W; 18 m; 25 Mar 1953. UMML 34334; 2(104.5–139.5); 6°25'N, 55°04'W; 7 m; 10 Jul 1968. FMNH 91109; (151); 6°24.5'N, 55°02.5'W; 27 m; 11 May 1957. USNM 313515; 3(136–152); 6°21'N, 54°28'W; 28 m; 29 Jun 1972. UMML 12310; 3(138.9–142.1); 6°11'N, 55°39'W; 15 m; 19 Feb 1963. FRENCH GUIANA: UMML 13301; 6(111.0–175); 6°00'N, 52°27'W; 64 m; 22 Feb 1963. UMML 13307; (166); 5°29'N, 51°37'W; 64 m; 23 Feb 1963. UF 83997; (143.1); 5°05'N, 51°58'W; 45 m; 11 Dec 1977. USNM 313516; (147); 4°47'N, 51°37'W; 33 m; 5 May 1975. UMML 34336; (160); off Cayenne; 4°46'N, 52°04'W; 51 m; 12 Dec 1977. BRAZIL: UMML 12265; (150); 2°20'S, 40°24'W; 40 m; 12 Mar 1963.

*Symphurus tessellatus* 523 specimens (13.4–220 mm SL).

**Counted and measured (23 specimens, 97.9–203 mm SL).** PUERTO RICO: UPRM 2717; (141.7); Puerto Rico; 8 m; 14 Mar 1966. UPRM 2760; (142.3); Mayaguez; 12 m; 15 Mar 1966. UPRM 2859; (111.0); Mayaguez Bay; 9 m; 29 Apr 1966. UPRM 3758; (130.4); Anasco River; 1–2 Jul 1953. UPRM 3759; 2(130.1–132.6); Mayaguez Bay, 1966. FRENCH GUIANA: UF 35275; (172); 5°14'N, 52°06'W; 45 m; 11 Dec 1977. BRAZIL: UFPB 143; 5(97.9–132.7); Rio Paraiba estuary, near Joao Pessoa (ca. 7°S, 37°W); 27 Apr 1978. MHNN 691; (140.3); Bahia (possible holotype or syntype of *Plagusia brasiliensis*). ANSP 121549; 10(108–203); Rio de Janeiro; July–August 1963.

**Counted (267 specimens, 82 lots).** PUERTO RICO: MCZ 28843; (91.8); Puerto Rico; 1898-99. UF 83996; (146.1); beach at Mani, just north of Mayaguez; 16 Apr 1964. UPRM 1590; 2(159–173); Mayaguez; 3 Mar 1962. UPRM 2743; 15(114–172); Mayaguez; 6 m; 15 Mar 1966. UPRM 3760; 2(128.0–143.2); Rio Anasco; 17 Aug 1951. UPRM 3761; 3(126.3–158); Mayaguez Bay; 1966. USNM 126448; (131.5); Mayaguez; 1899. CUBA: MCZ 11269; (111); Cuba. USNM 35108; (81.3); Havana. USNM 37750; (68.6);

Havana. USNM 154857; (131); Cuba. DOMINICAN REPUBLIC: USNM 108369; (123). USNM 108372; (126). HAITI: ANSP 81861; (97.7); Port-au-Prince; November 1949. ANSP 83626; 8(83.3–113); Port-au-Prince; 1949. ANSP 97661; 6(114–146); Port-au-Prince; 1936. UMMZ 142422; (127.4); Haiti; 15 Apr 1983. USNM 133671; 3(109–124); Port-au-Prince; 1–4 Jan 1947. USNM 164849; 2(87.7–132.6); Haiti; 1927. JAMAICA: LACM 6215; (142.0); 17°52'N, 77°53'W; 40 m; 15 May 1962. LACM 6217; 10(123.0–152); 17°46'N, 77°30'W; 16 m; 15 May 1962. UMML 4831; (114.7); Hunts Bay; 3 Aug 1958. UMML 34367; 3(118–160); 17°45'N, 77°38'W; 35 m; 15 May 1962. UMML 34368; (144); 17°55'N, 77°51'W; 39 m; 18 May 1965. USNM 37348; (79.9); Jamaica. USNM 291333; 6(128.1–161); 17°55'N, 77°51'W; 40 m; 18 May 1965. USNM 291347; 2(130.7–146.4); 17°53'N, 77°50'W; 42 m; 18 May 1965. USNM 291346; 2(128–138); 17°51'N, 77°49.5'W; 49 m; 18 May 1965. BELIZE: UMML 34354; 4(132–160); 17°12'N, 88°11.2'W; 19 m; 9 May 1967. UMML 34355; 9(134–160); 17°12'N, 88°11.2'W; 19 m; 18 May 1967. HONDURAS: FMNH 100384; 5(38.1–56.0); Brus Lagoon; 10 May 1975. FMNH 94819; 5(37.7–49.5); Brus Lagoon; 10 May 1975. UMML 34348; 2(130–134); 15°49.15'N, 83°44'W; 31 m; 7 Apr 1967. UMML 34349; 2(126–141); 15°48'N, 83°54'W; 24 m; 7 Apr 1967. UMML 34350; 5(111–164); 15°49.5'N, 83°44'W; 31 m; 7 Apr 1967. UMML 34351; 3(130–148); 15°54'N, 83°40'W; 37 m; 8 Apr 1967. UMML 34352; 3(132–155); 15°54'N, 83°40'W; 37 m; 8 Apr 1967. UMML 34353; 2(138–147); 15°45'N, 83°32'W; 35 m; 9 Apr 1967. PANAMA: FMNH 18251-57; 7(50.3–70.3); Panama. GCRL 12698; 2(13.4–65.8); Canal Zone; 5 Mar 1974. COLOMBIA: UMML 34369; 4(145–155); 10°53'N, 75°22'W; 42 m; 23 May 1964. USNM 316776; (134.5); 10°05'N, 75°40'W, 44 m; 27 Nov 1968. UMML 34356; (148); 9°30'N, 76°07.5'W; 41 m; 26 May 1964. USNM 291332; (147); 8°59'N, 76°27'W; 26 m; 29 Nov 1968. USNM 316775; 4(134.7–165); 8°59'N, 76°27'W; 26 m; 29 Nov 1968. VENEZUELA: ANSP 121394; 7(67.9–152); Venezuela; 15 Mar 1962. FMNH 88650; 16(155–200); 12°19'N, 70°34'W; 73 m; 27 Sep 1963. UMML 34370; (173); 11°52'N, 70°22'W; 35 m; 27 Jun 1968. UMML 34357; (171); 12°19'N, 70°34'W; 73 m; 27 Sep 1963. UMML 34358; (145.0); 10°29'N, 62°30'W; 9 m; 24 Oct 1963. TRINIDAD: UPRM 3762; (141.6); Trinidad; 4 May 1964. GUYANA: FMNH 86364; (162); 8°09'N, 58°23'W; 42 m; 29 Aug 1958. FMNH 90546; 23(152–204); 8°32'N, 59°10'W; 43 m; 28 Oct 1958. GCRL 3835; (196); 8°13'N, 58°40'W; 37 m; 27 Apr 1969. GCRL 3838; 3(192–202); 9°14'N, 60°19'W; 44 m; 25 Apr 1969. SURINAME: FMNH 86459; (161); Suriname; RV *Coquette* 1957. GCRL 23512; 6(164–196); 6°56'N, 54°05'W; 59 m; 2 May 1969. USNM 316774; (150); 6°23'N, 55°05'W; 28 m; 11 May 1957. USNM 291335; (168); 6°12'N, 53°23'W; 46 m; 1 Jul 1972. FRENCH GUIANA: USNM 316777; 3(150–172); 4°52'N, 51°49'W; 37 m; 5 May 1975. BRAZIL: FMNH 90544; 3(183–196); 1°57'N, 48°12'W; 55 m; 14 Nov 1957. FMNH 91129; (197); 2°29'N, 48°54'W; 86 m; 15 Nov 1957. UFPB 1120; 5(51.5–114.6); Rio Paraiba estuary, near Joao Pessoa (ca. 7°S, 37°W); 30 Aug 1981. USNM 324679; 9(55.7–122.6); Rio Paraiba estuary, near Joao Pessoa (ca. 7°S, 37°W); 13 Nov 1981. USNM 324680; 2(100.2–109.5); Rio Paraiba estuary, near Joao Pessoa (ca. 7°S, 37°W); 30 Jul 1981. UFPB 882; 5(36.0–115.0); Cabedelo; 29 Oct 1981. UFPB 993; 5(57.8–107.4); Ilha da Restinga, Rio Paraiba do Norte. USNM 159225; 2(182–187); 1°57'N, 48°12'W; 55 m; 17 Nov 1957. MCZ 11381; 14(93.9–202); Rio de Janeiro; 1865. MCZ 24939; (174); Rio de Janeiro; 1865. MCP 1198; (116.0); Florianopolis; 30 Oct 1968. MCP 5663; (180); Port Belo, Santa Catarina. MCP 2193; (156); Florianopolis; Oct 1968. MCP 2194; (112.5); Florianopolis; Oct 1968. MCP 1199; (113.8); Florianopolis; 30 Oct 1968. MCP 1202; (115.5); Florianopolis; 30 Oct 1968. MCP 7270; (127.8); Port Belo, Santa Catarina; 3–4 Nov 1973. MCP 7327; (126.0); Porto Belo, Santa Catarina; 1 Aug 1973. MCP 7345; (130.0); Porto Belo, Santa Catarina; 31 Jul–1 Aug 1973. MCP 1200; (118.4); Florianopolis; 30 Oct 1968. MCP 3139; (125.7); Florianopolis; Oct 1968. UF 19938; 3(109.4–133.3); São Paulo; 13 Jul 1961.

**Other material examined (233 specimens, 61 lots).** CUBA: IOH 1318; (158); ca. 23°00'N, 83°00'W. IOH 1313; (168); ca. 23°00'N, 83°00'W. MCZ 91961; (89.9); Cuba. HAITI: MNHN 1982-1126; 14(83.9–139.9); Baie de Saint Marc; 8 m. JAMAICA: LACM 6218; 43(95.1–170); 17°55'N, 77°53'W; 41 m; 15 May 1962. HONDURAS: UF 33892; 4(138–154); 15°45'N, 83°32'W; 35 m; 9 Apr 1967. USNM 291345; 6(136.5–161); 15°56'N, 83°55'W; 47 m; 2 Feb 1967. NICARAGUA: UMML 34359; 2(126–140); 11°51'N, 83°35'W; 20 m; 28 Jan 1971. UMML 34360; 9(56.4–142.5); 12°16'N, 83°31W; 12 m; 28 Jan 1971. PANAMA: GCRL 14930; 2(173–177); Colon; April 1974. MCZ 58656 (31.1); Panama; 9 Sep 1964. UF 75622; (57.5); Canal Zone; 1974. UF 76003; (62.8); Canal Zone; August 1974. UMML 26664; 2(123–141); 9°18.2–18.4'N, 80403.3–04'W; 24 m; 20 Jul 1966. USNM 81652; (89.4); Porto Bello; 24–28 Apr 1911. USNM 81653; 2(61.1–67.6); Fox Bay; 11 Jan 1911. USNM 81655; 2(38.1–43.5); Fox Bay; 27 Jan 1912. USNM 144792; (65.1); Canal Zone; 4 Mar 1937. USNM 291351; 3(170–208); 8°25'N, 79°56'W; 10 m; 19 Dec 1963. USNM 291354; 5(189–220); 8°25'N, 79°56'W; 10 m; 19 Dec 1963. COLOMBIA: USNM 291358; 5(126.3–141.9); 9°33'N, 76°02'W; 49 m; 28 Nov 1968. UMML 22247; 22(84–148); 8°48–46.8'N, 76°39.7–42.8'W; 20 m; 12 Jul 1966. UMML 31320; (133); 8°51.9–53.9'N, 76°37.2'W; 12 Jul 1966. USNM 291350; (152); 8°50'N, 76°48'W; 49 m; 2 Nov 1970. VENEZUELA: ANSP 120209; (133); Venezuela; 23 Jul 60–17 Mar 1962. GCRL 3837; (163); 8°52'N, 59°58'W; 29 m; 26 Apr 1969. MCZ 41081; (103.9); 10°17'N, 69°45'W; 1958. UMML 30197; 30(84–183); 11°25.1–25.8'N, 70°52.1–50'W; 18 m; 27 Jul 1968. UMML 30223; (160); 11°55–55.3'N, 71°00–59.9'W; 11 m; 28 Jul 1968. UMML 34361; 2(138–185); 10°49'N, 63°13'W; 48 m; 19 Jul 1968. UMML 34362; (187); 10°36'N, 68°12'W; 24 m; 25 Jul 1968. UMML 34363; 6(158–201); 10°11'N, 64°48'W; 35 m; 19 Oct 1963. USNM 291355; 10(143.5–197); 12°17'N, 70°34'W; 73 m; 27 Sep 1963. USNM 291348; 4(161–185); 11°50'N, 70°40'W; 59 m; 10 May 1965. USNM 123112; (179); Gulf of Paria. TRINIDAD: USNM 113251; (124); 10°37'N, 61°42'W; 60 m; 3 Feb 1884. SURINAME: IOH 1312; (156); 6°14'N, 55°24'W; 15 m; 14 Jan 1971. UMML 12251; (162); 6°18'N, 55°11'W; 18 m; 20 Feb 1963. USNM 291352; 3(162–178); 6°34'N, 54°28'W; 37 m; 28 Jun 1972. USNM 291353; (194); 6°46'N, 54°27'W; 49 m; 28 Jun 1972. USNM 159536; (177); 6°41'N, 54°17'W;

46 m; 14 Jun 1957. USNM 159567; (205); 6°42'N, 54°12.5'W; 44 m; 14 Jun 1951. USNM 159612; (204); 6°41.5 N, 54°14.5'W; 44 m; 14 Jun 1957. USNM 159618; (194); 6°42.5'N, 54°10'W; 42 m; 14 Jun 1957. USNM 291356; 9(191–207); 6°54'N, 53°58'W; 64 m; 30 Jun 1972. USNM 291349; (82.3); 5°30'N, 52°10'W; 51 m; 12 Sep 1958. FRENCH GUIANA: UF 44365; (168); 5°05'N, 51°58'W; 45 m; 11 Dec 1977. BRAZIL: UMML 13292; (186); 4°38'N, 51°05'W; 59 m; 26 Feb 1963. USNM 159237; 6(165–191); 2°00'N, 48°19'W; 46 m; 16 Nov 1957. UMML 13977; (157); 2°10'S, 42°24'W; 48 m; 11 Mar 1963. FMNH 88193; (160); Bahia; 13 Apr 1908. MCZ 11323; (105); Pernambuco. MCZ 11378; 3(68.7–96.1); Pernambuco. MCZ 11380; (91.7); Curuca. USNM 83172; (94.4); Rio de Janeiro. MCZ 889; 2(123–139); Rio de Janeiro. MCZ 11382; (137); Rio de Janeiro. MCZ 11149; (160); Rio de Janeiro. MCZ 11379; (147); Santos. URUGUAY: USNM 87772; (119); Montevideo. USNM 87773; (113); Montevideo.

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# Radiocarbon from nuclear testing applied to age validation of black drum, *Pogonias cromis*

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**Abstract.**—Radiocarbon ($^{14}C$) in the world's oceans increased sharply between 1950 and 1970 as a result of the atmospheric testing of nuclear weapons. Through comparison with the $^{14}C$ time series reconstructed from atmospheric measurements and marine carbonates, Kalish, in 1993, used the $^{14}C$ concentration measured in fish otolith cores as a means of confirming the annulus-based age estimates for some South Pacific fish species. Here we report the pre- and postbomb $^{14}C$ chronology of North Atlantic adult black drum (*Pogonias cromis*), assumed to be between 15 and 42 yr of age on the basis of otolith annulus counts. According to accelerator mass spectrometry (AMS) assays, $^{14}C$ in otolith cores increased sharply between 1958 and 1964, with a timing and magnitude which was very similar to that of the atmospheric bomb $^{14}C$ signal. The correspondence between the two $^{14}C$ chronologies indicates that the annulus-based age assignments were accurate on average to within 1–3 yr. Differences between the black drum $\Delta^{14}C$ chronology and that of other marine carbonates in the North Atlantic are explained by the estuarine habitat of young-of-the-year black drum and by the fact that estuarine $\Delta^{14}C$ values more closely reflect atmospheric values than surface ocean values. At present, there is no other age-validation technique that can confirm the absolute age of long-lived fish species with comparable levels of accuracy.

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Despite the international acceptance of otolith annuli as the best means for estimating the age of most fish species, the correct interpretation of annuli is far from easy and can result in serious and systematic ageing errors (Beamish and McFarlane, 1995). Indeed, aside from the use of tagged, hatchery-reared fish released into the wild, confirmation of the accuracy of a method of annulus interpretation for marine fish species is often problematic. Mark-recapture of chemically tagged individuals has generally been considered to be the most accurate means of confirming the frequency of formation of presumed annuli, owing to a correspondence between time at liberty and the number of annuli distal to the chemical check (Foreman, 1996). Although the approach is sound, extremely low recapture rates for fish at liberty more than 2–3 years can make it difficult to acquire sufficient samples for an adequate test. Moreover, the technique validates the time elapsed since tagging, not the absolute age of the fish. Alternatively, radiochemical dating based on $^{210}Pb$:$^{226}Ra$ or $^{228}Th$:$^{228}Ra$ ratios can be used to differentiate between very different age interpretations (Bennett et al., 1982; Campana et al., 1990), but these assays are too imprecise for detailed or individual age confirmations. The most widely used approach, that of the seasonal progression of marginal increments (Beckman and Wilson, 1995) is well suited only to fast-growing fish and suffers from the lack of an objective means of evaluation. Thus there is a well-defined gap in our ability to confirm the age interpretations of the majority of marine fish species, particularly those that are long-lived. However, the recent finding that nuclear testing left a dated mark in the otolith (Kalish, 1993) provides a significant breakthrough in our ability to determine accurate, absolute ages for individual long-lived fish.

Kalish (1993) was the first to describe the use of bomb radiocarbon ($^{14}C$ or carbon-14) as a dated marker in fish otoliths and its value for confirming age interpretations. His findings were based on earlier work that had documented a 100% increase in atmospheric radiocarbon as a result of the widespread atmo-

spheric testing of atomic bombs in the 1950's and 1960's (Nydal and Lovseth, 1983). This product of nuclear testing was subsequently incorporated into the world's oceans in a manner which has been well described at large spatial scales (Broecker et al., 1985; Duffy et al., 1995). Through analysis of annular growth rings in coral, other workers demonstrated that bomb radiocarbon was incorporated into the accreting coralline structure in concentrations proportional to those present in the water column (Druffel and Linick, 1978; Nozaki et al., 1978). Thus the time series of bomb radiocarbon in the coral was shown to reflect that present in the surface marine environment, which increased by about 20% between 1950 and 1970. Using accelerator mass spectrometry (AMS) as a sensitive and accurate assay tool, Kalish (1993) was able to demonstrate that the otoliths of a New Zealand fish species also incorporated $^{14}C$ and that the time series of radiocarbon reconstructed from the presumed otolith annuli was similar to that present in nearby corals. Thus he was able to infer that the otolith annuli had been interpreted and aged correctly because systematic under- or over-ageing would have resulted in a phase shift between the otolith $^{14}C$ and the coral $^{14}C$ time series.

Subsequent work by both Kalish (1995a, 1995b; Kalish et al., 1996) and Campana (1997) has confirmed the value of the bomb radiocarbon technique for solving problems of age validation in a variety of fish species. Furthermore, recent work by Campana (1997) has confirmed that the assumption of synchronicity between otolith and marine carbonate $^{14}C$ chronologies is justified, because the period of rapid increase in the $^{14}C$ chronology recorded in age-1 haddock (*Melanogrammus aeglefinus*) otoliths was synchronous with that reported for other taxa in the North Atlantic, whether based on corals (Druffel, 1989) or bivalves (Weidman and Jones, 1993). Such large-scale synchronicity implies that the $^{14}C$ time series reconstructed from the otolith cores of old fish can be compared to one of the other North Atlantic time series; errors in annulus-based age determinations would manifest themselves as noncoherent time series. The only constraint to such an age determination procedure is the requirement for otoliths of fish spawned during and adjacent to the 1958–65 period, so as to take advantage of the unique $^{14}C$ values during that period.

The black drum, *Pogonias cromis*, with its putative lifespan of some 60 yr and estuarine dependence during early life (Jones et al., 1997), is an ideal candidate for age validation with $^{14}C$. This large sciaenid is distributed along the east coast of the U.S. (Jones et al., 1997) and throughout the Gulf of Mexico, where it is fished commercially. However its relatively low abundance results in low recapture rates after tagging. Accordingly, attempts to validate annulus formation with mark-recapture techniques in the older age groups have been unsuccessful. Yet such validation is critical to the proper management of this fish in the Chesapeake Bay region, where the greatest numbers of presumably old fish are harvested.

Here we report the first pre- and post[atom]bomb $^{14}C$ otolith chronology for black drum, and the first such chronology for any long-lived fish species in the North Atlantic. We use this $^{14}C$ chronology to determine the absolute ages of individual fish, and through comparison with otolith annulus counts from the same fish, we then confirm the accuracy of otolith annuli as indicators of absolute age in this species.

## Materials and methods

Adult black drum ($n$=31) with a mean ±SE total length of 111 ±1 cm (range=95–119 cm) were collected with anchored and drifted gill nets during research surveys of the eastern shore of Chesapeake Bay in Apr–May 1990. To estimate age based on annuli, one randomly selected sagittal otolith of each otolith pair was sectioned transversely through the core, and the annuli were counted under reflected light. The radius of the presumed first annulus was confirmed through measurements of the dimensions of intact sagittae collected from young-of-the-year black drum, which indicated that the first annulus in a transverse section should be approximately 7 mm wide and 2 mm thick. After ageing with reflected light microscopy, the remaining halves of each otolith were stored dry in paper envelopes in preparation for $^{14}C$ assay.

To extract a sample of the first year's growth from each otolith, a transverse section 1-mm thick was made with an Isomet saw immediately adjacent to that made for ageing. Although this second section was adjacent to the otolith core, the length of the age-1 otolith (~8 mm) indicates that most of the first year's growth was still present in the section. After recording a digital image of the annuli, a Dremel tool was used to remove all otolith material distal to the first annulus. The remaining core material was then stored in aluminum foil and submitted for $^{14}C$ assay by AMS. All samples were also individually assayed for $\delta^{13}C$, which was used to correct for isotopic fractionation effects. Radiocarbon values were subsequently reported as $\Delta^{14}C$, which is the per mil (‰) deviation of the sample from the radiocarbon concentration of 19th-century wood, corrected for sample decay prior to 1950 according to methods outlined by Stuiver and Polach (1977).

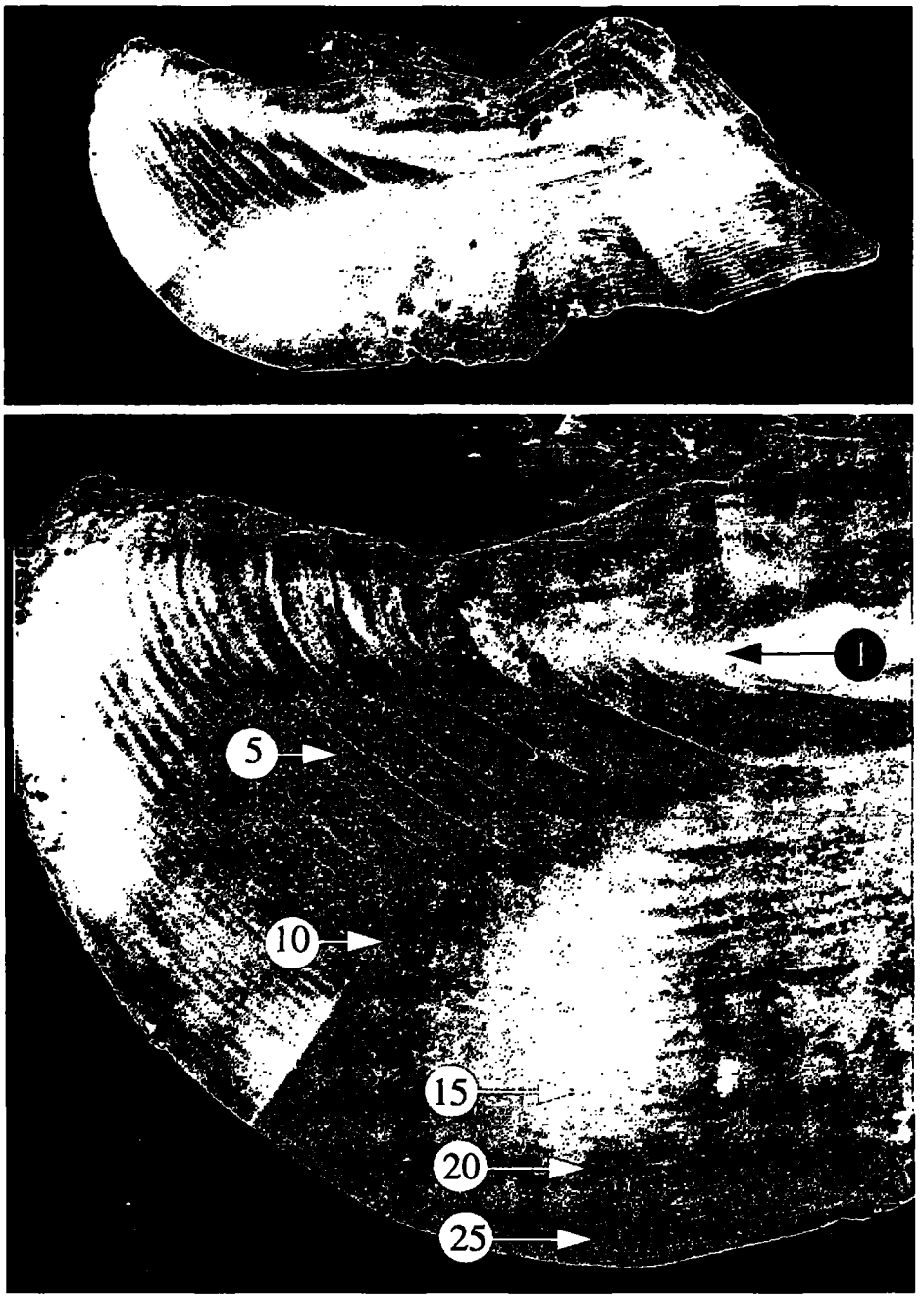


**Figure 1**

**(A)** Transverse section of an adult black drum otolith presumed to be 27 years old. **(B)** A magnified view of the ventral side of the sulcus, a region in which the annuli (indicated by arrows) tend to be most clear. Bar = 2 mm.

## Results

The presumed annuli in the black drum otolith sections were clear and unambiguous (Fig. 1). Age bias plots (Campana et al., 1995) of the counts of the two independent age readers showed no bias and high precision (CV=1.6%) over an age range of 15–42 years. Although the number of annuli was generally consistent on both the dorsal and ventral sides of the sulcus, the latter was usually the clearer of the

two. Therefore, all age and year-class estimates were based on annulus counts along the ventral aspect of the core-medial axis.

The assay results for mean $\delta^{13}C$ were consistent with those observed previously in fish otoliths (mean ± SD=–3.48±1.50‰) (Table 1). Although the presence of a slight but significant decrease across years ($b$= –0.09, $P$=0.04, $r^2$=0.13) was somewhat larger than the long-term ocean trend reported by Quay et al. (1992) and was of different slope than that reported for North Atlantic haddock otoliths (Campana, 1997), the biological significance of the observed trend is questionable given the relatively large coefficient of variation (CV=43%) among the samples. In contrast, $\Delta^{14}C$ differed strongly and systematically though time; concentrations were relatively low and constant prior to the late 1950's but increased sharply to a peak in the mid-1960's (Table 1; Fig. 2). Subsequent values continued to decline to the end of the time series in 1975. The maximum rate of increase occurred between 1958 and 1964 and was easily differentiated from the adjacent time periods. Therefore, the $\Delta^{14}C$ of the cores of the black drum otoliths was characteristic of the period of incorporation and could reasonably be considered a dated marker.

**Table 1**

Summary of $\Delta^{14}C$ and $\delta^{13}C$ assay results for each black drum otolith core.

| Year class | Annulus age (yr) | $\Delta^{14}C$ | SD | $\delta^{13}C$ |
|---|---|---|---|---|
| 1948 | 42 | –38.8 | 5.9 | –0.9 |
| 1950 | 40 | –78.2 | 8.3 | –2.7 |
| 1952 | 38 | –36.7 | 6.4 | –2.4 |
| 1954 | 36 | –71.9 | 5.9 | –5.9 |
| 1954 | 36 | –62.8 | 6.1 | –2.1 |
| 1957 | 33 | 1.9 | 4.6 | –2.7 |
| 1958 | 32 | 45.2 | 7.8 | –2.2 |
| 1959 | 31 | –3.1 | 6.4 | –3.0 |
| 1959 | 31 | 101.9 | 7.2 | –1.9 |
| 1960 | 30 | 46.1 | 6.8 | –3.3 |
| 1960 | 30 | 18.1 | 6.6 | –4.3 |
| 1960 | 30 | 70.8 | 6.8 | –1.9 |
| 1961 | 29 | 175.3 | 7.5 | –3.3 |
| 1962 | 28 | 62.4 | 4.5 | –5.9 |
| 1962 | 28 | 182.5 | 7.5 | –4.4 |
| 1963 | 27 | 299.3 | 8.5 | –0.8 |
| 1963 | 27 | 136.2 | 7.3 | –2.6 |
| 1963 | 27 | 95.7 | 7.1 | –5.8 |
| 1964 | 26 | 111.4 | 6.8 | –6.0 |
| 1964 | 26 | 194.2 | 7.6 | –2.3 |
| 1964 | 26 | 371.4 | 9.1 | –4.8 |
| 1965 | 25 | 340.6 | 8.6 | –4.4 |
| 1965 | 25 | 106.4 | 7.1 | –4.9 |
| 1966 | 24 | 366.5 | 9.1 | –4.4 |
| 1967 | 23 | 291.1 | 8.5 | –3.3 |
| 1968 | 22 | 297.2 | 10.2 | –2.9 |
| 1968 | 22 | 261.8 | 8.2 | –2.9 |
| 1968 | 22 | 207.5 | 8.0 | –3.2 |
| 1970 | 20 | 213.1 | 7.8 | –2.4 |
| 1973 | 17 | 255.2 | 8.1 | –4.0 |
| 1975 | 15 | 150.4 | 6.5 | –6.3 |

The $\Delta^{14}C$ from the otolith cores from the prebomb, pre-1957 year classes (–57.7±19.0‰) was very similar to that which has been measured in other North Atlantic otoliths, corals, and bivalves (Fig. 3). However, considerably more $^{14}C$ was incorporated into black drum otoliths during the 1960's than has been measured in most other marine carbonates. Indeed, peak $\Delta^{14}C$ values in black drum (~340‰; Fig. 2) were almost twice as high as those recorded in contemporaneous corals, and almost four times as high as those measured in haddock otoliths of the same year classes. After normalizing the black drum and marine carbonate time series to the same scale, the black drum $\Delta^{14}C$ chronology appeared to both begin its increase and reach a peak approximately 2–3 yr before that of the other carbonates. In addition, unlike the $\Delta^{14}C$ in the other taxa, the $\Delta^{14}C$ in the black drum otoliths declined significantly (to +150‰ in 1975) after reaching a peak in the mid-1960's. Thus in terms of phase coherence, peak magnitude, and subsequent decline, the black drum $\Delta^{14}C$ chronology more closely resembled that of the atmosphere than of other marine carbonates.

To assess the level of correspondence between the black drum $\Delta^{14}C$ chronology and that of the atmosphere, the two time series were scaled to comparable magnitudes. The resulting correspondence was striking (Fig. 4), both in its rate of increase and subsequent decline. The phase shift between the two chronologies was approximately 1 yr, with black drum lagging behind atmosphere.

## Discussion

In light of the sharp rate of increase of the $^{14}C$ signal associated with the onset of nuclear testing, interpretation of the $^{14}C$ chronology in otolith cores is relatively simple; the otolith chronology should match other published chronologies for the region as long as the annular age assignments (=year class) are correct. Any under-ageing would phase-shift the otolith $^{14}C$ chronology towards more recent years, whereas over-ageing would phase-shift it towards earlier years. Because marine waters with $\Delta^{14}C$ values greater than 0‰ did not generally exist prior to the late 1950's, coastal fish otolith cores with subzero values must have formed before the late 1950's. Contamination with material of more recent origin

could only increase the $\Delta^{14}C$ value, not decrease it. Thus the $\Delta^{14}C$ value sets a minimum age for the sample, and the years 1958–65 become the most sensitive years for $\Delta^{14}C$-based ageing. It is on this basis that workers in other disciplines have used bomb radiocarbon assays to infer age and the frequency of growth-ring formation in both bivalves (Turekian et al., 1982; Peck and Brey, 1996) and mammals (Bada et al., 1990).

The coherence between the otolith-based $^{14}C$ time series reconstruction reported here and that reported elsewhere in the North Atlantic for bivalves (Weidman and Jones, 1993), corals (Druffel, 1989), and haddock otoliths (Campana, 1997) indicates that black drum age assignments were, on average, reasonably accurate (Fig. 3). The similar prebomb $\Delta^{14}C$ histories for these taxa reflect a common baseline value, whereas differences in post-1970 histories reflect geographic variability in water mixing times (Weidman and Jones, 1993). However, the differences in phase, magnitude, and postbomb decline among the various $\Delta^{14}C$ chronologies are both significant and meaningful and suggest that more accurate age interpretations may be possible. To improve ageing accuracy, however, three additional assumptions must be met: 1) the extracted otolith core must not be contaminated with material of more recent origin; 2) annulus interpretations and any associated errors must be made consistently across all ages examined; 3) the $^{14}C$ "reference" chronologies must be synchronous with that of the fish species under study. The first assumption has only been tested by Campana (1997) for haddock but was found to hold in part; intact age-1 otoliths and the extracted core of older fish from the same year class were characterized by similar $\Delta^{14}C$ values, although there was a tendency for more recent $\Delta^{14}C$ values to be found in the older cores, suggesting limited contamination. The second assumption is implicit in all ageing studies, because it implies that a given growth increment is interpreted in the same way, whether observed in a young or an old fish. However, the third assumption, that of synchronicity among all North Atlantic $^{14}C$ chronologies, is more interesting. This assumption has been tested and found to hold in all $^{14}C$

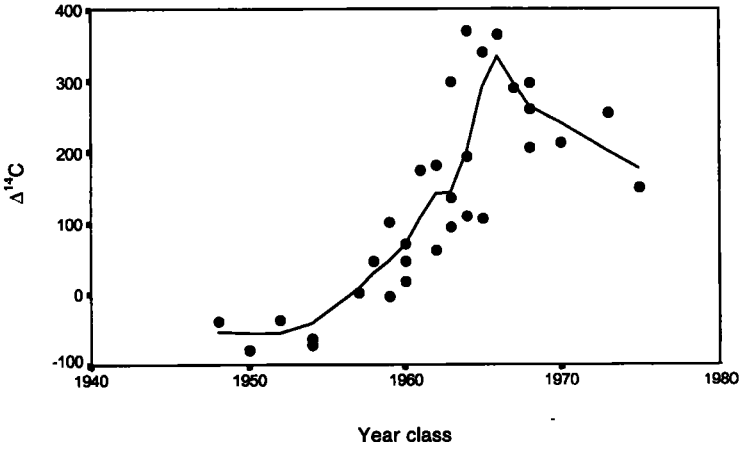


**Figure 2**

$\Delta^{14}C$ in the otolith cores of adult black drum in relation to the year class estimated from counts of presumed annuli. The $\Delta^{14}C$ values have been fitted with a LOWESS curve.

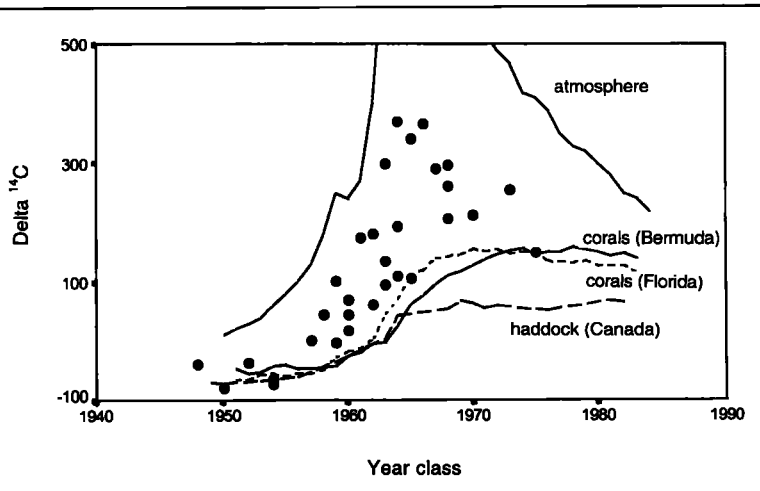


**Figure 3**

$\Delta^{14}C$ values in the otolith cores of adult black drum in relation to published $\Delta^{14}C$ chronologies for the atmosphere, corals from Bermuda and Florida, and haddock otoliths from eastern Canada. Whereas peak $\Delta^{14}C$ values differed among the time series, all shared a similar period of increasing values, with the source of the $^{14}C$ (the atmosphere) predating the coral and haddock time series by 2–4 years. The black drum chronology lies intermediate in phase and value to the atmospheric and marine carbonate time series, reflecting an estuarine origin. The two coral chronologies are drawn from Druffel (1989), and the chronologies for the atmosphere and haddock are from Nydal (1993) and Campana (1997), respectively.

otolith ageing studies reported to date, whether in the North Atlantic (Fig. 3) or in the South Pacific (Kalish, 1993, 1995a, 1995b; Kalish et al., 1996). However, the $\Delta^{14}C$ chronology reconstructed from the black drum otoliths was noticeably different; whereas prebomb $^{14}C$ values were comparable among all taxa, all postbomb year classes of black drum were significantly higher than those observed in any other open-ocean carbonate, and appeared to be phase-shifted 2–4 yr towards earlier years. This difference cannot be explained on the basis of ageing error, because the peak $\Delta^{14}C$ values in the otolith were as much as four times higher than those recorded in any year of any other open-ocean species. However, the apparent anomaly is fully explicable when the life history of the black drum is considered. The black drum is a marine fish but spends the first year of its life in rivers or estuaries (Richards, 1973). Thus the elemental and isotopic composition of the otolith core reflects the riverine or estuarine environment, not that of the open ocean. Because estuaries are shallow, well-mixed areas with strong riverine input, there is a rapid and relatively complete exchange of radiocarbon between the atmosphere and the water. As a result, the $^{14}C$ chronology of an estuary is a much closer reflection of the atmospheric chronology than of the marine chronology (Erlenkeuser, 1976; Spiker, 1980; Tanaka et al., 1986). Thus it is to be expected that the $\Delta^{14}C$ values of the black drum otolith core would lie intermediate, in magnitude and phase, to those of the atmosphere and the marine series, although closer to the former. This is indeed what was observed; thus black drum age assignments based on annular counts appear to be considerably more accurate than was originally thought, and not biased by 2–4 yr as would have been indicated by comparison with the marine carbonate chronologies. Nonetheless, the black drum measurements are the first demonstration of this phenomenon in fish and confirm Kalish's (1995b) suggestion that precise age calibrations against bomb radiocarbon signals must take into account the nature of the habitat in which the young fish has lived.

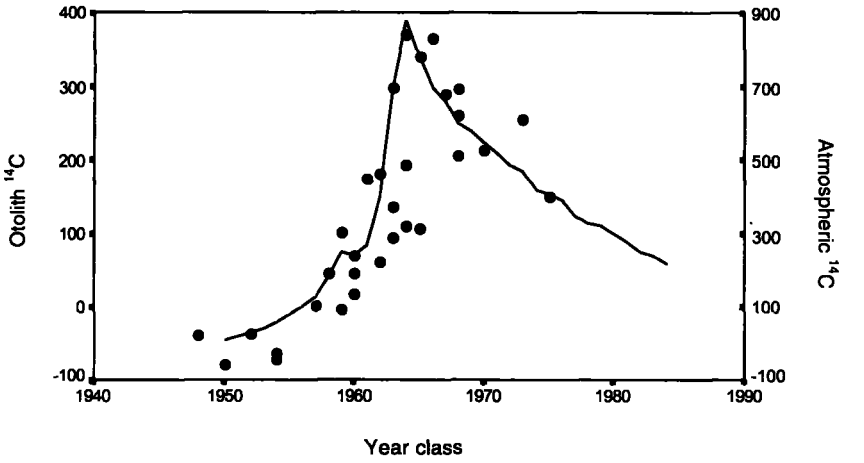


**Figure 4**

$\Delta^{14}C$ values in the otolith cores of adult black drum in relation to the published $\Delta^{14}C$ chronology for the atmosphere (data from Nydal [1993]). The data have been scaled so as to emphasize the similarities in the rate of increase and decline in the two time series. Otolith cores formed in riverine or estuarine waters would be expected to reflect more closely the atmospheric pattern of $\Delta^{14}C$ than that found in marine carbonates.

Whereas the the collection of black drum cores provided an unambiguous view of the period of $\Delta^{14}C$ increase, individual variability within any given year class was large and greatly exceeded the analytical error of the $^{14}C$ assays. Individual ageing errors undoubtedly contributed to this variability because even a 1-yr ageing error (in a 30-yr-old fish) would have resulted in a $\Delta^{14}C$ change of about 40 during the early 1960's. A similar argument applies to errors associated with the isolation of the otolith core from the surrounding, more recent, material. However, we believe that environmental heterogeneity and estuarine food sources were the dominant source of variability in the year-class-specific measurements. Variability in the isotopic composition of estuarine waters can be much larger than that of the open ocean: Spiker (1980) documented nearly twofold variability in the $\Delta^{14}C$ of total dissolved inorganic carbon (DIC) among locations in the Chesapeake Bay nursery area of black drum. The potential for variability due to diet in an estuary is also large. Because terrigenous carbon sources reflect atmospheric (enriched) $\Delta^{14}C$ in their isotopic composition and because terrigenous input and $\Delta^{14}C$ tend to decrease with increasing salinity, the isotopic composition of an animal's diet is bound to be more variable in an estuary than in a more homogeneous environment like the open ocean. Approximately half of the carbon incorporated into the shells of estuarine bivalves is derived from $^{14}C$-enriched metabolic (dietary) sources, as opposed to DIC, with the result that there is a high variability among individuals (Erlenkeuser, 1976; Tanaka et al., 1986). Similar arguments undoubtedly apply to fish otoliths because metabolic

carbon is thought to provide about one third of the carbon to the otoliths (Kalish, 1991; Schwarcz et al., 1998).

Although the $^{14}C$ assays reported here provided absolute age determinations for black drum between the ages of 15 and 42 yr, they were of greater value for their use in confirming the accuracy of the criteria generally used to interpret otolith annuli. Compared with otoliths of many other fish species, black drum otoliths form remarkably clear annuli; thus it would have been somewhat surprising if their interpretation had proven to be incorrect. Indeed, on the basis of marginal increment analysis, an annual rate of otolith annulus formation has already been demonstrated for black drum (Beckman et al., 1990), as well as for the closely related red drum, *Sciaenops ocellatus* (Murphy and Taylor, 1991). An annual rate of formation has also been reported for annuli in young black drum scales (Matlock et al., 1993), despite the fact that scale annuli indicate a maximum age of only 10 yr for black drum in Chesapeake Bay. In any event, confirmation of the frequency of annulus formation cannot be used to infer absolute age with the same accuracy as a direct measure of absolute age. In light of the statistical uncertainty around the correspondence between the black drum $^{14}C$ chronology and that expected of an estuary, it appears reasonable to conclude that otolith annuli can be used to determine the age of a sample of black drum with an accuracy of at least ±1–3 yr, corresponding to 3–7% for a collection of 40-yr-old fish. The confidence interval for an individual fish would be, of course, somewhat larger.

Although techniques such as the mark-recapture of chemically tagged fish can be used to validate the annual frequency of formation of growth increments in the otolith accurately, especially in young or abundant fishes, only radiocarbon from nuclear testing has the potential to confirm both annulus formation and absolute age in individual fish. The results of this study suggest that bomb radiocarbon can be used to determine the accuracy of an alternative ageing technique to within 1–3 yr. In addition, the presence of a strong phase coherence across a broad array of organisms and areas has excellent implications for the age determination of other North Atlantic fish species. The only constraints to this procedure are the relatively high costs (~$700–$1,000 per otolith) and the requirement for fish hatched during the 1958–65 period, so as to take advantage of the unique $^{14}C$ values during that period. Although the availability of suitable otolith samples may limit the applicability of this approach to specific stocks and species, use of bomb-derived radiocarbon as a dated otolith marker appears to provide one of the most accurate and logistically feasible methods for age validation that is currently available.

## Acknowledgments

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# Discerning patterns in patchy data: a categorical approach using gulf menhaden, *Brevoortia patronus*, bycatch

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**Abstract.**—We use two categorical techniques to explore patchy data on releasable bycatch in the U.S. Gulf of Mexico menhaden fishery. With no previous statistical studies on releasable bycatch, this paper serves both as an analysis of patchy data with categorical techniques and as a quantitative description of a biologically important portion of the menhaden bycatch.

By means of exploratory analyses with loglinear and logit models, we determined spatial and temporal patterns in bycatch of the menhaden fishery. Contrasts revealed that at fishing grounds east of the Mississippi River, the probability of observing fishing sets with high bycatch rates in spring and summer were greater than in the fall. Furthermore, spring bycatch rates were higher in fishing areas east of 89°W than in fishing areas west of 93°W.

Correspondence analysis indicated that the fate of the releasable bycatch could be classified into three major groupings. The first group, species associated with being gilled, was composed primarily of *Micropogonias undulatus, Trichiurus lepturus, Chloroscombrus chrysurus,* and *Cynoscion arenarius.* The second group consisted of species associated with being dead or disoriented; it included the requiem sharks *Caranx hippos* and *Sciaenops ocellatus.* The third group included those fish that were associated with being put into the hold, those kept by the crew, or those whose fate was unknown. These included *Arius felis, Bagre marinus,* and *Scomberomorus maculatus.*

Seasonal and spatial associations of bycatch species were also examined with correspondence analysis. From April through August, two distinct bycatch species assemblages were observed that separated the fishery at a longitude of 91°W. From September through October, a shift in the species assemblage indicated that the western region of the fishery (west of 93°W) appeared to have a assemblage distinct from the rest of the fishery.

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Statistical analyses of fisheries data often require consideration of the patchy distribution of aquatic organisms (e.g. Andrew and Pepperell, 1992). This is especially true with standard regression and ANOVA techniques because they rely on the assumptions of normality of residuals and homogeneous variances. Often, transformations of the response variable can be used to satisfy these assumptions (Underwood, 1981). However, in many instances suitable transformations cannot be found. In such cases, the use of standard regression and ANOVA techniques will result in gross violations of the model assumptions and affect the results of the analysis (Underwood, 1981). Where suitable transformations cannot be found, nonparametric techniques such as the Kruskal-Wallis one-way ANOVA or ANOVA on the ranked data have been used. As Underwood (1981) has noted, one of the implied assumptions of these methods, that of equal variances among treatments, is usually not satisfied when dealing with patchy data. A further problem with such techniques is that one cannot explore significant differences with the use of contrasts or multiple comparison tests, except with the Kruskal-Wallis one-way ANOVA. Therefore, when using these techniques, one is limited to the use of empirical methods to examine significant differences.

Studies on fisheries bycatch have used a variety of statistical methods. Andrew et al. (1995) used ANOVA with suitable transformations to evaluate the bycatch in an Australian stow-net fishery for school prawns, and Austin et al. (1994) used the Kruskal-Wallis one-way ANOVA to examine geographical differences in the bycatch of the Atlantic menhaden fishery. Hudson (1990), examining the shrimp and fish bycatch assemblages of the Canadian Eastern Arctic, used an intermediate linkage clustering algorithm to examine abundance patterns and species associations among different regions. More unique solutions have been pre-

sented by Richards et al. (1994), who proposed the use of a modified generalized logit model to carry out a categorical form of response surface analysis, allowing the estimation of transformation parameters on the explanatory variables along with other parameters. Perkins and Edwards (1996) have used mixture models, consisting of the negative binomial distribution with added zeros, as a solution to analyzing bycatch with many zero observations.

In this paper we use loglinear and logit models to examine patchy data with bycatch from the gulf menhaden, *Brevoortia patronus*, fishery. Menhaden bycatch can be classified into two groups: 1) bycatch that is pumped directly into the hold with the menhaden and that is termed "automatically retained bycatch"; and 2) all other bycatch that is termed "releasable bycatch." In this paper we analyze only releasable bycatch. With the exception of Christmas et al. (1960) and Condrey,[1] previous studies on menhaden bycatch have not taken releasable bycatch into account. Furthermore, all previous work has been qualitative in nature. Our examination of releasable bycatch, however, serves both as an analysis of patchy data with categorical techniques and as a quantitative description of a biologically important portion of the menhaden bycatch.

Species taken as bycatch may be caught because they are associated with the target species or simply because they were encountered on a random basis (Hall, 1996). An analysis of the structure of bycatch species assemblages associated with a fishery can provide valuable information for both management and ecological purposes. Hudson (1990), examining shrimp and fish bycatch assemblages in the Canadian Eastern Arctic, observed three associations that she proposed were related to the origin of the predominant water masses in the region. Harris and Poiner (1991) documented changes in the species composition of demersal fish fauna over a 20-year period in the Gulf of Carpentaria, Australia, and suggested that increases in the benthopelagic taxa over this period could be partially explained by discard of bycatch in the banana prawn fishery. Because little information on spatial and temporal associations for species assemblages of the menhaden fishery exists, we describe areal and temporal associations for these species, together with the fate of these species, as a first step in accruing such information. We have used correspondence analysis, a categorical form of ordination, to describe these association patterns.

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## The fishery

The U.S. Gulf of Mexico menhaden fishery has existed since the late 1800's (Nicholson, 1978) and is the largest fishery in tonnage in the northwestern Gulf of Mexico. Estimates of menhaden landings for the 1994 fishing season were approximately 0.7 million metric tons (t) (Leard et al., 1995). Although gulf menhaden is the primary clupeid sought, finescale menhaden, *B. gunteri*, yellowfin menhaden, *B. smithi*, and Atlantic thread herring, *Opisthonema oglinum*, are occasionally taken opportunistically (Leard et al., 1995).

Schools of menhaden are located visually by the senior crew aboard the fishing vessel or with the help of spotter planes. A purse seine, deployed from a pair of small (12.2-m) purse-seine boats, is used to encircle the school. Once the school is encircled, the bottom of the net is drawn up to hold the catch. The seine is then retrieved mechanically by each purse-seine boat until the fish are confined to a small section of the net. The catch is then pumped into the refrigerated hold of a larger (43 to 61 m) carrier vessel. The number of times the purse net is set each day depends on the availability and size of schools. Schools contain from 3 to 100 t of menhaden (Leard et al., 1995). Once the hold of a vessel is full, or a trip is otherwise complete, the menhaden are transported to one of the processing plants located from Moss Point, MS, to Cameron, LA. Although the fishing area extends from Apalachicola, FL, to Freeport, TX, more than 86% of the menhaden caught from 1990 to 1994 were taken off Louisiana (Leard et al., 1995).

## Materials and methods

### Loglinear and logit models

As reviewed in Agresti (1990) and Freeman (1987), loglinear and logit models are special cases of the generalized linear models introduced by Nelder and Wedderburn (1972). Agresti (1990) summarizes a generalized linear model as "a linear model for a transformed mean of a variable having a distribution in the natural exponential family."

Loglinear models describe association patterns among categorical variables. With this approach, cell counts in a contingency table are modeled in terms of association among the variables. Loglinear models may be viewed as analogous to correlation analysis where cell counts in a loglinear contingency table are treated as independent Poisson variables.

In a $I \times J$ table, where $N = IJ$ cells consisting of $n$ multinomial samples, let $n_k$ denote the count of the

$k^{th}$ cell, and let $m_k = E(n_k)$ represent the expected value where $k = 1.....N$. The probabilities $\{\pi_{ij}\}$ for that multinomial distribution form the joint distribution of two categorical responses. These two responses are statistically independent when $\pi_{ij} = \pi_{i+}\,\pi_{+j}$ for all $i$ and $j$.

If there is a dependence between the two variables, then all expected values of each cell ($m_{ij}$) are > 0. The loglinear model for this two-way table can be written as

$$\log m_{ij} = \mu + \lambda_i^x + \lambda_j^y + \lambda_{ij}^{xy},$$

where $\mu = \Sigma_i \Sigma_j \log m_{ij} / IJ$;
$\lambda_i^x = \Sigma_j \log m_{ij} / J - \mu$;
$\lambda_j^y = \Sigma_i \log m_{ij} / I - \mu$; and
$\lambda_{ij}^{xy} = \log m_{ij} - \lambda_i^x - \lambda_j^y + \mu$.

This model perfectly describes any set of positive expected frequencies and is referred to as the saturated model. The right-hand side of this equation resembles the formula for the cell-means ANOVA. The parameters $\{\lambda_i^x\}$ and $\{\lambda_j^y\}$ are deviations about a mean and $\Sigma_i \lambda_{ij}^{xy} = \Sigma_j \lambda_{ij}^{xy} = \Sigma_i \lambda_i^x = \Sigma_j \lambda_j^y = 0$. This model can also be described in the notation form as $[XY]$.

A saturated loglinear model always expresses a given table of categorical data perfectly. This model has the maximum achievable log likelihood because it is the most general model, with as many parameters as observations. However, it is possible that a simpler model may provide a fit as statistically good as that of the saturated model. How well this model fits is represented by the scaled deviance, a function of twice the difference in the log likelihoods of the saturated model and the simpler model. In addition to testing the fit of a model, one can use the deviance to diagnose lack of fit through residual analysis.

For example, consider a three-dimensional saturated model with variables $X$, $Y$, and $Z$. For this model $[XYZ]$, $\log m_{ijk} = \mu + \lambda_i^x + \lambda_j^y + \lambda_k^z + \lambda_{ij}^{xy} + \lambda_{ik}^{xz} + \lambda_{jk}^{yz} + \lambda_{ijk}^{xyz}$. When $\lambda_{ijk}^{xyz} = 0$, there is no three-factor interaction, and the association between two variables is identical at each level of the third variable and reduces to the loglinear model $[XY\,XZ\,YZ]$. Further, if $\lambda_{ijk}^{xyz} = 0$ and $\lambda_{jk}^{yz} = 0$, then for any given level of $X$, $Y$ and $Z$ are conditionally independent $[XY\,XZ]$. Similarly if $\lambda_{ijk}^{xyz} = 0$, $\lambda_{jk}^{yz} = 0$ and $\lambda_{ik}^{xz} = 0$, then $Z$ is jointly independent of $X$ and $Y$ $[XY\,Z]$. Finally if $\lambda_{ijk}^{xyz} = 0$, $\lambda_{jk}^{yz} = 0$, $\lambda_{ik}^{xz} = 0$, and $\lambda_{ij}^{xy} = 0$, then $X$, $Y$, and $Z$ are mutually independent $[X\,Y\,Z]$. With these criteria and beginning with a saturated model, we used a stepwise model selection procedure with deviance in the form of the $G^2$ test statistic to find a simpler model that fits as well as the saturated model. This simpler model would enable one to explore multidimensional tables to find simpler representations of the information contained therein.

**Table 1**

Hypothetical example used to explain odds ratios and conditional probabilities. $\pi_{j1|i}$ is the conditional probability of observing bycatch given a particular area. $\pi_{j2|i}$ is the conditional probability of observing no bycatch given a particular area.

| | Bycatch | | | Conditional probabilities | |
|---|---|---|---|---|---|
| | Presence ($j_1$) | Absence ($j_2$) | Total sets | $\pi_{j1\|i}$ | $\pi_{j2\|i}$ |
| Area A ($i_1$) | 4 | 6 | 10 | 0.40 | 0.60 |
| Area B ($i_2$) | 2 | 4 | 6 | 0.33 | 0.67 |
| Total | 6 | 10 | 16 | | |

Another advantage of loglinear models is that when one of the variables can be modeled as a response, and the others as explanatory variables, certain loglinear models are equivalent to logit models with categorical explanatory variables. Such logit models enable us to study the problem of interest in a manner analogous to ANOVA.

Many categorical response variables have only two categories. The response can be classified either as a success or a failure. The Bernoulli distribution, which belongs to the natural exponential family, forms the basis of modeling the logit model. For such a dichotomous variable, the probability of observing response 0 can be defined as $P(Y=0) = \pi$, and the probability of observing response 1, as $P(Y=1) = 1 - \pi$. The link function for this model, $\log \pi_i / (1-\pi_i)$, known as the logit, is equivalent to the log odds.

Consider the following example, where we examine the presence or absence of bycatch in two areas. In this example (Table 1), the 2 × 2 table has rows $i_1$(*area* 1), and $i_2$ (*area* 2) and columns $j_1$ (*presence of bycatch*) and $j_2$ (*absence of bycatch*). The counts in the cells of the table are the number of units of effort (individual sets) observed in each category.

In this case, the odds, $\Omega_{i1}$, of observing $j_1$ (*presence of bycatch*) given you are in category $i_1$ (*area* 1) is computed as the ratio of the conditional probabilities of observing a set with bycatch to that of observing a set with no bycatch in area 1:

$$\left\{\pi_{j1|i1}/\pi_{j2|i1}\right\} \text{ is } 0.4/0.6 = 0.67.$$

Similarly, the odds, $\Omega_{i2}$, of observing $j_1$(*presence of bycatch*) given you are in category $i_2$ (*area* 2) is computed as the ratio of the conditional probabilities of

observing a set with bycatch to that of observing a set with no bycatch in area 2:

$$\left\{\pi_{j1|i2}/\pi_{j2|i2}\right\} \text{ is } 0.33/0.67 = 0.5.$$

The odds ratio, θ, is computed as

$$\Omega_{i1}/\Omega_{i2} \text{ is } 0.67/0.5 = 1.34.$$

Thus, the odds of observing response $j_1$ *(presence of bycatch)* is 1.34 times more likely for row $i_1$ *(area 1)* than for row $i_2$ *(area 2)*. An odds ratio of 1 indicates that you are equally likely to observe response $j_1$*(presence of bycatch)* for row $i_1$ *(area 1)* and row $i_2$ *(area 2)* and thus indicates independence between the rows and columns of the table.

The logit model has two forms. One form occurs where the explanatory variables are continuous and is the logistic regression model. The second occurs where the explanatory variables are categorical. The logistic regression model is analogous to a regression model, whereas the second type is analogous to an ANOVA model.

For the previous example, a model with a single categorical explanatory factor (area), the logit form of the model is

$$\log(\pi_{j1|i}/\pi_{j2|i}) = \alpha + \beta_i^{Area},$$

where $\alpha$ = the mean of the logits; and
$\beta_i^{Area}$ = the deviation from the mean for row $i$.

$\beta_i$ describes the effects of the factor on the response. For this model the higher $\beta_i$ becomes, the higher the logit in row $i$, and the higher the value of $\pi_{j1|i}$. The constraints on this model are $\Sigma\ \beta_i = 0$. In this case the right-hand side of the equation resembles the cell-means model of a one-way ANOVA. This logit model would be equivalent to $\log(m_{ij1}) - \log(m_{ij2}) = 2\lambda_i^{Area} + 2\lambda_{j1}^{Bycatch} + 2\lambda_{ij1}^{AreaBycatch}$ in loglinear form.

## Bycatch sampling and data set description

Bycatch from the gulf menhaden fishery was sampled April through October 1995 by two to three onboard samplers on a total of twenty-seven week-long trips aboard vessels operating from menhaden processing plants in the U.S. Gulf of Mexico. To maximize coverage of the Gulf, samplers boarded vessels from ports in the western, central, and eastern regions in a given week as often as possible. During each sampling trip, all sets made by the vessel were alternatively sampled, either for releasable bycatch or automatically retained bycatch. For all sets sampled, the presence of dolphins in the vicinity was also noted by the observers. In addition, the boat captains visually estimated catch in standard menhaden (1,000 standard menhaden [~305 kg]) and recorded the latitude and longitude of a set location. The location was used to identify in which National Marine Fisheries Service (NMFS) statistical zone (Fig. 1) the set was made (after Kutkuhn, 1962).

To collect releasable bycatch data, samplers observed the purse seine from the time it was brought alongside the carrier ship and throughout the pumping procedure, until the net was emptied and cleaned. During this time, the species, number, and fate of the releasable bycatch were recorded. The seven categories of bycatch fate were as follows: gilled in the net (gilled); kept by the crew for consumption (kept); released with no apparent harm (released healthy); released seriously injured or dead (released dead); released after being bruised or after being kept in the set for a long time (released disoriented); collected by the crew from the net or deck and put into the hold (caught and put in hold); and observed in the net but fate unknown (unknown).

## Statistical analysis

**Preliminary analysis** For the variables bycatch number, bycatch percentage, and estimated catch, we calculated a series of commonly used statistical descriptors, namely the mean, standard deviation, 95% confidence intervals, median, skewness, and kurtosis. In addition, we also calculated the winsorized mean and its standard deviation.

We initially attempted to examine spatial and temporal patterns in the bycatch with a two-way ANOVA model. For the analysis, data were classified into season (S) consisting of three groups: 1) spring (April through June), 2) summer (July through August), and 3) fall (September through October). Adjacent NMFS zones (Fig. 1) were combined to form four area (A) groups: 11–12, 13–14, 15–16, and 17–18.

Bycatch patterns were examined with two response variables: 1) bycatch numbers; and 2) bycatch percentage ([bycatch number/total catch] × 100). For each of these two response variables, spatial and temporal patterns were examined by using the ANOVA model with season, area, and their interaction term as independent variables. Because we anticipated that neither model would satisfy the model assumptions of normality of residuals and homogeneous variances, we also examined the models by using the log and square-root transformations for both response variables. In addition we also used 2 arcsin $\sqrt{}$ (bycatch/menhaden catch) suggested by Neter et al. (1990) for transformation of proportions. All seven

models were examined to determine if model assumptions were met.

**Spatial and temporal patterns in bycatch** For our analysis using loglinear and logit models with categorical explanatory variables, we used a four-way contingency table with a unit of effort (the set) as the count. Our main interest was 1) to examine the spatial and temporal patterns in bycatch and 2) to determine if the presence of dolphins in the vicinity when the set was made might be an indicator of bycatch patterns.

**Exploratory analysis with loglinear and logit models** To examine bycatch as a response of interest with categorical models, a new dichotomous categorical variable, bycatch, based on the median bycatch percentage, was created. Each set was classified either as high bycatch if the bycatch rate of the set was greater than the median value of all sets or as low bycatch if the bycatch rate of the set was less than or equal to the median bycatch of all the sets. We used the median rate because it is a robust measure of central tendency. In deciding on possible criteria for defining this variable, more extreme conditions, such as bycatch rates greater than the 75$^{th}$ percentile, were considered. However, by choosing more extreme values, we increased the number of sparse cells and thus affected the validity of the $G^2$ test statistic.

In analyzing contingency tables, it is necessary that the number of cell counts with zero frequencies be low (a minimum expected value of 1 is satisfactory as long as <20% of cells have counts of 5 or less) for the test statistic to be valid (Agresti, 1990). To reduce the number of cells with zero frequencies, months and zones were combined, generating two new variables, season and area, corresponding to those used in the ANOVA. The presence of dolphins was used as a dichotomous variable, dolphins ($D$).

To identify the most appropriate and simplest loglinear model for the data using the variables season, area, bycatch, and dolphins, we employed a stepwise backward solution procedure commencing with the saturated loglinear model (Agresti, 1990). Here the saturated model

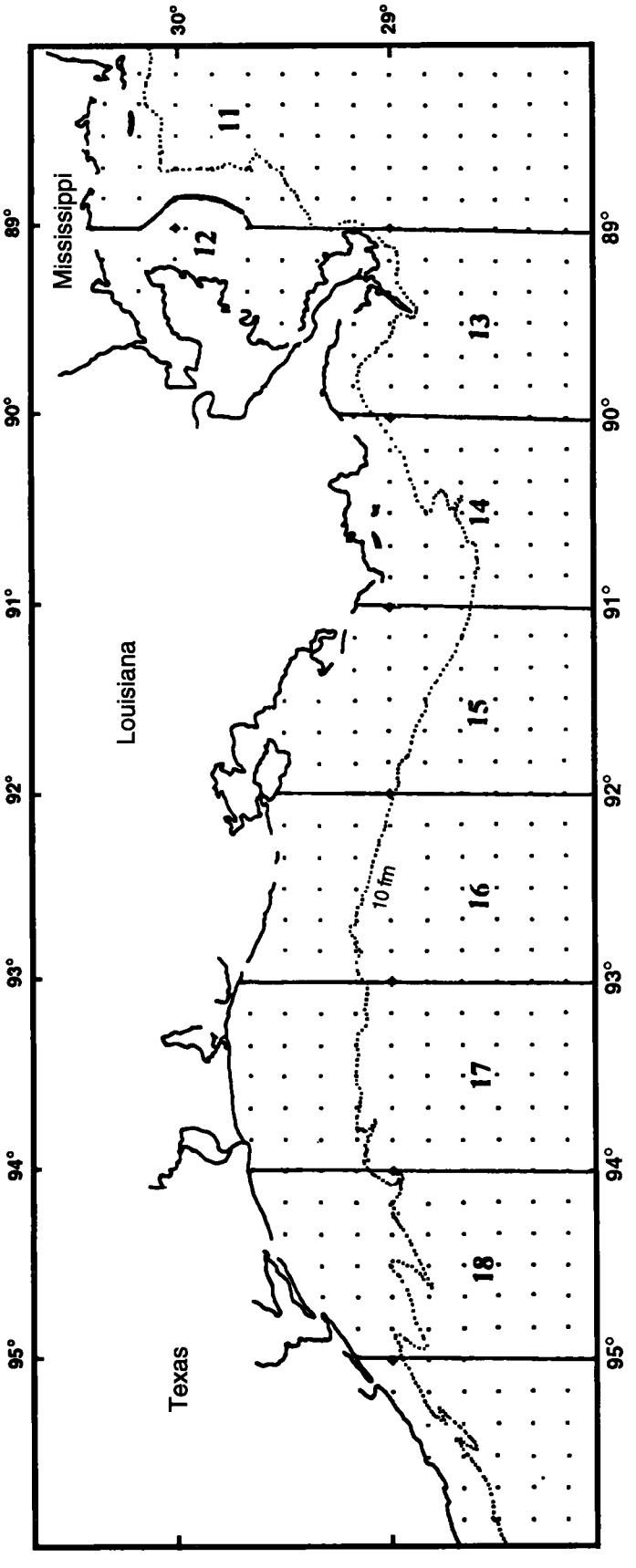


**Figure 1**
Map encompassing the extent of the U.S. gulf menhaden fishery from the Texas to Alabama coasts. The eight fishing zones numbered 11–18 are from NMFS (after Kutkuhn, 1962).

is denoted as [*SABD*] were *S* stands for season, *A* for area, *B* for bycatch, and *D* for dolphins, and the model includes all possible interactions up to and including the four-way interaction. Because the saturated model would naturally provide the best fit, we were interested in determining if a simpler model could be found that would also satisfy the criteria of a logit model with bycatch as the response variable. The standardized residuals of the resulting model were then examined to ensure that lack of fit was not a problem.

**Contrasts** We anticipated that we would have significant interaction terms in our analyses that would require detailed examination of interactions. For the logit form of the selected model, we constructed a series of contrasts that might help to explain the nature of these potential interactions. The contrasts of interest had two general forms:

1 Given a specific area, are the odds of observing a set with high bycatch the same between any two different seasons. This results in three unique contrasts for each area (spring vs. summer, spring vs. fall, summer vs. fall) and a total of 12 contrasts.

Let $F_{ij}$ be the logit of high bycatch for season $i$ and area $j$ and let $F_{hj}$ be the logit of high bycatch for season $h$ and area $j$.

The hypotheses being tested were

$$H_0: F_{ij} - F_{hj} = 0,$$

where $F_{ij} = \alpha + \beta_i^S + \beta_j^A + \beta_{ij}^{SA}$;
$F_{hj} = \alpha + \beta_h^S + \beta_j^A + \beta_{hj}^{SA}$; and
$h$ and $i$ = spring, summer, and fall, such that $h \neq i$ for each $j$, and $j$ = area 11–12, area 13–14, area 15–16, and area 17–18.

2 Given a specific season, are the odds of observing a set with high bycatch the same between any two different areas. This results in six unique contrasts for a given season and a total of 18 contrasts (11–12 vs. 13–14, 11–12 vs. 15–16, 11–12 vs. 17–18, ..... ,15–16 vs. 17–18).

Let $F_{ij}$ be the logit of high bycatch for season $i$ and area $j$ and let $F_{ik}$ be the logit of high bycatch for season $i$ and area $k$.

The hypotheses being tested were

$$H_0: F_{ij} - F_{ik} = 0,$$

where $F_{ij} = \alpha + \beta_i^S + \beta_j^A + \beta_{ij}^{SA}$;
$F_{ik} = \alpha + \beta_i^S + \beta_k^A + \beta_{ik}^{SA}$; and
$j$ and $k$ = area 11–12, area 13–14, area 15–16, and area 17–18, such that $j \neq k$ for each $i$, where $i$ = spring, summer, and fall.

Because 30 contrasts were performed, the type-I error level of 0.10 was adjusted by using the Bonferroni technique, and only *P*-values less than 0.0033 were considered significant. The estimated odds ratios for the conditions associated with the hypotheses were calculated from the parameter estimates given by the analysis.

**Bycatch species associations** To examine the association between species and fates of the releasable bycatch, we used correspondence analysis on a species-by-fate table for all seasons and areas combined. Area and species associations of the releasable bycatch were also examined for each of the three seasons with correspondence analysis on species-by-area tables.

For all correspondence analyses we defined two groups of species. The first group, consisting of those species that were common in terms of number and occurrence, was used in the main table. Releasable bycatch species falling into this group had a minimum of 230 individuals and were found in at least 30% of the sets. The second group of species consisted of releasable bycatch that were less common; these were species for which a minimum of 30 individuals were observed, which occurred in at least 4% of the sets, and which did not meet our criteria for well represented species. These species were included as supplementary variables in our analysis (Greenacre, 1984). Supplementary variables are represented as points in the joint row and column space but are not used in determining the locations of the active rows and columns of the table. Species included in the main and supplementary table accounted for 97% of the total number of organisms observed during the study period. Species that did not meet these criteria were not used in the analyses.

## Results

### Preliminary analysis

A total of 15,579 bycatch organisms representing 62 species or species groups were observed as releasable bycatch in 257 sets. The estimated catch of standard menhaden per set ranged from 5,000 to 500,000 with a median, mean, and standard deviation of 50,000, 67,000, and 61,000 respectively. Skewness and kurtosis values of 2.5 and 10.7 indicated that the distribution of the estimated menhaden catch was positively skewed (Fig. 2).

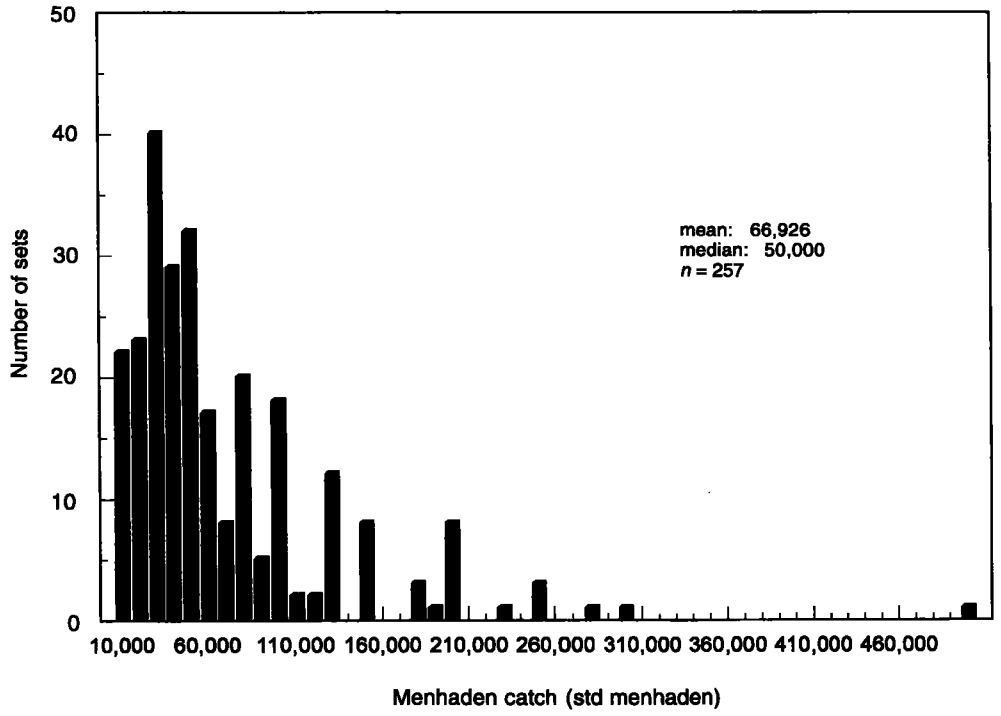


**Figure 2**

Distribution of menhaden catch sampled during the 1995 gulf menhaden fishing season. std = standard (1,000 standard menhaden ~ 305 kg).

The number of bycatch observed in each set ranged from 0 to 1,600 organisms, with a median, mean, and standard deviation of 15, 61, and 153 respectively. The winsorized mean and its standard deviation values were 53 and 6.9 respectively. The 95% confidence interval of the mean was between 41.8 and 79.3. The distribution of bycatch organisms was strongly positively skewed (5.9) and peaked sharply with a Kurtosis value of 47.2 (Fig. 3).

The bycatch percentage ranged from 0% to 4% with a median, mean, and standard deviation of 0.033%, 0.168%, and 0.48 respectively. The winsorized mean bycatch percentage and its standard deviation were 0.14% and 0.02, respectively. The 95% confidence interval of the mean was between 0.11% and 0.22%. The distribution of the bycatch percentage was also found to be positively skewed and strongly peaked, with skewness and kurtosis values of 5.4 and 32.7 respectively (Fig. 4).

Analysis of variance with bycatch, bycatch percentage, and their respective transformations, together with the arcsine transformation, did not meet model assumptions. In all cases the modified Levene's test indicated that the variances were nonhomogeneous, and both the residual plots and Shapiro-Wilk test indicated that the assumption of normality of residuals were not met. For example, for the response log (bycatch percentage + 1), the residuals of the model were not normally distributed (Shapiro-Wilk $W$=0.678, $P<W$=0.0001), and the residual plot indicated nonhomogenous variances. Furthermore, a modified Levine's test indicated that the variances were nonhomogeneous ($F$=6.21, df=11, df-error=245, $P>F$=0.0001). These characteristics suggest that the model assumptions were grossly violated and that ANOVA may not be an appropriate form of analysis in this case.

## Spatial and temporal patterns in bycatch

**Exploratory analysis using loglinear models** With the backward selection procedure, loglinear models [SAB SAD DB] and [SAB SAD] (as defined in Table 2) satisfied the criteria for a logit model and had good fit (Table 2). The simplest of these models, [SAB SAD], was selected; this loglinear model corresponds to the logit model with categorical explanatory variables of the form

$$\log\frac{\pi_{highlik}}{\pi_{lowlik}} = \alpha + \beta_i^A + \beta_k^S + \beta_{ik}^{AS}, \quad (1)$$

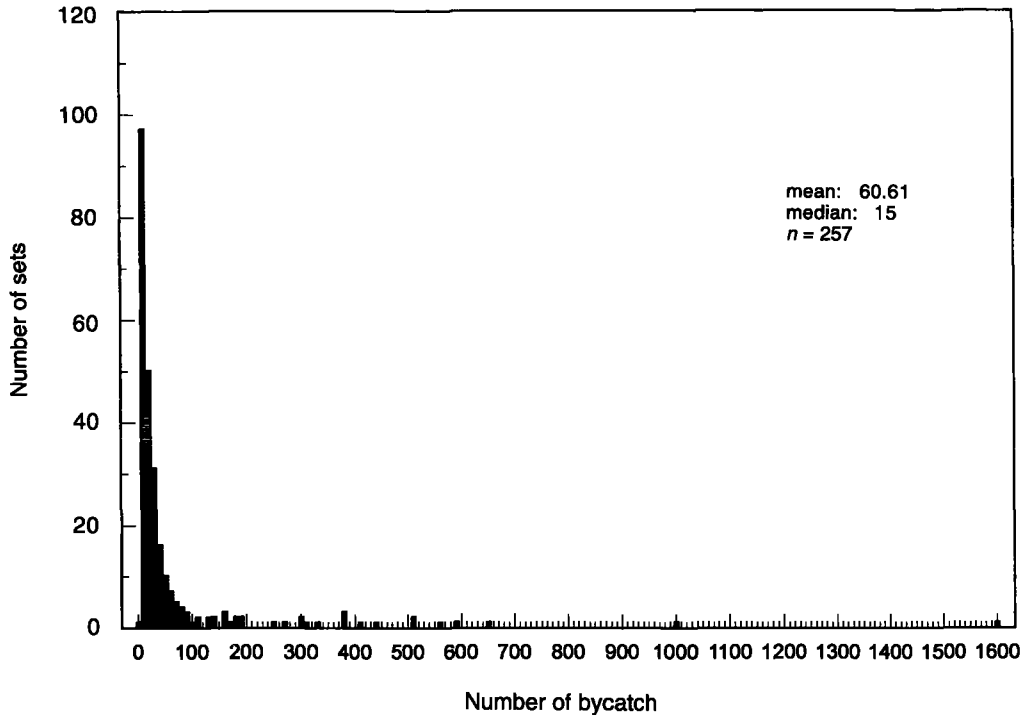


**Figure 3**

Distribution of bycatch sampled during the 1995 gulf menhaden fishing season.

**Table 2**

Summary statistics of loglinear models examined through the stepwise selection procedure. Models with fits as good as the saturated model are marked ns. (A=area, B=bycatch, D=dolphins, S=season). Models are presented hierarchically from most complex to simplest.

| Loglinear model | df | $G^2$ | $P$-value |
|---|---|---|---|
| Model without the four-way interaction term | | | |
| ADB SDB SAB SAD | 6 | 11.64 | 0.0706 |
| Selected models with 3 three-way interaction terms | | | |
| ADB SDB SAB | 12 | 26.58 | 0.0089 |
| ADB SDB SAD | 12 | 27.62 | 0.0063 |
| SDB SAB SAD$^{ns}$ | 9 | 13.41 | 0.1449 |
| SAB SAD ADB | 14 | 27.90 | 0.0147 |
| Selected models with 2 three-way and 1 two-way interaction terms | | | |
| SDB SAB DA | 15 | 29.38 | 0.0144 |
| SAB SAD DB$^{ns}$ | 11 | 15.65 | 0.1547 |
| Selected models with 2 three-way interaction terms | | | |
| SAB SAD$^{ns}$ | 12 | 17.82 | 0.1213 |
| SDB SAB | 18 | 45.83 | 0.0003 |
| Selected models with 1 three-way and 2 two-way interaction terms | | | |
| SAB SD AD | 18 | 34.89 | 0.0097 |
| SAD SB AB | 18 | 34.30 | 0.0116 |

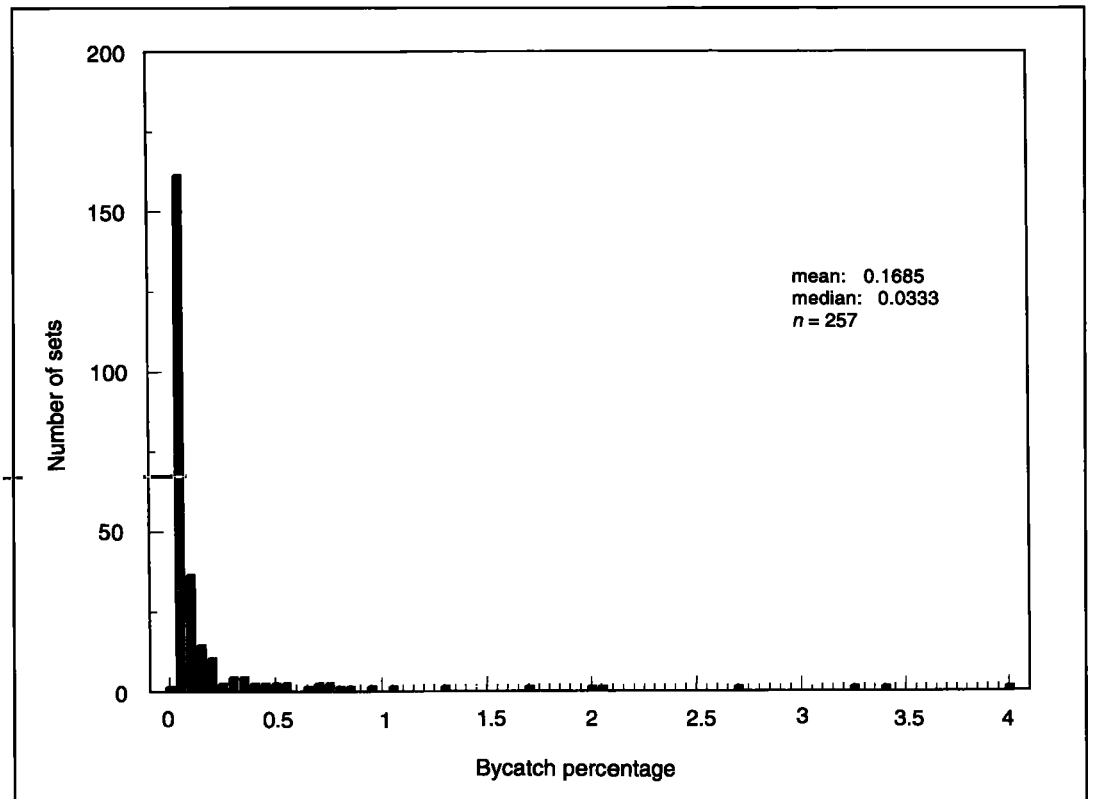


**Figure 4**

Distribution of the bycatch percentage in fishing sets sampled during the 1995 gulf menhaden fishing season.

where $\pi_{high\,|\,ik}$ = the probability of observing a set with high bycatch given area $i$ and season $k$; and

$\pi_{low\,|\,ik}$ = the probability of observing a set with low bycatch given area $i$ and season $k$.

This model, in loglinear and logit forms, had a $G^2$=17.82, with 12 df and a $P$-value=0.1213. Examination of the standardized residuals of the logit form revealed that none of the residuals had an absolute value greater than 1.45 and thus showed no evidence of lack of fit.

For the logit model, there was a significant interaction between season and area (Wald chi-square ($\chi^2$)=14.65, df=6, $P$=0.0232). This interaction is reflected in the plot of probabilities of high (greater than 0.033%) bycatch for the area-season combinations (Fig. 5).

**Contrasts** The contrasts of the odds of high bycatch between seasons for a given area indicate that the hypothesis of spring and summer seasons being the same for all four areas could not be rejected. Wald $\chi^2$ values are presented in Table 3. The contrasts of the spring and fall seasons suggest that the only signifi-

**Table 3**

Estimated odds ratios and Wald chi-square ($\chi^2$) values of contrasts of observing high bycatch between seasons, given a set was made in a certain area. For example, the odds of observing high bycatch is 11.761 times greater during the spring season than during the fall season for area 11–12. * indicates a ratio significantly different from 1. Wald $\chi^2$ values are in parenthesis. For all contrasts, Wald $\chi^2$ df = 1.

| Season | Area | Spring | | Fall | |
|---|---|---|---|---|---|
| Fall | 11–12 | 11.761* | (10.03) | | |
| Summer | 11–12 | 1.142 | (0.05) | 0.097* | (9.25) |
| Fall | 13–14 | 4.444 | (2.24) | | |
| Summer | 13–14 | 0.555 | (0.19) | 0.125 | (2.41) |
| Fall | 15–16 | 0.699 | (0.48) | | |
| Summer | 15–16 | 0.414 | (4.29) | 0.592 | (0.97) |
| Fall | 17–18 | 0.312 | (2.11) | | |
| Summer | 17–18 | 0.218 | (2.47) | 0.899 | (0.02) |

cant differences between these two seasons existed for area 11–12 (Wald $\chi^2$=10.03, df=1, $P>\chi^2$=0.0015). When the summer and fall seasons were contrasted, a significant difference between seasons was observed only for area 11–12 (Wald $\chi^2$=9.25, df=1, $P>\chi^2$=0.0024).

For contrasts of the odds of high bycatch between areas for a given season, significant differences between areas 11–12 and 17–18 in the spring season were observed (Wald $\chi^2$=9.29, df=1, $P>\chi^2$=0.0023). All other contrasts between areas for the spring, summer, and fall seasons were not significant. Wald $\chi^2$ values for these contrasts are presented in Table 4.

The estimated odds ratios for the conditions associated with the hypotheses are also given in Tables 3 and 4. Only estimated odds ratios of contrasts for the rejected hypotheses of no difference are examined in detail.

If a fishing boat was in area 11–12, the odds of observing a set with high bycatch are about 11.8 times higher if a boat was fishing in the spring rather than the fall. Also, if a fishing boat was in area 11–12, the odds of observing a set with high bycatch are about 0.1 times (or approximately 10.3 times lower) in the fall than in the summer. It appears that for area 11–12, the odds of observing a set with high bycatch in the fall are significantly lower than in the spring or summer.

The third significant contrast indicated that for a vessel fishing in the spring, the odds of observing a set with high bycatch are about 10.8 times higher in area 11–12 than in area 17–18.

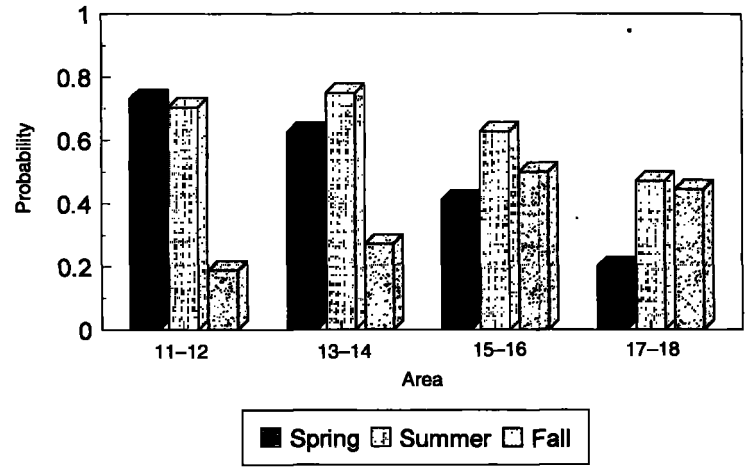


**Figure 5**

Probabilities of observing a set with high bycatch (> 0.033%) for the season-area combinations.

**Table 4**

Estimated odds ratios and Wald chi-square ($\chi^2$) values for contrasts (in parentheses) for observing high bycatch between areas, given a set was made in a certain season. For example, the odds of observing high bycatch are 1.628 times greater in area 11–12 than in area 13–14. * indicates a ratio significantly different from 1. Wald $\chi^2$ values are in parenthesis. For all contrasts, $\chi^2$ df=1.

| | | Area | | |
|---|---|---|---|---|
| Season | Area | 11–12 | 13–14 | 15–16 |
| Spring | | | | |
| | 13–14 | 1.628 (0.33) | | |
| | 15–16 | 3.877 (6.64) | 2.380 (1.23) | |
| | 17–18 | 10.857* (9.29) | 6.666 (3.79) | 2.799 (2.13) |
| Summer | | | | |
| | 13–14 | 0.791 (0.04) | | |
| | 15–16 | 1.407 (0.42) | 1.777 (0.23) | |
| | 17–18 | 2.671 (2.33) | 3.374 (0.94) | 1.898 (1.22) |
| Fall | | | | |
| | 13–14 | 0.615 (0.27) | | |
| | 15–16 | 0.230 (3.63) | 0.375 (1.50) | |
| | 17–18 | 0.288 (2.43) | 0.468 (0.84) | 1.250 (0.12) |

**Refining the final model** We were interested, on the basis of our contrasts, in determining if a model with simpler dichotomous classes for areas and seasons would provide as good a statistical fit as this "full model" (Eq. 1). We compared three potential models that had one or both of these variables with reduced classes against the full model (Table 5). For these models we classified area into two groups: 1) east of the Mississippi River; and 2) west of the Mississippi River. Season was also classified into two groups; 1) early—sets sampled April through August; and 2) late—sets sampled September through October.

All three reduced models provided a fit as good as that of our full model (Table 5); therefore we chose the model that had reduced classes for season and area because it was the simplest. Four contrasts of interest were examined:

1 Test for seasonal differences in the odds of observing a set with high bycatch given the set was sampled east of the Mississippi River;

2 Test for seasonal differences in the odds of observing a set with high bycatch given the set was sampled west of the Mississippi River;
3 Test for area differences in the odds of observing a set with high bycatch given the set was sampled in the early season; and
4 Test for area differences in the odds of observing a set with high bycatch given the set was sampled in the late season.

The contrasts were written similarly to those for the "full model." For the four contrasts, we used an $\alpha$ level of 0.025 as significant.

Of the four contrasts, two were significant. The first indicated that in areas east of the river, the odds of observing a set with high bycatch was significantly different between sets sampled in the early season and sets sampled in the late season (Wald $\chi^2$=11.41, df=1, $P>\chi^2$= 0.0007). The odds of observing a set with high bycatch east of the river in the early season was 11 times greater than the odds of observing a set with high bycatch in the late season. The second significant contrast indicated that for sets sampled in the early season, the odds of observing a set with high bycatch east of the river was significantly different from the odds of observing a set with high bycatch west of the river (Wald $\chi^2$=7.99, df=1, $P>\chi^2$=0.0047). In the early season, the odds of observing a set with high bycatch east of the river was 2.7 times greater than observing a set with high bycatch west of the river during the same period.

**Table 5**

Comparison of reduced logit models with the full model. Diff = difference between full model and reduced model.

| | Likelihood ratio statistics | | | Model comparisons | | |
|---|---|---|---|---|---|---|
| | df | $G^2$ | $P > G^2$ | Diff (df) | Diff ($G^2$) | $P$-Value |
| Full model<br>Season= Apr–Jun, Jul–Aug, Sep–Oct<br>Area = 11–12, 13–14, 15–16, 17–18 | 12 | 17.82 | 0.1213 | | | |
| Reduced model I<br>Season=spring, summer, fall<br>Area = 11–12, 13–18 | 6 | 9.76 | 0.1352 | 6 | 8.06 | 0.237 |
| Reduced model II<br>Season=Apr–Aug, Sep–Oct<br>Area = 11–12, 13–14, 15–16, 17–18 | 8 | 9.99 | 0.2659 | 4 | 7.83 | 0.098 |
| Reduced model III<br>Season= Apr–Aug, Sep–Oct<br>Area = 11–12, 13–18 | 4 | 7.54 | 0.1100 | 8 | 10.28 | 0.246 |

## Bycatch species associations

Of the 62 species groups observed, 20 occurred in two or fewer sets. The most frequently occurring species were Atlantic cutlassfish, *Trichiurus lepturus* (44% of sets), Atlantic croaker, *Micropogonias undulatus* (38% of sets), Spanish mackerel, *Scomberomorus maculatus* (36% of sets), sand seatrout, *Cynoscion arenarius* (35% of sets), and gafftopsail catfish, *Bagre marinus* (34% of sets). In terms of total abundance (Table 6), Atlantic croaker, sand seatrout, and Atlantic bumper, *Chloroscombrus chrysurus*, accounted for 71% of the total releasable bycatch.

Species included in the main table were Atlantic croaker, sand seatrout, crevalle jack, *Caranx hippos*, gafftopsail catfish, Spanish mackerel, and Atlantic cutlassfish (Table 6 ). Species included as supplementary variables were striped mullet *Mugil cephalus*, unidentified requiem sharks, gulf butterfish, *Peprilus burti*, cownose ray, *Rhinoptera bonasus*, spotted seatrout, *Cynoscion nebulosus*, Atlantic bumper, blacktip shark, *Carcharhinus limbatus*, red drum, *Sciaenops ocellatus*, unidentified penaeid shrimp, hardhead catfish, *Arius felis*, brown shrimp, *Panaeus aztecus*, cabbage head jellyfish, *Stomolophus meleagris*, bull shark, *Carcharhinus leucas*, and unidentified tonguefish (Soleidae) (Table 6).

**The fate of releasable bycatch** Correspondence analysis on the fate-by-species table for the entire fishing season indicated that the first two axes explained 97% of the total inertia (conceptually similar to variance) and offered a good representation of the fate-species associations. From the two-dimensional plot (Fig. 6) we discerned three major and one minor groupings.

Species primarily associated with being released dead or disoriented were unidentified requiem sharks, red drum, crevalle jack, and bull sharks. Species secondarily associated with being released dead or disoriented were cownose rays and blacktip sharks. These last two species were primarily associated with being released healthy and appeared to form their own minor grouping.

**Table 6**

Species used in correspondence analyses. (M) signifies species used in main table and (S) in supplementary table (see "Materials and methods" section. Areas (11–12, 13–14, etc. are shown under each season. Counts are number of organisms observed. Unid. = unidentified.

| | Spring | | | | Summer | | | | Fall | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 11–12 | 13–14 | 15–16 | 17–18 | 11–12 | 13–14 | 15–16 | 17–18 | 11–12 | 13–14 | 15–16 | 17–18 | Total |
| Atlantic croaker (M) | 132 | 20 | 50 | 1 | 554 | 1,604 | 1,732 | 212 | 40 | 97 | 51 | 612 | 5,105 |
| sand seatrout (M) | 104 | 26 | 17 | 0 | 813 | 1,500 | 572 | 2 | 91 | 91 | 197 | 53 | 3,466 |
| gafftopsail catfish (M) | 255 | 70 | 72 | 24 | 161 | 0 | 96 | 48 | 8 | 28 | 33 | 1 | 796 |
| Atlantic cutlassfish (M) | 41 | 28 | 209 | 22 | 5 | 1 | 53 | 55 | 7 | 0 | 13 | 36 | 470 |
| crevalle jack (M) | 71 | 12 | 133 | 17 | 5 | 0 | 31 | 9 | 22 | 41 | 8 | 0 | 349 |
| Spanish mackerel (M) | 22 | 11 | 34 | 33 | 29 | 0 | 56 | 33 | 0 | 7 | 6 | 10 | 241 |
| Atlantic bumper (S) | 0 | 0 | 0 | 0 | 0 | 0 | 2,166 | 330 | 0 | 0 | 1 | 0 | 2,497 |
| striped mullet (S) | 344 | 31 | 0 | 0 | 511 | 0 | 0 | 0 | 0 | 9 | 0 | 0 | 895 |
| red drum (S) | 21 | 0 | 34 | 0 | 23 | 0 | 24 | 6 | 0 | 12 | 9 | 116 | 245 |
| hardhead catfish (S) | 36 | 5 | 3 | 0 | 100 | 3 | 38 | 3 | 12 | 1 | 3 | 2 | 206 |
| tonguefish spp. (S) | 0 | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 200 | 1 | 204 |
| blacktip shark (S) | 37 | 0 | 54 | 1 | 20 | 0 | 19 | 52 | 0 | 0 | 0 | 1 | 184 |
| cownose ray (S) | 27 | 2 | 26 | 0 | 3 | 0 | 4 | 7 | 0 | 0 | 1 | 0 | 70 |
| brown shrimp (S) | 0 | 0 | 1 | 2 | 0 | 0 | 39 | 0 | 0 | 0 | 10 | 13 | 65 |
| cabbbagehead jellyfish (S) | 0 | 0 | 5 | 12 | 0 | 0 | 33 | 0 | 1 | 0 | 4 | 6 | 61 |
| unid. requiem sharks (S) | 0 | 0 | 23 | 2 | 3 | 0 | 16 | 0 | 0 | 6 | 1 | 6 | 57 |
| spotted seatrout (S) | 2 | 8 | 0 | 0 | 31 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 41 |
| gulf butterfish (S) | 2 | 0 | 3 | 0 | 0 | 0 | 6 | 3 | 0 | 0 | 0 | 26 | 40 |
| bull shark (S) | 5 | 0 | 0 | 0 | 31 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 39 |
| unid. penaeid shrimp (S) | 0 | 0 | 1 | 9 | 5 | 0 | 0 | 0 | 1 | 0 | 0 | 16 | 32 |
| Others (not used in CA) | 80 | 5 | 86 | 11 | 147 | 5 | 56 | 24 | 13 | 8 | 72 | 9 | 516 |
| Column Total | 1,179 | 218 | 753 | 134 | 2,441 | 3,113 | 4,944 | 784 | 195 | 300 | 609 | 909 | 15,579 |

The second group, species primarily associated with being gilled, were Atlantic croaker, sand seatrout, and unidentified tonguefish. Other species that were associated with being gilled were unidentified penaeid shrimp, Atlantic cutlassfish, gulf butterfish, and Atlantic bumper. These four species were also associated with the third group, species kept by the crew, and those whose fate was unknown. Other species associated with this third group were hardhead catfish, brown shrimp, Spanish mackerel, gafftopsail catfish, striped mullet, and the cabbage head jellyfish.

## Temporal and spatial patterns of bycatch species

**Spring** Correspondence analysis of area by species for spring indicated that the first two axes explained 97% of the inertia and offered a good representation of species-area associations. From the two-dimensional plot (Fig. 7), we discerned three major groupings. The first axis separates the eastern areas of the fishery (zone groups 11–12 and 13–14) from the western areas (zone groups 15–16 and 17–18). The second axis also separates zone group 15–16 from zone group 17–18.

The eastern areas are associated with Atlantic croaker, gafftopsail catfish, sand seatrout, hardhead catfish, bull shark, striped mullet, and spotted seatrout.

Zone group 15–16 is primarily associated with unidentified tonguefish, red drum, crevalle jacks, blacktip shark, unidentified requiem sharks, gulf butterfish, and Atlantic cutlassfish. Zone group 17–18 was associated with Spanish mackerel, brown shrimp, cabbage head jellyfish, and unidentified shrimp.

**Summer** For the summer, correspondence analysis indicated that the two axes accounted for 94% of total inertia. As in spring, three major species area groupings were observed (Fig. 8). Notable differences in these grouping were that zone group 15–16 appeared to be closer to the eastern groups (13–14 and 11–12). Furthermore, group 13–14 was separated further from zone group 11–12.

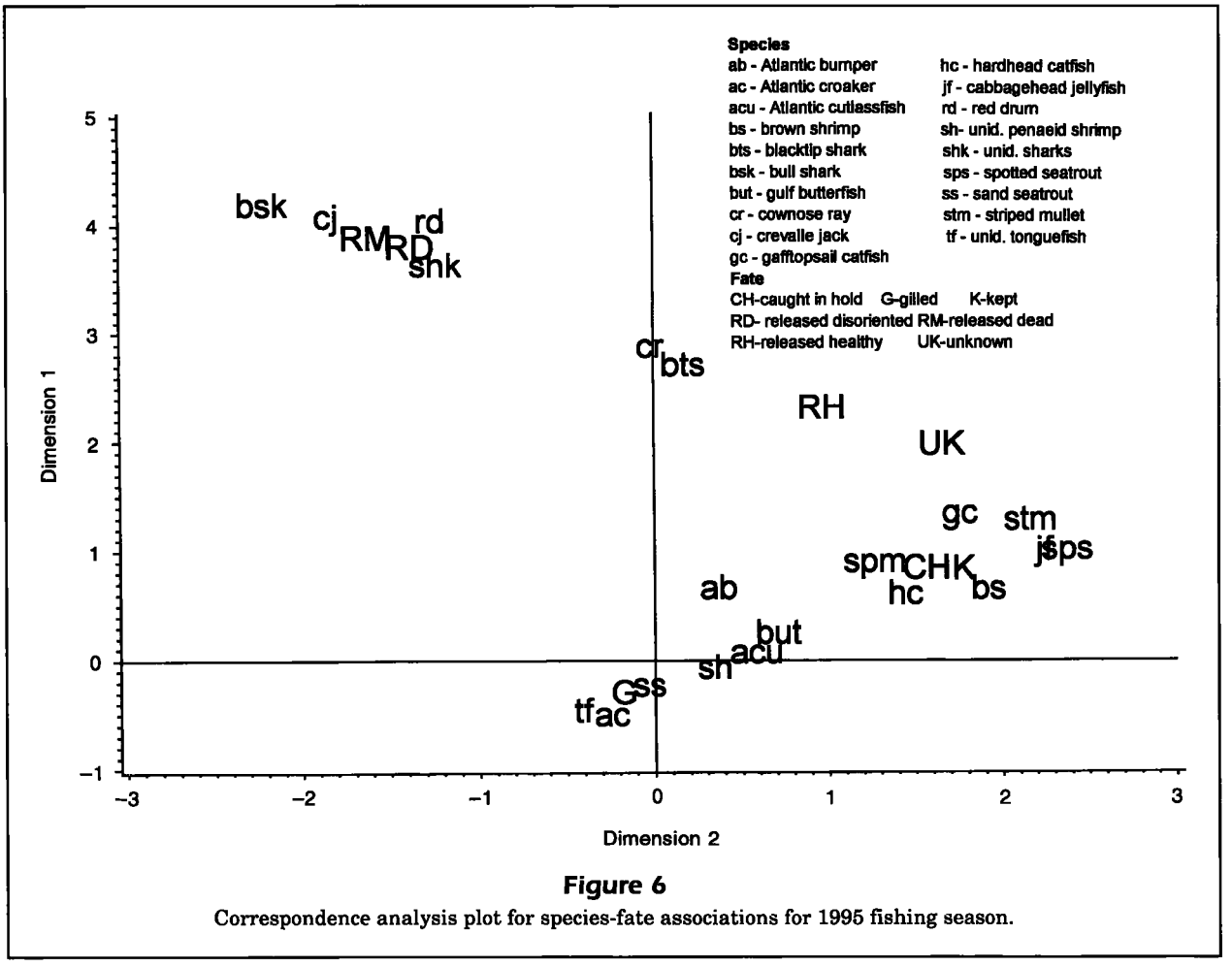


**Figure 6**

Correspondence analysis plot for species-fate associations for 1995 fishing season.

Zone groups 11–12 and 13–14 were primarily associated with sand seatrout and, to a lesser extent, Atlantic croaker. In addition, zone group 11–12 was also associated with bull shark, striped mullet, spotted seatrout, unidentified shrimp, and hardhead catfish.

Zone group 15–16 was also associated with Atlantic croaker. Other species associated with this area were cabbage head jellyfish, brown shrimp, unidentified tonguefish, Atlantic bumper, unidentified requiem sharks, gulf butterfish, and crevalle jack. Zone group 17–18 was associated with Spanish mackerel, Atlantic cutlassfish, cownose ray, blacktip shark, red drum, and gafftopsail catfish. Secondarily associated species with this area were gulf butterfish and crevalle jack.

**Fall** The first two axes of the fall analysis explained 97% of the total inertia, once again presenting a good fit of the table. By fall, two major groupings were observed (Fig. 9). Areas from zone group 11–12 to 15–16 formed one group and were separated from the most westerly zone group 17–18.

Zone group 17–18 was primarily associated with Atlantic croaker, red drum, bull shark, blacktip shark, gulf butterfish, unidentified shrimp, and, to a lesser extent, cabbage head jellyfish, brown shrimp, spotted seatrout, Spanish mackerel, and unidentified requiem sharks.

Zone groups 11–12 to 15–16 were associated with hardhead catfish, gafftopsail catfish, sand seatrout, and, to a lesser degree, Spanish mackerel. In addition zone group 13–14 was also associated with crevalle jack and striped mullet and zone group 15–16 with cownose ray, unidentified tonguefish, and Atlantic bumper.

## Discussion

Bycatch studies of the menhaden industry were conducted in 1894 on the Atlantic menhaden, *Brevoortia tyrannus*, fishery (Christmas et al., 1960) and in 1948 in the U.S. Gulf of Mexico (Miles and Simmons, 1950). Automatically retained bycatch percentage estimates

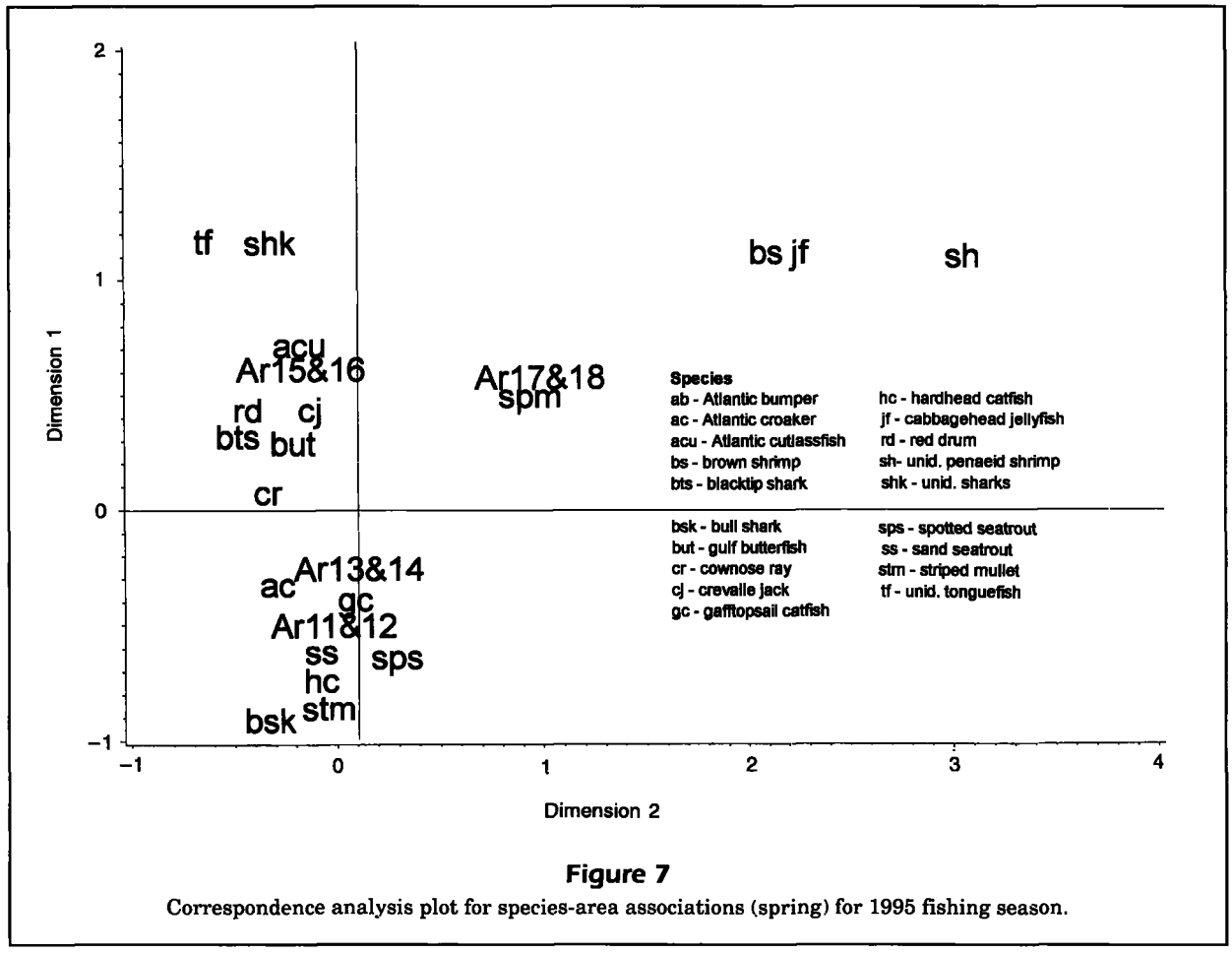


**Figure 7**

Correspondence analysis plot for species-area associations (spring) for 1995 fishing season.

have ranged from 0.05% (Dunham, 1972) to 3.90% (Christmas et al., 1960) by number, and 1.0% (Condrey[1]) to 2.80% (Christmas et al., 1960) by weight. However, these values are based on bycatch retained in the fish hold. No estimates of the releasable bycatch are available. Based on our analysis, releasable bycatch estimates for the U.S. Gulf of Mexico menhaden fishery range from 0.033% (median) to 0.17% (mean) and reflect the strong positively skewed distribution of the bycatch. Values based on the winsorized mean are intermediate to those of the mean and median and are associated with a lower standard deviation than that for the mean.

As a result of the patchy distribution of menhaden bycatch, examination of the relationship of bycatch to other factors is made more complex. Even after the transformation of our data, gross violations of the ANOVA model assumptions made it an unsatisfactory technique. Because we could not find a suitable transformation, our solution to examining such data would be to convert the variable of interest into a categorical variable and to use categorical techniques in analyzing the data. In our case, the use of loglinear models to identify statistically important interactions was found to be a useful tool in exploring such data. This solution can be considered to fall between studies that can use ANOVA techniques (e.g. Andrew et al., 1995) and those based on the modified negative binomial model as used by Perkins and Edwards (1996).

Legendre (1987) noted that the responses of living organisms to environmental change is nonlinear and in instances nonmonotonic. As loglinear models are insensitive to the shape of the relationship among the variables, Legendre (1987) noted that they are well suited for examining nonmonotically related variables. A further advantage of this type of analysis is that because biological variables respond to interacting environmental variables, they can be used to examine such relationships in detail. By using loglinear models we can include a set of potential interactions in our saturated model, and through a stepwise selection procedure, find those interactions that are statistically important. In our study, bycatch was the issue of interest and the variable that we treated as a response. In effect, we were trying to

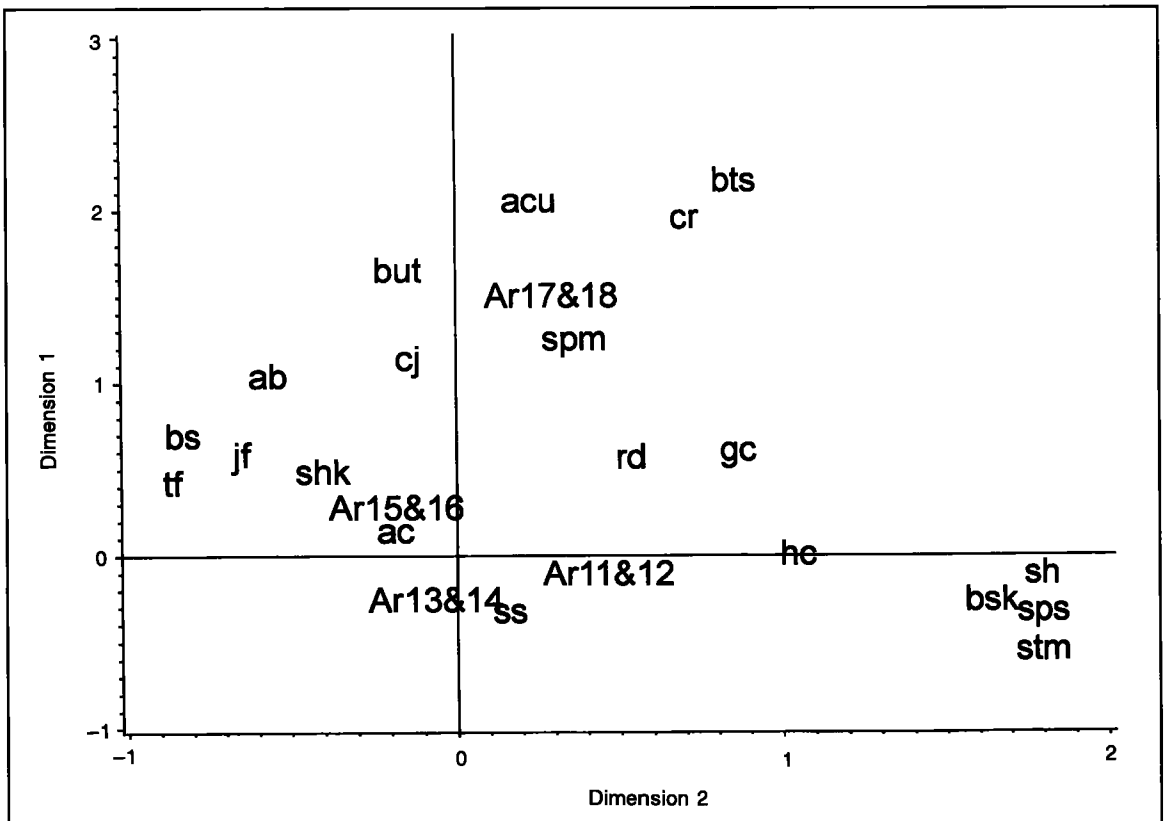


**Figure 8**
Correspondence analysis plot for species-area associations (summer) for 1995 fishing season.

find factors that could explain the bycatch, and we used loglinear models to find a suitable model that was associated with occurrences of bycatch greater than the median level for the fishery.

By using both loglinear models and logit models with categorical explanatory variables, we have used the loglinear model for model selection and the logit model for a detailed examination of the model of our choice in a manner analogous to ANOVA.

With the stepwise selection procedure, [SAB SAD] was found to be the most suitable loglinear model. We had hypothesized that the presence of dolphins in the fishing area could indicate the presence of high bycatch. Had this been true, the presence of dolphins in the vicinity could have been used by fishermen to avoid setting nets in certain areas. However, such a relation between dolphins and bycatch was found not to exist.

At first glance the issue of bycatch in Gulf of Mexico menhaden fishery may seem to be negligible, given the low bycatch percentage. However the fishery had the second highest annual U.S. commercial landings of 472,000 t in 1995 (U.S. Dep. Commerce, 1996). Further, given the strong positively skewed distribution of releasable bycatch, a small percentage of the total fishing effort would account for much of the take. By structuring our analysis around bycatch rates that were greater than the median, we have attempted to identify the potential "hot spots" in the fishery in terms of areas and seasons. One of the solutions for reducing bycatch in the fishery is to identify such areas and thereby offer the industry a tool for managing their take of bycatch by minimizing fishing effort in these "hot spots."

Our philosophy has been that consideration of all bycatch as a single entity is not the best approach. Although we felt the need to address the total bycatch in our first analysis, we also wanted to take individual species into consideration. We approached this multispecies aspect of our study using correspondence analysis, which we used to identify the commonly associated species in different zones and areas, as well as the different fates. Our results suggest that this approach can have general appeal not only in identifying areas and species of concern but also in suggesting approaches to solutions. For example, our "hot spot" fishing zone and season were

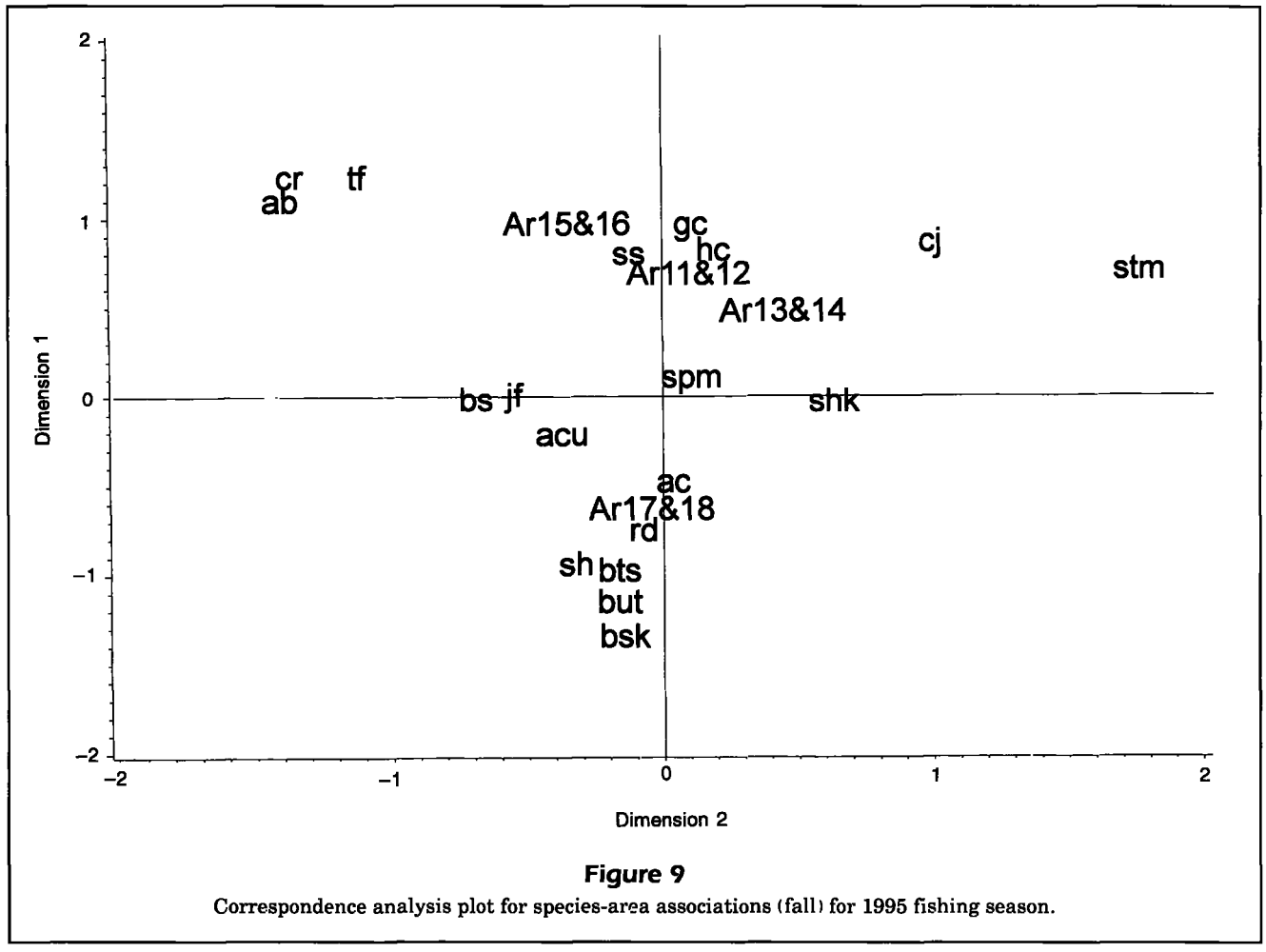


**Figure 9**

Correspondence analysis plot for species-area associations (fall) for 1995 fishing season.

east of the Mississippi River and April–August. This hot spot was associated with the bycatch of Atlantic croaker, sand seatrout, hardhead catfish, spotted seatrout, and bull sharks. Of these, Atlantic croaker and sand seatrout were the most commonly occurring species in the releasable bycatch and were associated with being gilled. If a reduction in the mortality of these species in the menhaden bycatch were necessary, our study suggests it would require gear modification in the purse seine. A species associated with our hot spot, more likely to require attention, is the bull shark given its life history characteristics. Species-fate associations indicated that bull sharks were primarily associated with being released dead. If a reduction in the mortality of bull sharks as menhaden bycatch were mandated, solutions should be centered around reducing the number of sharks released dead. Rester (1996) has suggested that this could be achieved through modifications to the fish pumping equipment for fish 1 meter in length or larger.

## Acknowledgments

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# Estimated tuna discard from dolphin, school, and log sets in the eastern tropical Pacific Ocean, 1989–1992

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**Abstract.**—Pressure to reduce fishery-related dolphin mortality in the tuna purse-seine fishery of the eastern tropical Pacific Ocean (ETP) may alter fishing patterns from the current situation, in which most tuna is caught in association with dolphins, to a situation in which these "dolphin sets" are replaced by sets on unassociated schools of tuna (school sets) or on floating objects (log sets). Although not likely to effect any substantial change in dolphin population dynamics, owing to current low levels of dolphin mortality, such a change in fishing pattern could damage the commercial stock of yellowfin tuna and perhaps stocks of other tuna species because, unlike dolphin sets which generate almost no unwanted catch, school and log sets capture moderate to large amounts of undersized or otherwise undesirable tuna that are subsequently discarded at sea.

In this study, we examined the differences between set types (in short tons of tuna discarded per set by U.S. vessels fishing in the ETP during 1989–92) and then predicted the increase in short tons of tuna discarded per set (all tuna species combined) that would likely result from replacing the dolphin sets with an equivalent number of school or log sets (or both).

Expected discard weight of tuna was 100 times higher for log sets and 10 times higher for school sets than for dolphin sets. Average expected tuna discard per set was 0.06 short tons for dolphin sets, 1.15 short tons for school sets, and 10.5 short tons for log sets. Hypothetically, redistributing all dolphin sets to log sets increased estimated average discard of tuna by the international fleet in the ETP by about 337%.

A hypothetical replacement of all dolphin sets with log sets would lead to estimated discards of 10–25% of the estimated average number of yellowfin recruits to the fishery each year. If this discard is combined with an estimated 25% reduction in tons of yellowfin tuna caught that would result from concommitant changes in size structure of the landed fish (Punsley et al., 1994), the fishery could lose 30–50% of the approximately 98 million individual yellowfin tuna estimated to recruit to the fishery each year. Sustained removals of this magnitude, combined with environmental variability, could pose problems for long-term sustainability of the ETP yellowfin tuna stock; moreover, the change in fishing-effort patterns leading to this effect on yellowfin tuna would likely contribute little to recovery or sustainability of ETP dolphin stocks.

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Fishery Bulletin 96: 210–222 (1998).

Tuna purse-seiners fishing in the eastern tropical Pacific Ocean (ETP) conduct three different types of sets on tuna schools: dolphin sets, school sets, and log sets (IATTC[1,2]). Set types differ only in the technique used to capture the fish; the net used is the same in all cases. Dolphin sets include all sets in which the tuna were captured in association with dolphins. School sets include all sets on tuna schools not associated with either floating objects or with dolphins. "Log" sets as defined in our study include all sets on any floating object encountered by the purse seiner, including natural objects such as trees and tree limbs, dead whales, and other large animals, or other natural debris, as well as human-generated objects such as rafts and discarded trash.

The overwhelming majority of dolphins caught during purse-seining activities in the ETP are caught during dolphin sets, the only set type during which dolphins are captured intentionally. A few dolphins (generally fewer than 25–50) are captured accidentally each year in a few school or log sets or both (generally fewer than 5–10 dolphins), usually because the dolphins were not observed prior to making the set. School sets tend to catch free-swimming schools of moderately small yellowfin tuna, *Thunnus albacares* (about 7–8 kg, 60 cm total length, and not associated with dolphins and with other, unwanted fish), or mixed schools of yellowfin and skipjack tuna (*Katsuwonus pelamis*), and little else. Dolphin sets catch relatively large yellowfin tuna (15–25 kg and 75–125 cm) associated with dolphins (Punsley[3]), some or (rarely) all of the associated dolphins, and very little else. Log sets have tended historically to catch small, prereproductive yellowfin tuna smaller than about 5 kg and less than about 50 cm fork length or skipjack tuna (or a mixture of both tuna), together with a wide variety and large quantity of other biota including sharks, billfish, other large and small sportfish, and a variety of other small noncommercial tunas.

Dolphin sets traditionally have been preferred by tuna fishermen because the associated yellowfin tuna are abundant, large, relatively easy to locate and capture, not associated with unwanted (nontarget)

[1] IATTC (Inter-American Tropical Tuna Commission) Annual Report. 1988. Inter-American Tropical Tuna Commission, c/o Scripps Institute of Oceanography, La Jolla, CA 92038, 288 p.

[2] IATTC Annual Report. 1990. Inter-American Tropical Tuna Commission, c/o Scripps Institute of Oceanography, La Jolla, CA 92038, 261 p.

[3] More recently (1995 onward), some log sets have begun to capture some bigeye tuna and larger yellowfin although the majority of logs still capture mostly smaller fish. Punsley, R. 1995. Inter-American Tropical Tuna Commission, La Jolla, CA 92038. Personal commun.

fish, and generally have been more valuable per pound than the smaller school- or log-associated tuna. Dolphin sets traditionally have been opposed by conservationists because large numbers of dolphins have died annually as a result of net entanglement during these sets. Fishery-related dolphin mortalities began occurring in the ETP with the advent in the late 1950's and early 1960's of the tuna purse-seine fishery. At that time, new net-hauling equipment and net materials made large-scale purse seining practical for the first time. Within a few years, the earlier practice of catching tuna by pole and line was replaced almost entirely by purse seining. Estimates of dolphin mortality during the 1960's and early 1970's were on the order of 300,000–400,000 dolphins annually. Mortality estimates exceeded 100,000 per year until 1977, when the effects of dolphin mortality limits and improvements in fishing practices finally brought mortality below 50,000 per year. Mortality estimates decreased through 1983 to about 12,000 per year but increased significantly again to over 130,000 in 1986 when U.S. vessels left the ETP to move to the western Pacific and were replaced by vessels from countries with less experience in purse-seining techniques. Following a number of new restrictions on fishing methods and limits on allowable species composition of dolphin mortality, enacted by the U.S. congress in the late 1980's and early 1990's, mortality decreased again to about 25,000 per year in 1991.

Obviously, eliminating dolphin sets would virtually eliminate dolphin captures and associated dolphin mortality in the fishery. Recognizing this simple fact, the U.S. congress in 1992 passed legislation designed to eliminate fishing on dolphins by eliminating the U.S. market for tuna caught in association with dolphins while leaving the market open to tuna caught by other methods in the ETP, i.e. by school and log fishing. It was assumed that all effort previously directed to sets involving dolphins would simply be transferred to sets on schools and logs.

It is probably fortunate for the commercial stock of yellowfin tuna in the ETP, as well as for a host of other species, that the legislation did not affect the fishery in the manner expected. More or less concurrent with the changes in U.S. laws, the majority of the countries practicing purse-seining in the ETP, with the help and leadership of the Inter-American Tropical Tuna Commission, formed in 1992 a voluntary agreement (the Panama Declaration) to limit dolphin mortality dramatically in the tuna fishery. A major factor influencing the remarkable success of this program was the introduction of dolphin mortality limits on a per-vessel basis. Under this system, the total mortality quota for a given year is divided equally among all the vessels fishing that year. In addition, annual quotas were adopted that decreased annually to zero mortality by the year 2005.

Results during the first year that this system was fully operational (1993) far exceeded the stated limits of the Panama Declaration (annual mortality quota of 15,000 dolphins). Annual dolphin mortality during 1993 dropped to about 3,600 animals. Annual dolphin mortality has continued to decrease since then, to less than 2,600 animals during 1996. This decrease in mortality was not accomplished by decreasing the number of sets on dolphins, but rather by significantly decreasing dolphin mortality per set, from about 5 animals per set in 1986 to about 0.3 per set in 1996. The number of dolphin sets remains around 8,000 per year, down only about 20% from the approximately 10,000 sets per year that were practiced from the early 1970's through the early 1990's. At the current time, annual dolphin mortality is between 0.1% and 0.2% of estimated abundances of all dolphin stocks affected by the fishery, compared with annual net reproductive rates of 2–4% per year. Thus, fishery-related dolphin mortality at present is negligible compared with estimated current abundances and replacement rates.

This decrease in dolphin mortality, achieved by decreasing kill-per-set rather than decreasing the number of dolphin sets, has probably been fortunate for the commercial stock of yellowfin tuna and other biota in the ETP because it has apparently forestalled any major shift of fishing effort from dolphin sets to school or log sets.

The remainder of this paper focuses on the potential changes in tuna bycatch (discard) that could have been expected had dolphin set effort actually been transferred to school and log sets. We focus on tuna discard because bycatch data for tuna were the only available data to us when this study began.[4] Provided that the currently low levels of dolphin mortality are maintained, so that maintaining effort on dolphin sets does not appear to endanger dolphin population status or dynamics, the results presented here imply that encouraging such a change in effort patterns would be ecologically unsound.

This study presents the first report characterizing patterns and extent of tuna discard from the U.S. tuna purse-seine fishery in the ETP. We describe here general characteristics of the discard data available to us and apply statistical methods described elsewhere (Perkins and Edwards, 1996) to estimate average discard per set for each set type. We use these estimates of discard per set to estimate average an-

[4] The Inter-American Tropical Tuna Commission initiated in 1993 a large-scale bycatch monitoring program in the ETP, but those data are still being collected and analyzed by that agency.

nual discard by the U.S. fleet during the study period (1989–92) for observed patterns and to predict discards that would have resulted if sets on dolphins were redirected to school or log sets. We then predict annual average discard from the international fleet (of which the U.S. was only a small part) under the same redistributions of effort and discard rates assumed for the U.S. fleet.

Although providing the ultimate impetus for the current study, we consider here only briefly the change in dolphin bycatch that would result from replacing dolphin sets with school and log sets because the effect is quite easy to estimate and is currently almost irrelevant in terms of dolphin population dynamics. The effect is easy to estimate because dolphin mortality is almost nonexistent in school and log sets. Thus replacing dolphin sets with school or log sets (or both) will virtually eliminate fishery-related dolphin deaths. This result is irrelevant in a population dynamics sense because annual fishery-related dolphin mortality is currently less than 5% of estimated annual replacement rates (compared with dolphin mortality rates approaching 100% of annual replacement rates during most years prior to 1993). Current mortality levels are about 2,600 dolphins per year from a variety of stocks composing an overall abundance of about 9.5 million dolphins in the ETP. Even for the stock most commonly affected by the fishery, the northeastern spotted dolphin (*Stenella attenuata*), current kill levels are about 800/year from a stock of about 700,000 animals with an estimated replacement rate of 14,000–28,000 animals/year.

Thus, replacing all dolphin sets with school or log sets would likely have little effect on dolphin stock dynamics, given current levels of fishery-related mortality. However, it appears very likely from our analysis that such a replacement could substantially reduce the abundance and biomass of the commercial tuna stock by substantially increasing the bycatch of yellowfin tuna that are too small for market sale. Discarding these small fish affects both current catch and future size composition. Thus we focus here on the potentially detrimental effects on the commercial stock of ETP yellowfin tuna that could result from redirecting dolphin sets to school and log sets, rather than on the negligible effects such effort changes are likely to have on ETP dolphin stock dynamics.

## Methods

### Data collection

As part of a bycatch study initiated in 1989 by the Inter-American Tropical Tuna Commission (IATTC), data were collected by scientific observers from either the National Marine Fisheries Service (NMFS) or IATTC, placed aboard U.S. tuna purse seiners during routine fishing trips to the ETP. Observed purse seiners included only those with greater than 400 short-t holding capacity. Those with a smaller capacity do operate in the ETP and are numerous for some countries but are not included in the ETP observer program (IATTC[1,2,5,6]).

Each agency contributed about 50% of the observers. Agencies alternated sending observers on departing trips. Observers recorded time, position, and set type of all sets made by U.S. vessels during the 31-month "study period" from 1 September 1989 through 30 March 1992. Position data were used to allocate each set to one of three geographic areas of fishing effort, as explained below.

Short tons of tuna discarded per set was calculated by subtracting the reported "total tons tuna loaded" from the reported " total tons tuna captured." After completing the original analysis of these data (Perkins and Edwards, 1996), we were informed that the data set we had been provided for analysis did not distinguish between true discard and those cases in which the calculated discard also included some tuna that were transferred to another vessel rather than loaded by the capture vessel because the capture vessel had reached capacity during that set. Thus in our original analysis we missed a small number of sets in which some of the captured fish were transferred to another vessel and became part of the commercial catch rather than discard. We recalculated the discard estimates for this paper using the corrected data; therefore the estimated average discard (and associated parameters) reported here differ slightly from our earlier paper. Because the problem occurred in only a few sets, it led to very little change between the estimated model parameters presented in Perkins and Edwards (1996) and those presented here. The largest change (approximately 10%) occurred in the parameter $\mu$ for estimating discard from dolphin sets, but this change has almost no effect on subsequent analyses or conclusions because so little discard overall occurs from dolphin sets.

Observers recorded discard data for only 50% of the sets made during the period 1 September 1989 through 30 July 1990 because only IATTC observers were collecting discard data during this period. During the remaining period, 1 August 1990 through 30

[5] IATTC Annual Rep. 1991. Inter-American Tropical Tuna Commission, c/o Scripps Institute of Oceanography, La Jolla, CA 92038, 271 p.

[6] IATTC Annual Rep. 1992. Inter-American Tropical Tuna Commission, c/o Scripps Institute of Oceanography, La Jolla, CA 92038, 315 p.

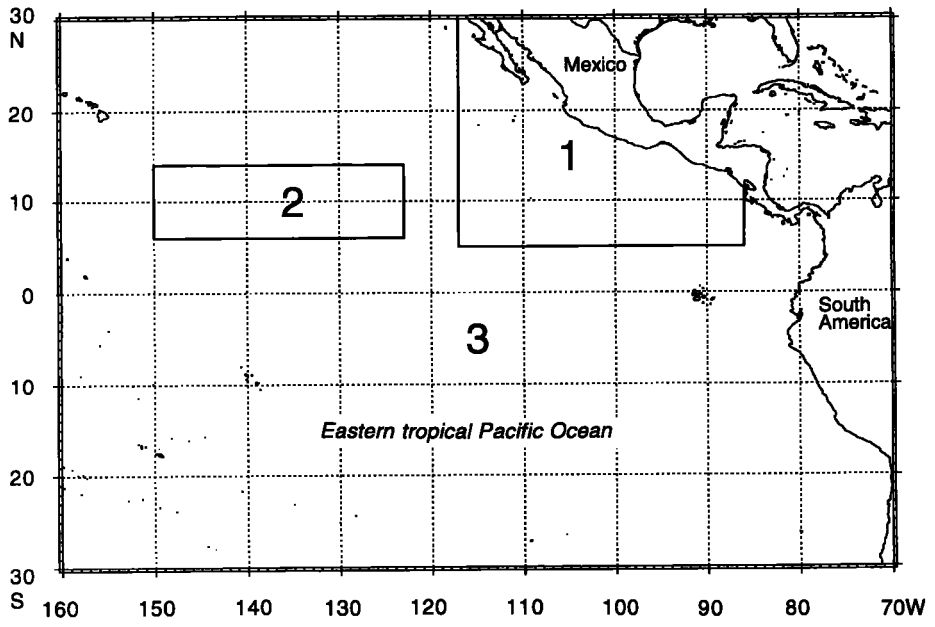


**Figure 1**

Geographic strata used in estimating average annual discard per set by the U.S. tuna purse-seine fleet fishing in the eastern tropical Pacific Ocean, 1989–92.

March 1992, observers from both agencies collected discard data for all observed sets. Because complete records of discard were missing for the early part of the study period, it was necessary to estimate discard during the study period rather than to measure it directly.

Complete details of data collection and statistical modeling methods and rationale appear in Perkins and Edwards (1996). In summary, we chose to model the data using a modified negative binomial (NB) distribution (the negative binomial with added zeros, Johnson and Kotz, 1969) because this distribution was sufficiently flexible to describe with a single form the disparate catch per set distributions for the three set types. The modified NB was able to accommodate the preponderance of zeros and the long tails (extreme skewness) in the dolphin-set and school-set discard data as well as the more strictly negative binomial distribution of the discard data from log sets.

Readily apparent differences in tuna discard per set type in different areas contributed to our stratification of the data into three geographic areas (Fig. 1), the same areas used currently to determine comparability of U.S. and non-U.S. dolphin mortality rates (Federal Register, 1989). For the purposes of estimating overall discard rates, we ignored school and log fishing in area 2 because no school sets and only ten log sets occurred there (Table 1).

**Table 1**

Effort data (number of sets on logs, schools, and dolphins) for the U.S. tuna purse-seine fishery in the eastern tropical Pacific Ocean 1989–92. Geographic areas as defined in Federal Register (1989). $N$ = number of sets in a given area, $n$ = number of sets examined for discard, and $n^+$ = number of sets examined for discard in which discard actually occurred.

| Set type | Area | | $N$ | $n$ | $n+$ |
|---|---|---|---|---|---|
| Dolphin | 1 | | 2,496 | 1,445 | 10 |
| | 2 | | 498 | 272 | 5 |
| | 3 | | 596 | 393 | 4 |
| | | Total | 3,590 | 2,110 | 19 |
| School | 1 | | 399 | 279 | 32 |
| | 2 | | 0 | 0 | 0 |
| | 3 | | 867 | 681 | 48 |
| | | Total | 1,266 | 960 | 80 |
| Log | 1 | | 537 | 326 | 257 |
| | 2 | | 10 | 4 | 4 |
| | 3 | | 791 | 672 | 393 |
| | | Total | 1,338 | 1,002 | 654 |

There was no distinct difference in discard rates among months for any of the three set types, and we did not include a monthly or seasonal effect in our analyses. Although the sample of sets was unbalanced with respect to months (i.e. the period Sep-

tember through March occurred three times during the study period, whereas the period April through August occurred only twice), the magnitude of the imbalance during the study period was not large. Data were too few to examine any annual effects.

We used maximum-likelihood estimates of model parameters from the best-fit models to estimate expected discard per set for each set type. We calculated estimates for individual geographic areas where model fits indicated significant areal effects on parameter values (i.e. for school and log sets), then calculated a "pooled" estimate of expected discard per set from the area-specific estimates. Where no areal stratification was appropriate (i.e. for dolphin sets), we calculated only one "pooled" estimate using the maximum-likelihood estimates of parameter values for the unstratified model.

We estimated standard errors for expected discard per set by bootstrapping rather than by using analytic formulae because only bootstrap methods could be efficiently applied to all three set types. Analytic methods could be easily applied only in the case where no areal stratification was appropriate (i.e. dolphin sets, where we fitted a single model for all areas) and in the case where complete areal stratification was appropriate (i.e. log sets, where we fit separate models in each of the geographic areas).

We estimated annual discard and standard errors of those estimates for the U.S. fleet as observed during the study period by multiplying the estimated overall discard rate for each set type by the corresponding average annual number of sets.

To investigate the effect of entirely eliminating dolphin sets, we predicted potential discard after redirecting all dolphin sets to school or log sets (or both). We used three hypothetical redistributions: 1) all dolphin sets were reassigned to school sets; 2) half of dolphin sets were reassigned to school sets, the remaining half were reassigned to log sets; and 3) all dolphin sets were reassigned to log sets. Sets were reassigned in proportion to the observed proportions of set types by the U.S. fleet in each geographic area; therefore the pooled estimates of expected discard per set could be used for each set type.[7]

We predicted total redistributed discard during the study period by multiplying pooled estimates of expected discard per set for school and log sets by the redistributed number of sets for each type. This procedure assumes that the redirected effort did not change the fishing habits, geographic patterns of the fleet, or the discard per set realized during the redirected effort.

[7] The geographic distribution of set types by U.S. vessels tends to differ from the geographic distribution with international fleet as a whole because U.S. vessels are largely restricted from the nearshore Exclusive Economic Zones (EEZ's) of coastal nations. If data for the geographic distribution of effort by the international fleet had been available, it would have been more appropriate to use that. However, the general results of the present study would likely remain unchanged (see "Caveats" in "Discussion" section).

## Results

### Patterns in set-type distributions

Several patterns are evident in the number of sets of each type. During the study period, about half the sets by U.S. boats were made on dolphins, about one quarter were made on school sets, and one quarter on log sets (Table 1). Sets were most common in the relatively nearshore area 1, rare in the offshore equatorial area 2, and moderate in the remaining area 3. Only dolphin sets were made with any frequency in area 2 (Table 1; Fig. 2). All three set types were common in areas 1 and 3.

About 70% of school sets were observed in area 3 (Table 1: Fig. 2). Of those sets, most occurred during April and May (59% of sets), between the hours of 8 am and 4 pm local time (68% of sets). Observed school sets in area 1 also occurred primarily between 8 am and 4 pm (76% of sets) but were distributed more homogeneously throughout the year and were much less common than in area 3. No school sets were observed in area 2.

Log sets were also observed primarily in area 3 (58% of sets, Table 1), although fewer sets were observed here during the period June–September (Fig. 2). Observed log sets decreased during summer and winter months in area 1. Log sets usually occurred early in the day in all areas (80% before noon, 56% before 8 am, Fig. 2). Less than 1% of observed log-set effort occurred in area 2.

Contrary to school-set and log-set effort, dolphin sets were observed primarily in area 1 (66% of sets, Table 1) with a small but important number of sets observed in area 2 (17% of sets). Effort in area 2 obviously replaced effort in area 1 during the months of June and July (Fig. 2). Only 1.6% of effort in area 1 but 78% of effort in area 2 occurred during these two months, and all effort in area 2 occurred between June and October. In all three areas, dolphin sets were observed primarily (79%) between the hours of 8 am and 4 pm during which greater effort was evident before noon.

### Discard patterns

Estimated tuna discard from U.S. vessels was recorded for 59% (Table 1) of observed dolphin sets,

76% of observed school sets, and 75% of observed log sets. The set data reported 134, 1,098, and 9,819 tons of observed discard, respectively. A nonzero amount of discard was reported in 65% (Table 1) of log sets where discard was recorded, but in only 8% of school sets and only 0.7% of dolphin sets where discard was recorded. Frequency distributions for tons of tuna discarded per set were clustered near zero for dolphin sets, were somewhat wider for school sets, and were much wider for log sets (Fig. 3), indicating the increasing frequency and increasing tonnage of tuna discard from dolphin, school, and log sets, respectively.

Geographic patterns in discard reflected geographic patterns in effort devoted to the three different set types. Both effort and positive discard occurred most frequently in area 1 for dolphin sets and in area 3 for school and log sets (Table 1).

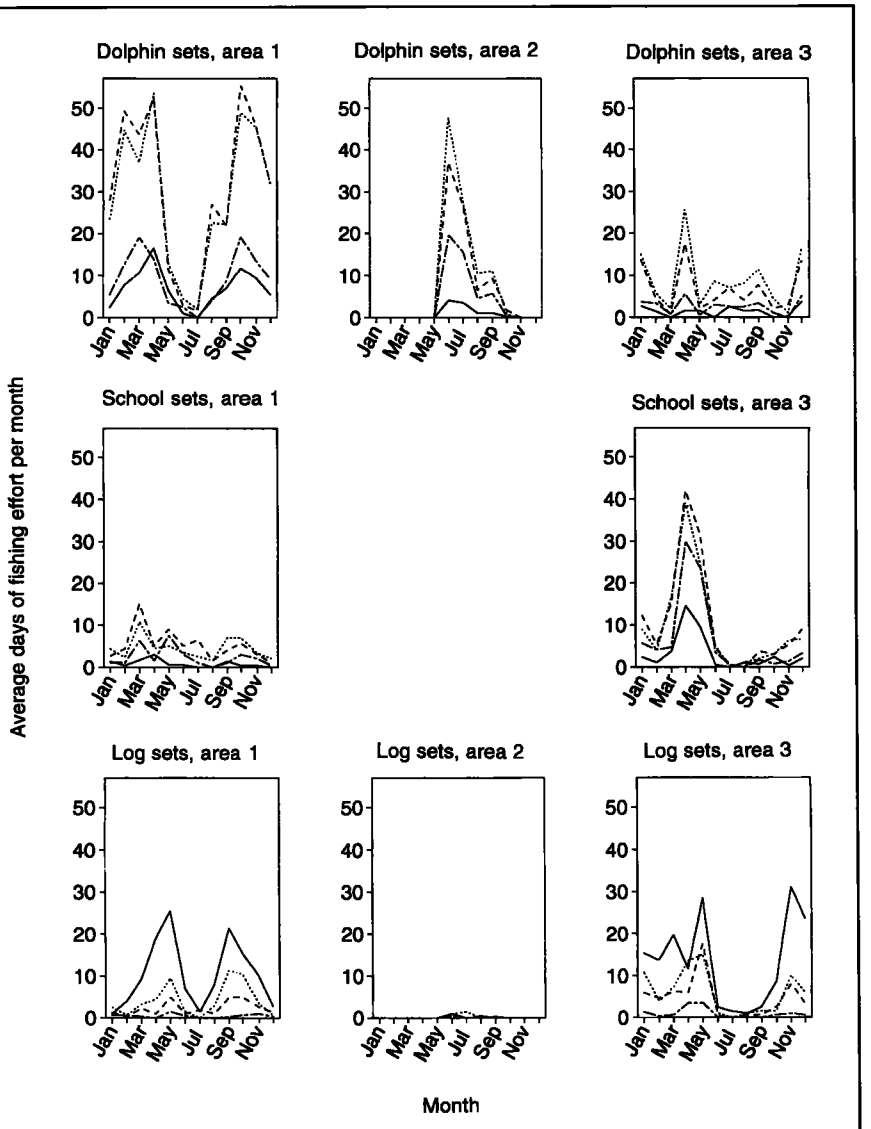


**Figure 2**

Daily, monthly, and geographic (areas 1, 2, and 3) patterns in fishing effort (number of sets) made on dolphin, school, and log sets by the U.S. tuna purse-seine fleet fishing in the eastern tropical Pacific Ocean, 1989–92. Solid line = before 0800 hours, dotted line = 0800–1200 hours, dashed line = 1200–1600 hours, and dot-dashed line = after 1600 hours.

## Expected discard per set

Expected discard per set for log sets was 10.5 short tons of tuna (all tuna species combined; SE= 0.83, $n$=998, means range 7.1–15.4 short-t depending on geographic area; Fig. 4). Expected discard per set for school sets was 1.15 short tons of tuna (SE=0.24, $n$=960, means range 0.97–1.57 short-t) depending on geographic area). Expected discard per set for dolphin sets was 0.06 short tons of tuna (SE=0.2, $n$=2,110 fishery wide).

## Estimated average annual discard

Despite the much larger number of sets (greater fishing effort) on dolphins than on school or logs (Table 1), estimated average annual discard was much greater for log sets than for school or dolphin sets, reflecting the enormous difference between set types in expected discard per set. Estimated average annual discard for the entire U.S. fleet during the study period was 88 short tons per year (SE=29, $n$=2,110) from dolphin sets, 595 short tons per year (SE=125, $n$=960) from school sets, and 5,400 short tons of tuna (all species combined) per year (SE=426, $n$=998) from log sets, based on observed patterns of effort (Fig. 5).

Redistributing the great number of dolphin sets to either of the other set types considerably increased predicted annual discard of tuna from school or log sets (or both), and from the U.S. fleet as a whole.

Redistributing all dolphins sets to school sets increased predicted annual discard of tuna from school

sets by the U.S. fleet from 595 to 2,190 short tons per year. Redistributing all dolphin sets to log sets had by far the greatest effect, increasing predicted annual discard of tuna from log sets by the U.S. fleet from 5,400 to 19,900 short tons.

Predicted total annual discards of tuna from the U.S. fleet for all set types combined were 7,500, 14,000, and 20,500 short tons for redistribution of dolphin sets to all school sets, combined school and log sets, and all log sets, respectively (Fig. 5), representing increases of 1.25 (7,580/6,080), 2.31 (14,000/6,080), and 3.34 (20,500/6,080) times, respectively.

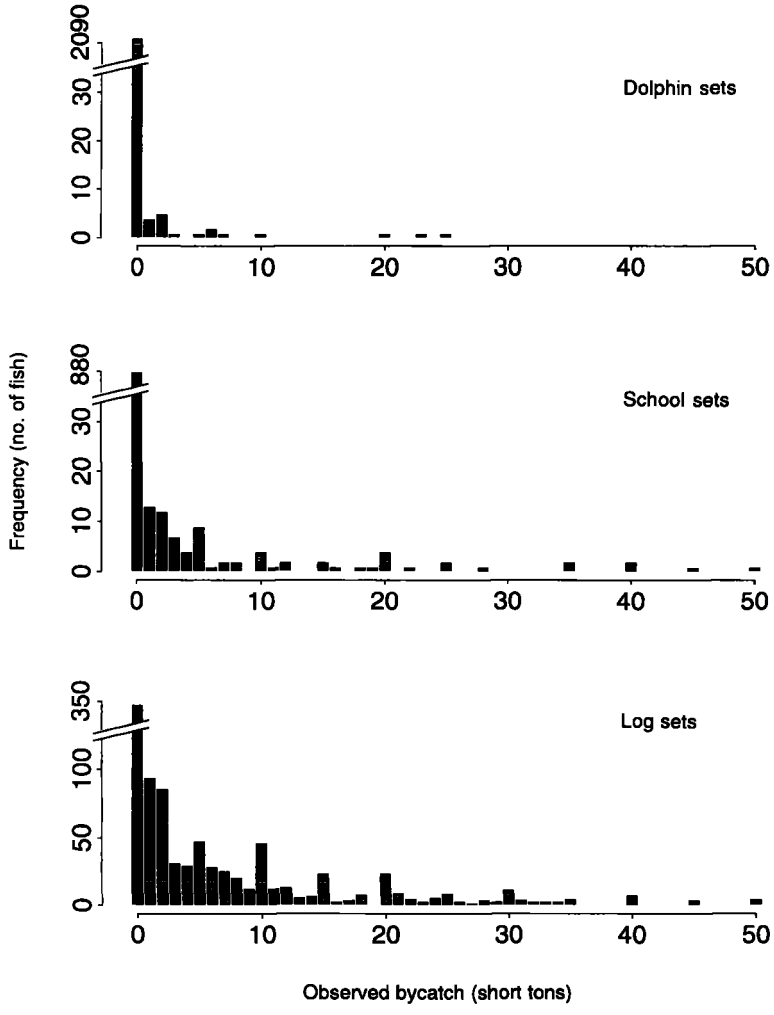


**Figure 3**

Frequency distributions of observed discard per set for dolphin, school, and log sets by the U.S. tuna purse-seine fleet fishing in the eastern tropical Pacific Ocean, 1989–92. The scale for school sets does not show 3 school sets exceeding 50 short tons per set, totaling 310 short tons, and representing 30% of total catch on school sets, with maximum catch per school set = 150 short tons. The scale for log sets does not show 25 sets exceeding 50 tons per set, totaling 3,221 short tons, and representing 33% of the total catch on log sets, with maximum catch per log set = 325 short tons.

## Discussion

### Comparison with other discard data

Although the data used in this report consist of estimates made "by eye" (i.e. estimated by visually noting the volume of discarded tuna and mentally comparing that volume to the volume of tuna in some container of known size, e.g. the vessel's brailer) and could not be analyzed in hindsight for inter-observer reliability, our results are reasonably similar in magnitude, especially in relative magnitude (expressed as tonnages) between set types, to data collected during 1993 and 1994 by the IATTC as part of a greatly expanded bycatch sampling program in the ETP. Average short tons of tuna discarded per set during these 2 years for dolphin, school, and log sets was 0.17 (no difference between years), 0.58 (0.5 in 1993, 0.9 in 1994), and 8.3 (5 in 1993, 11 in 1994), respectively (Hall[8]). These values are reasonably comparable to our estimates of 0.06, 1.2, and 10.5 short tons of tuna discard per set for dolphin, school, and log sets, respectively. The apparently large differences between the IATTC and NMFS estimates for dolphin sets, and to some extent for school sets, are relatively unimportant because the overall discards for these set types are so low. In addition, annual differences can be substantial although still low in relation to log sets.

### Implications for the ETP yellowfin fishery

Our results imply that historically, tuna discard from the U.S. tuna

[8] Hall, M. 1995. Inter-American Tropical Tuna Commission, c/o Scripps Institute of Oceanography, La Jolla, CA 92038. Personal commun.

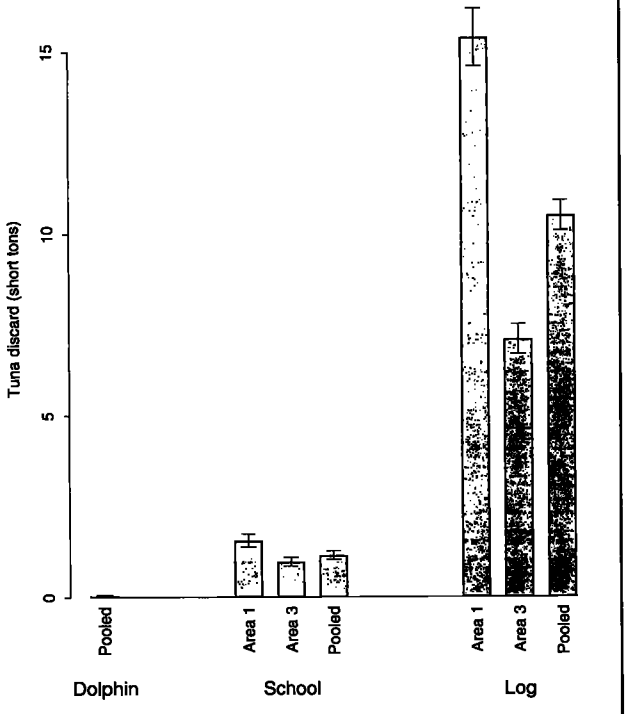


**Figure 4**

Estimated expected tuna discard per set by the U.S. tuna purse-seine fleet fishing in the eastern tropical Pacific Ocean, 1989–92, in specified geographic strata (Federal Register, 1989) and in all areas pooled. Standard errors indicated by vertical bars.

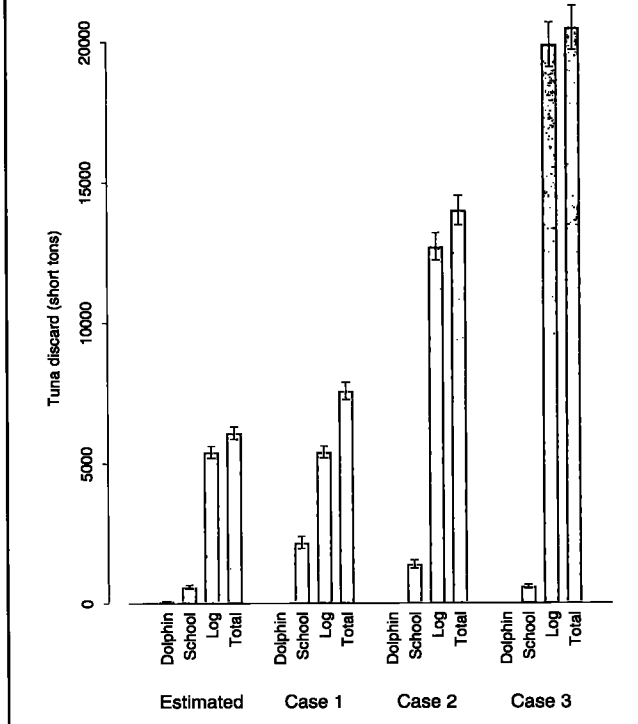


**Figure 5**

Estimated annual tuna discard by the US tuna purse-seine fleet fishing in the eastern tropical Pacific Ocean, 1989–92, under observed effort patterns and redistributed effort patterns where all dolphin sets were redistributed exclusively to school sets (case 1), equally to school and log sets (case 2), and exclusively to log sets (case 3).

purse-seine fleet in the ETP was probably relatively minor (although local effects might have been large at some times). From the fishery's inception in the early 1960's through the mid-1980's, the majority of U.S. vessels (which during that period represented over 90% of the international fleet) targeted tuna associated with dolphins, a strategy that generates very little tuna discard.

The situation has changed dramatically in the past few years, in particular since 1) passage, in 1988, of stringent new amendments to the Marine Mammal Protection Act, 2) the decision by U.S. canneries in April 1990 to buy only "dolphin-safe" tuna, and 3) the passage of the International Dolphin Conservation Act of 1992 (IDCA). The 1988 amendments required non-U.S. fleets to meet strict comparability criteria related to dolphin mortality rates in order to export tuna to the U.S. The cannery decision for dolphin-safe tuna (adopted also by European Community nations in 1993) means that the canneries involved will now buy only tuna that is certified not to have been caught either in association with dolphins or by drift gill nets on the high seas. The IDCA places increasing pressure on both U.S. and non-U.S. fleets to reduce dolphin mortality and to eliminate it altogether by 1999.

Largely in response to these events, most U.S. vessels have left the ETP, either to change flags, retire from fishing altogether, or to fish in the western Pacific Ocean under license from various island nations. Of those U.S. vessels remaining (4 vessels in 1994), all fish on school and floating logs. This change to school and log fishing will have greatly increased the U.S. discard of small immature tuna, although the overall effect on the tuna stocks due to changes in fishing practices by the U.S. fleet is probably small because very few U.S. vessels are currently fishing for tuna in the ETP using any of these set types.

However, the decrease in the size of the U.S. fleet has been offset by increases in the sizes of non-U.S. fleets so that the overall size of the international fleet has remained relatively constant since the mid-1980's. Although many of the non-U.S. vessels are still fishing "on dolphin," increasing numbers of vessels changed during the study period to school and

log fishing in response to pressures from the canneries, the MMPA, and the IDCA. Because all large ETP purse-seiners use the same type of gear, fishing procedures, and vessels, a rough estimate of tuna discard for the entire international fleet can be obtained by simply applying the ratio of discard of total catch for the U.S. fleet to total catches reported for the international fleet, under the assumption that non-U.S. fleets discarded tuna in the same manner as the U.S. fleet[9] during the study period.

Average annual commercial catch (short tons landed, all tuna species combined) by U.S. vessels fishing in the ETP during 1989–91 was 76,425 short tons.[10] Estimated average annual discard for the U.S. fleet during the study period was 6,080 short tons. Thus, estimated total annual discard by the U.S. fleet under observed patterns of effort was 7.96% (6,080/76,425 × 100) of the average annual commercial catch (Hall[11]). As noted previously, predicted total annual discards from the U.S. fleet for redistributions of dolphin sets to log or school sets (or both) increased predicted total discard by 1.25 times for redistribution to school sets, 2.31 times for redistribution to a combination of log and school sets, and 3.37 times for redistribution to log sets (Fig. 5).

Average annual commercial catch for the international fleet during the study period was 395,768 short tons.[12] If observed effort patterns of the U.S. fleet during the period were the same as effort patterns of the international fleet, then discard from the international fleet under hypothetical redistributions of dolphin effort can be simply estimated as 7.96% of 395,768 short tons, i.e. 31,500 short tons. Assuming that changes in effort would affect discard in the same way for the international fleet as for the U.S. fleet, then discard under hypothetical redistributions of dolphin effort can be predicted as 1.25 times, 2.31 times, and 3.37 times 31,500 short tons, for redistributions to all school sets, combined school and log sets, and all log sets, respectively. The predictions are then 39,200, 72,700, and 106,000 short tons of tuna discarded, respectively (Fig. 6).

The significance of these discard predictions for future tuna resources depends on their magnitude in relation to the total stocks of tuna in the ETP. Although the amount of tuna that is potentially discarded appears high, it will not be particularly important if it represents only a few percent of the to-

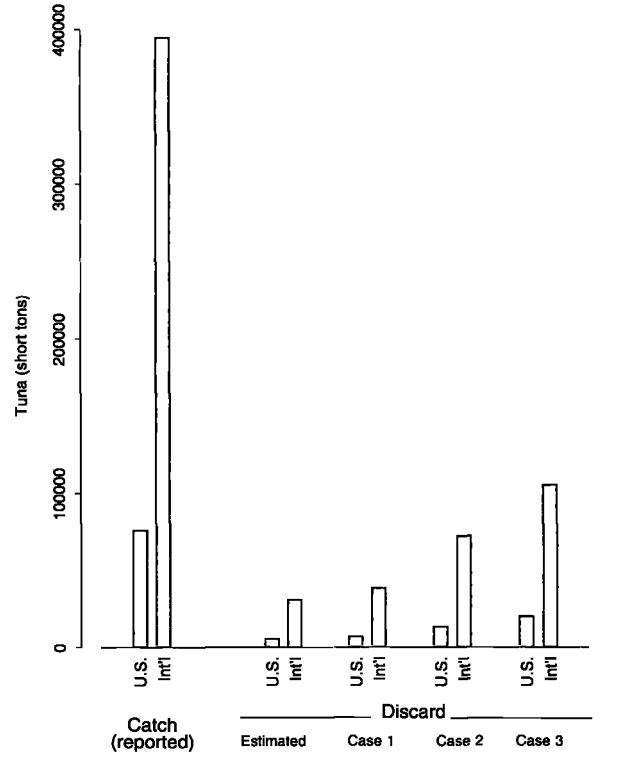


**Figure 6**

Average annual commercial tuna catch and estimated average annual tuna discard by the U.S. and international purse-seine fleet fishing in the eastern tropical Pacific Ocean, 1989–92, under observed effort patterns and redistributed effort patterns where all dolphin sets were redistributed exclusively to school sets (case 1), equally to school and log sets (case 2), and exclusively to log sets (case 3).

[9] Although we cannot test this assumption at present, presumably all vessels selling fish to canneries serving international markets have the same constraints on acceptable sizes for individual tuna retained for sale. It is possible that smaller sizes may be acceptable by canneries located in individual countries, but we are not aware of any such policy. The implications for population dynamics of affected tuna will be the same regardless of whether the fish are marketed or not (they are removed from the population in either case).

We also assume here that the effort distribution is the same for both the international and U.S. fleets. That is not strictly true, but the main difference tends to be that the international fleet, composed mostly of Mexican vessels, fishes more inshore areas (i.e. more in area 1) than does the U.S. fleet alone. Fishing more inshore would increase the fraction of school and log sets in the data. Thus, extrapolation from the U.S. data will, if anything, underestimate the extent of bycatch on school and logs.

[10] Estimated annual catches of tuna (all species combined, surface fishing only) for the U.S. fleet were 110,981, 79,530, and 38,765 short tons for the years 1989, 1990, and 1991, respectively (IATTC, 1991), averaging 76,425 short tons annually for the period.

[11] This compared well with IATTC data showing 7.4% of all sampled tuna captured during 1993 and 1994 were discarded (13,500 short tons of tuna discarded from 181,422 short tons of tuna caught) (Hall, M. 1995. Inter-American Tropical Tuna Commission, c/o Scripps Institute of Oceanography, La Jolla, CA 92037. Unpubl. data).

[12] Estimated annual catches of tuna (all species combined, surface fishing only) for the international fleet were 441015, 407445, and 338,385 short tons for the years 1989, 1990, and 1991 respectively (IATTC[5]), averaging 395,768 short tons annually for the period.

tal fish currently in the ecosystem, or a few percent of annual fishery recruitment (i.e. new young fish becoming vulnerable to purse-seine fishing each year), or individuals from a stock with very short life span and high annual ability to restock. Potential significance of discard calculations can be determined by combining estimates of recruitment with information about the species and size composition of fish discarded. These calculations are a rough estimate of the number of fish discarded (i.e. lost from the future commercial population) in relation to fish available for commercial catch. Estimates of discards of young, small fish are especially important in terms of future resources because these young fish have the most biomass to gain per individual, as well as the greatest reproductive potential.

Data recently collected by the IATTC as part of their bycatch investigations indicate that both the fraction and the size composition of yellowfin tuna discards change dramatically with set type (Hall and Deriso[13]). These data can be used to estimate the numbers of yellowfin tuna discarded under various fishing regimes.

IATTC data show that yellowfin tuna composed 92% (by weight) of tuna discard from dolphin sets, 50% of discard from school sets, and 22% of discard from log sets during the years 1993 and 1994 (Table 2).

[13] Hall, M., and R. Deriso. 1995. Inter-American Tropical Tuna Commission, c/o Scripps Institute of Oceanography, La Jolla, CA, 92038. Personal commun.

Of this yellowfin tuna discard, small yellowfin tuna (defined as less than 2.5 kg, or 5 lb) discarded from log sets were by far the most serious type of loss, particularly in the scenario where all dolphin-set effort was redistributed to log sets. Although small yellowfin tuna composed only 3% and 17% (by weight) of yellowfin tuna discards from dolphin and school sets, they composed about 76% of the discard from log sets (Table 2).

These data can be used to predict yellowfin tuna discard under different fishing regimes, given the percentage of total effort devoted to each of the set types. Assuming, as before, that effort patterns of the international fleet were similar to effort patterns of the U.S. fleet during the study period, we can use the percentages of total observed discard resulting from each set type in the U.S. fleet to estimate tonnages of discard from each set type for the international fleet during the same period.

Of the total annual discard of 6,080 short tons from the U.S. fleet under observed patterns of effort, 88 short tons (1.44%) resulted from dolphin sets, 595 short tons resulted from school sets (9.78%) and 5,400 short tons resulted from log sets (88.8%). Application of these percentages to the estimated total annual discard of 31,500 short tons of tuna from the international fleet produces estimates of 454 (31,500 × 1.44%), 3,079 (31,500 × 9.78%) and 28,000 (31,500 × 88.8%) short tons of tuna discarded annually from dolphin, school, and log sets by the international fleet (Table 2). The percentages of discard composed of

**Table 2**

Steps in estimating number of individual yellowfin tuna of different sizes discarded from each set type. "% yellowfin" is the sum of all yellowfin bycatch divided by the sum of all tuna bycatch for the years 1993–94 in the IATTC bycatch data base. "% small yellowfin" is the average of percent values for 1993 and 1994; "% medium yellowfin" and "% large yellowfin" were calculated similarly. "Small" yellowfin are less than 2.5 kg. "Medium" yellowfin are 5–15 kg. "Large" yellowfin are greater than 15 kg. Weights are expressed in short tons.

| Set type | Total tuna discard (tons) | % yellowfin | Yellowfin discard (tons) | % small yellowfin | % medium yellowfin | % large yellowfin | Small yellowfin (tons) | Medium yellowfin (tons) | Large yellowfin (tons) |
|---|---|---|---|---|---|---|---|---|---|
| dolphin | 475 | 92 | 437 | 3 | 31 | 66 | 13 | 135 | 288 |
| school | 2,976 | 50 | 1,488 | 17 | 31 | 53 | 253 | 461 | 789 |
| log | 28,177 | 22 | 6,199 | 76 | 24 | 1 | 4,711 | 1,488 | 62 |

Ranges of percent values:
(left = 1993, right =1994)

| Set type | % yellowfin | % small yellowfin | % medium yellowfin | % large yellowfin |
|---|---|---|---|---|
| dolphin | (92–99) | (1–5) | (20–42) | (57–74) |
| school | (49–50) | (16–17) | (25–36) | (48–57) |
| log | (19–29) | (73–78) | (20–27) | (0.2) |

yellowfin tuna can be applied to these set-specific tuna tonnages to produce estimates of 418, 1,540, and 6,150 short tons of yellowfin tuna discarded annually by the international fleet, under the assumption of observed U.S. effort patterns (Table 2). These estimates compare reasonably well with estimates of total short tons of yellowfin tuna discarded by the international fleet during 1993 and 1994 of 449–917 short tons from dolphin sets, 606–2,108 short tons from school sets, and 3,802–4,150 short tons from log sets (IATTC[14]).

Yellowfin tuna discards under redistributed patterns of effort can be predicted from tonnages predicted under the different effort regimes. The "worst-case" discards will obviously occur when all dolphin sets are redirected to log sets. The total tonnage of tuna discard in this circumstance is the sum of discards from dolphin sets (by definition 0, because we redistributed the dolphin sets effort to log sets), school sets (3,080 short tons, the same as under observed effort patterns because school effort is assumed to be unchanged), and log sets (103,000 short tons; estimated as log discard from observed patterns, 28,000 short tons, multiplied by 3.69, the increase factor for discard observed in U.S. data when redistributing all dolphin sets to log sets). The tonnage of yellowfin tuna in each of these set categories is $0 \times 0.92 = 0$ short tons for dolphin sets, $3080 \times 0.5 = 1{,}540$ short tons for school sets, and $103{,}000 \times 0.22 = 22{,}700$ short tons for log sets, with the "fraction yellowfin" from IATTC's data base.

Obviously, changing entirely from dolphin sets to an equal number of log sets dramatically increases predicted total bycatch of yellowfin tuna. A particularly unfortunate feature of this increase is the number of small yellowfin tuna involved; the vast majority of log-set yellowfin tuna discards are new recruits to the fishery that have grown just large enough to be caught in the seine (Table 2). This increase in yellowfin tuna bycatch is unfortunate for two reasons: first, removing these small fish removes their potential to grow larger and more valuable, thus reducing overall yield per recruit for the fishery (Punsly et al., 1994); second, these small fish are prereproductive. No stock-recruitment relationship has yet been demonstrated for yellowfin tuna in the ETP, but if one exists, these increased losses to bycatch might become troublesome over long periods of time.

The actual effect of these discards of small fish on future yield per recruit depends on the number discarded in comparison with the number recruited. Fortunately, the annual recruitment of yellowfin tuna has been estimated by the IATTC.[5] The number of small fish discarded can be estimated from the weight discarded by assuming that all small discarded yellowfin are new recruits (Table 2). This is reasonable because the "small" size class of discards is defined in the IATTC bycatch data base as fish less than 2.5 kg (Table 2), and Cole (1980) reported that yellowfin tuna recruit to the ETP tuna purse-seine fishery at sizes ranging from 0.7 to 2.0 kg. Thus a short ton of "small" discarded yellowfin tuna, at 907 kg per ton, should include between 454 and 1,296 individual fish.

According to inferred effort patterns, estimated average annual discard of small yellowfin tuna by the international fleet was 4,950 short tons , representing 2.3–6.4 million fish (Table 2). If all dolphin sets are assumed to be replaced by an equal number of log sets, then predicted discard of small yellowfin tuna increased to 17,562 short tons, representing 8.0–22.7 million fish (0 short tons from dolphin sets plus 262 short tons from school sets plus 17,300 short tons from log sets).

By comparison, the estimated annual recruitment of small yellowfin tuna to the ETP fishery for 1983–91 was 98 million fish (IATTC[5]); thus observed effort patterns may have been generating discards representing 2–7% of total recruitment each year. On the other hand, a redistribution of all dolphin-set effort to log sets could increase discards to 8–24% of annual recruitment, depending on the actual sizes of the discarded fish (smaller fish would lead to greater losses per ton of discard, although the increase in catchability with size in this range suggests that much of the discard might be closer to 2 kg than 0.7 kg).

These estimated discards would occur in addition to an expected 25% reduction in yellowfin tuna catch biomass if all dolphin-fishing effort were redistributed to log-fishing effort (Punsly et al., 1994). By implication, a change entirely to log fishing could reduce yellowfin tuna catch in the ETP by as much as 30–50%. A change to a combination of school and log fishing would be less detrimental, but the actual effect would depend on the ratio of school-set effort to log fishing effort. Historical patterns of purse-seine fishing in the ETP, in which 50% or more of effort was directed to dolphin sets, obviously minimized any removal of new recruits from the fishery. Replacement of the entire dolphin-set effort with log-set effort would reverse that characteristic of the fishery, with potentially troublesome effects. Losses to "observed" recruitment as high as 50% may not be likely (Deriso[15]), but it is not difficult to imagine that sus-

[14] IATTC Third Quarter Report. 1995. Table 10. Inter-American Tropical Tuna Commission, c/o Scripps Institute of Oceanography, 8604 La Jolla Shores Drive, La Jolla, CA 92038.

[15] It is also possible that a shift to log fishing could make some areas, particularly offshore areas, uneconomical to fish so that

*continued on next page*

tained losses of even 30% annually might pose long-term problems for the fishery.

### Caveats

Our results are based on a number of assumptions, including among others 1) similarity between effort patterns of the U.S. and international fleets in the ETP and 2) constancy in discard per set within each set type, regardless of changes in ecological or economic forces (e.g. oceanographic conditions, fish prices, or both), proportions of effort devoted to each set type, or times and areas fished. In addition, our study does not address possible limitations on the availability of nondolphin sets, e.g. limitations on the number of available schools or logs, possible changes in fleet sizes with the elimination of dolphin sets (e.g. seiners leaving the ETP), or the possibility of greater emphasis on log fishing through increased use of FAD's (fish aggregating devices). Our analysis also assumes that the catch per vessel, the number of vessels in the fleet, and the geographic distribution of set types would remain constant regardless of the amount of effort expended within each set type.

One or more of these assumptions may be invalid (e.g. Punsly et al., 1994), but at present the effects of violating them cannot be assessed quantitatively. For example, relatively greater effort in area 1 would increase tuna discard more than we have estimated in the present study, but increased competition for logs might decrease overall fishing success. Conversely, increased availability of "logs" (where the population of logs has been increased by deployment of FAD's) could mitigate this competition and lead to an increase in fishing success. Conversely yet again, increased availability of logs might "dilute" the available tuna resource per log, leading to decreased fishing success. The actual system response cannot be ascertained at this time.

In addition, the fine-scale size structure of the discards, particularly from log sets, is unknown. The estimated number of individuals potentially lost per short ton varies by a factor of three; at the lower estimate, only about 8% of recruits would be lost to discard; at the higher estimate, closer to 25% would be lost. More estimates await subsampling studies not yet completed. However, even a moderate estimate of 15% loss per year is difficult to dismiss as unimportant, particularly in combination with the significant increase in landed recruits that will result from increased log fishing.

More detailed data on size structure of the bycatch would also make it possible to address the issue of changes in the discard of medium to large yellowfin tuna that might occur in response to changes in effort distribution. Large and medium yellowfin can only become discard in the event that they grow to medium or large size; increases in log fishing will decrease survival of young yellowfin tuna and decrease the probability that these fish will show up later either as direct catch or as discards. Such detailed size-structure data would also make it possible to translate all discard data to a standardized age, making it easier to compare discards between size classes (e.g. a single 2-year-old yellowfin tuna might be found to be equivalent to 100 or more 6-month-old fish if mortality remained the assumed constant average over time). These more detailed studies should be possible in future given the intensive discard sampling program initiated recently by the IATTC (Deriso).[16]

## Conclusions

The work presented here provides only a general overview of the apparent situation based on data available to date, but the implications of our simple study are serious and merit further consideration. Our calculations, although only approximate, imply strongly that a change from dolphin to school or (especially) log fishing (or both), although it might alleviate the problem of dolphin mortality, could have significantly detrimental effects on other components of the eastern tropical Pacific Ocean ecosystem, not the least of which is the commercial resource upon which the fishery rests.

## Acknowledgments

We thank Al Jackson, for his help and advice about data collection methods and data form interpretation, and the Inter-American Tropical Tuna Commission, for generously making available their summary data on tuna discards from the ETP tuna purse-seine fleet. We also thank Richard Deriso, Martin Hall, and

[15] *continued*
the predicted redistribution of log and school effort to those areas might not occur. Instead, the fishery would likely contract to more nearshore areas, similar to the situation during the 1960's. Yellowfin tuna resident in the offshore zones would escape all exploitation with the resulting appearance of a much smaller stock—on the order of another 25% reduction in recruitment (Deriso, R. 1995. IATTC, c/o Scripps Institute of Oceanography, 8604 La Jolla Shores Drive, La Jolla, CA, 92038. Personal commun.).

[16] Deriso, R. 1996. IATTC, c/o Scripps Institute of Oceanography, 8604 La Jolla Shores Road, La Jolla, CA 92038. Personal commun.

Rick Punsley of the IATTC and Robert Brownell and Pierre Kleiber of NMFS, for their insightful and helpful comments on various drafts of this manuscript.

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# Reproductive dynamics of southern bluefin tuna, *Thunnus maccoyii*

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**Abstract.**—We investigated the spawning dynamics of southern bluefin tuna, *Thunnus maccoyii*, using ovaries obtained from fish caught on the spawning ground in the northeast Indian Ocean and their main feeding grounds in the Southern Ocean, between October 1992 and June 1995. Only sexually mature southern bluefin tuna were taken on the spawning ground and were caught in every month except July, although relative abundance was low from May to August. Peaks in abundance occurred during October and February. Individuals do not spawn over the whole season, and there is a turnover of fish on the spawning ground. The presence of oocytes in all stages of development and the absence of a hiatus in the oocyte size-frequency distributions between unyolked and early yolked oocytes indicate that southern bluefin tuna have asynchronous oocyte development and indeterminate annual fecundity. The presence of either migratory nucleus or hydrated oocytes and postovulatory follicles in the ovaries of many females indicates that southern bluefin tuna are capable of multiple spawning. On the basis of the proportion of females with postovulatory follicles, it appears that females spawn on average every 1.1 days. The average spawning batch fecundity, estimated from counts of hydrated oocytes, was 6.0 million oocytes or 57 oocytes per gram of body weight.

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Fishery Bulletin 96: 223–236 (1998).

Southern bluefin tuna, *Thunnus maccoyii,* are large, migratory pelagic fish with a circumglobal distribution between 30°S and 50°S. Stocks are considered to be overexploited, and parental stocks, in particular, are considered depleted (Caton et al., 1990; Anonymous[1]). Of all the tunas, bluefin tunas (*T. maccoyii* and *T. thunnus*) are the best adapted to cold water (Carey, 1973) and thus are able to occupy the rich feeding grounds of the temperate oceans. However, like other tunas, the early life history of southern bluefin tuna is restricted to warm waters, and the only known spawning area is in the tropical east Indian Ocean where surface water temperatures exceed 24°C during the spawning period (Yukinawa and Miyabe, 1984; Yukinawa, 1987) (Fig. 1). Juveniles leave the spawning grounds within a few months of hatching and move south along the continental shelf of Western Australia. This movement is probably assisted by the Leeuwin Current (Shingu, 1967; Maxwell and Cresswell, 1981). Juveniles first appear in the warm waters of the Great Australian Bight as one-years-olds in summer and then disperse along the West Wind Drift in winter.

Ichthyoplankton surveys have been used to define southern bluefin tuna spawning grounds and season of spawning. Southern bluefin tuna larvae have been caught within latitudes 7° and 20°S and longitudes 102° and 124°E from September to March (Ueyanagi, 1969; Yonemori and Morita, 1978; Yukinawa and Miyabe, 1984; Nishikawa et al., 1985; Yukinawa and Koido, 1985; Yukinawa, 1987; Davis et al., 1990). However, the northerly limit of spawning is not clear because there has been little sampling effort in Indonesian territorial waters. Apart from a general understanding of the location and timing of spawning and the associated migration patterns, little detailed information is available on the reproductive dynamics of southern bluefin tuna. To understand spawning seasonality, spawning frequency, and batch fecundity with greater accuracy, we analyzed ovarian samples from fish captured on spawning grounds in the northeast Indian Ocean and feeding grounds in the Southern Ocean (in waters off Tasmania, New Zealand, and South Africa)

## Materials and methods

Southern bluefin tuna ovaries were obtained from two sources: Indonesian-based longlining vessels fishing on the northern part of the spawning

[1] Anonymous. 1994a. Report of the thirteenth meeting of Australian, Japanese and New Zealand scientists on southern bluefin tuna. Report to management, 20–29 April 1994, Ministry of Agriculture and Fisheries, Wellington, New Zealand, 13 p.

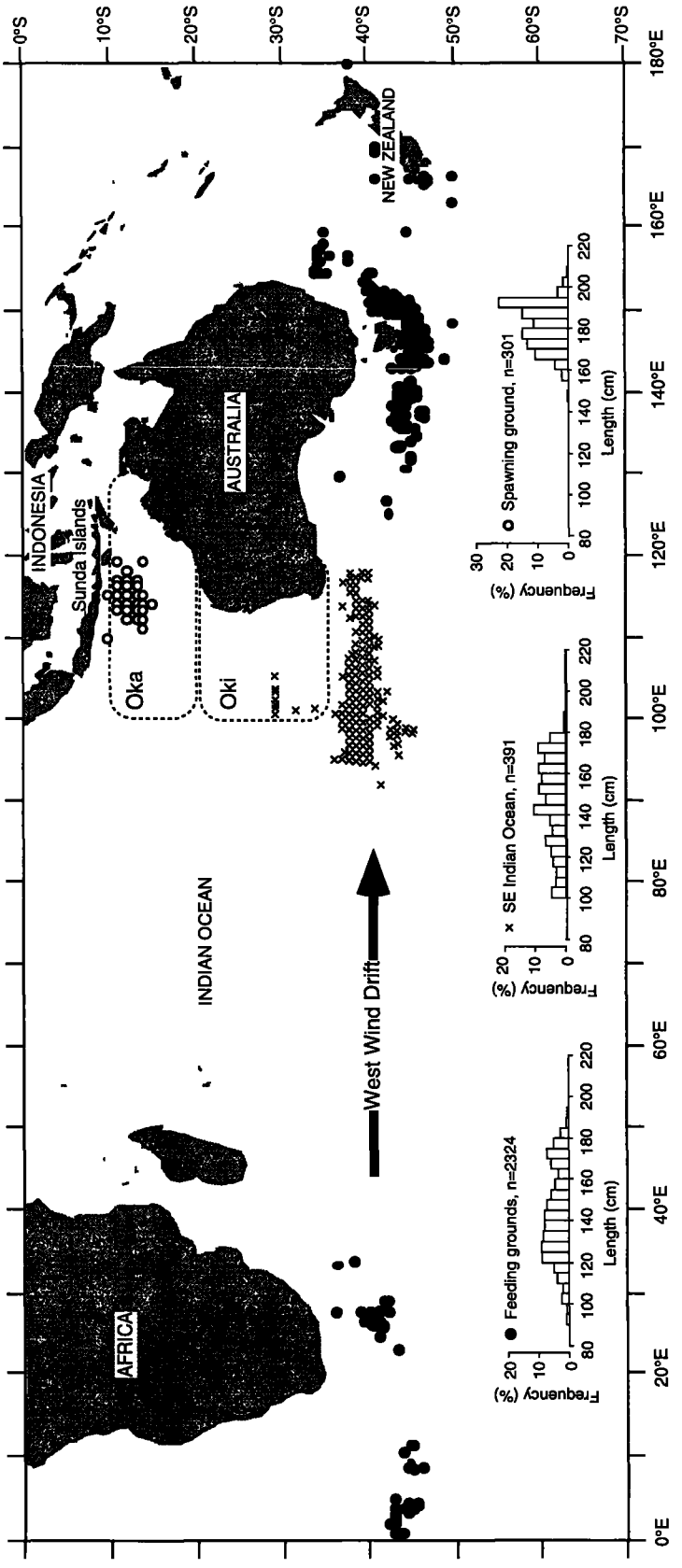


**Figure 1**

Locations where southern bluefin tuna ovaries were collected. Length-frequency distributions are shown for tuna sampled on the spawning grounds (○) in the northeast Indian Ocean; in the SE Indian Ocean (×) through which the spawning grounds are accessed; and on the feeding grounds along the West Wind Drift (•) in waters off Tasmania, New Zealand, and South Africa. The "Oka" and "Oki" fishing grounds referred to by previous researchers (Kikawa, 1964a, 1964 b; Shingu, 1970) are shown.

ground in the northeast Indian Ocean; and Japanese longine vessels operating in the Southern Ocean (on feeding grounds off Tasmania, New Zealand, and South Africa and on staging grounds in the southeast Indian Ocean) (Fig 1).

The ovaries of 475 females were collected from the complete size range of southern bluefin tuna caught on the spawning ground. Ovaries were removed at sea, labelled, stored on ice, and matched with the corresponding tuna carcass at Benoa in the Sunda Islands. Dressed weight (where fish was gilled, gutted, its fins removed, and its tail stock left intact) was measured to the nearest kg, and fork lengths of most fish to the nearest cm. A subsample was removed from 200 ovaries and fixed in 10% buffered formalin. The ovaries were frozen and flown by airfreight, along with the subsample, to Australia. In addition, up to 30% of all longline catches landed at Benoa were monitored and the individual weights and lengths of southern bluefin tuna were recorded.

Ovaries from the Southern Ocean were collected at sea from the fishing grounds around Tasmania, New Zealand, South Africa, and the southeast Indian Ocean. The areas around Tasmania, New Zealand, and South Africa are considered to be feeding grounds for immature and adult southern bluefin tuna, whereas the southeast Indian Ocean is the area where pre- and postspawning fish are caught during the spawning season. In total, ovaries were collected from 2,340 females from the feeding grounds in the Southern Ocean and from 393 females from the southeast Indian Ocean. Ovaries were frozen immediately after collection. Fork lengths were measured to the nearest cm.

In the laboratory, a core subsample was taken from each ovary while frozen. Subsamples were fixed in 10% buffered formalin, embedded in paraffin, and standard sections were prepared for histological examination (cut to 6 μm and stained with Harris's haematoxylin and eosin). All ovaries collected on the spawning grounds and 53 of the ovaries collected from the Southern Ocean were processed in this way.

Ovaries were thawed, trimmed of fat, blotted dry, and weighed to the nearest g. The mean diameter (random axis to the nearest μm) of five oocytes from the most advanced group of oocytes (MAGO) was determined for each ovary with a video coordinate digitizer connected to an Ikegami video camera mounted on a stereomicroscope at 50× magnification. Gonad index was calculated as

$$GI = W/L^3 \times 10^4,$$

where $W$ = gonad weight in g; and
$L$ = length to caudal fork in cm (Kikawa, 1964a; Shingu, 1970).

All ovaries were examined for residual hydrated oocytes as evidence of spawning activity.

## Histological classification and spawning frequency

Because many of the ovaries were frozen before a subsample could be removed, it was necessary to assess whether histological sections prepared from frozen ovarian material could be used to determine gonad stage and spawning activity. A comparison was made between histological sections prepared from 200 ovaries which were subsampled both before and after freezing. Although considerable cell destruction was observed in the histological sections from frozen tissue, oocytes, atretic oocytes, and postovulatory follicles were still distinguishable and could be classified.

Histological sections were classified with criteria similar to those developed for northern anchovy, *Engraulis mordax* (Hunter and Goldberg, 1980; Hunter and Macewicz, 1980, 1985a, 1985b), skipjack tuna, *Katsuwonus pelamis* (Hunter et al., 1986) and yellowfin tuna, *Thunnus albacares* (Schaefer, 1996). Each ovary was staged by the most advanced group of oocytes present into one of five classes: unyolked, early yolked, advanced yolked (Fig. 2A), migratory nucleus (Fig. 2B), or hydrated (Fig. 2C). In order to determine the relation between atresia (resorption of oocytes) and spawning, ovaries were also classified by the level of α and β stage of atresia in advanced yolked oocytes. During the α stage of atresia, yolk resorption takes place (Fig. 2D). During the β stage of atresia, the remaining granulosa and thecal cells are reorganized and resorbed leaving a compact structure containing several intercellular vacuoles.

Ovaries were classified into one of the following five atretic states:

0 no α atresia present, but advanced yolked oocytes are;
1 <10% of advanced yolked oocytes are in the α stage of atresia;
2 10–50% of advanced yolked oocytes are in the α stage of atresia;
3 >50% of advanced yolked oocytes are in the α stage of atresia;
4 100% of advanced yolked oocytes are in the α stage of atresia, or no advanced yolked oocytes are present but oocytes in the β stage of atresia are present.

Spawning frequency was determined by the postovulatory follicle method of Hunter and Macewicz (1985a). This method uses the incidence of females with postovulatory follicles less than 24 hours old to define the fraction of the population spawning. Because the time of capture was not available, we could not assign ages to postovulatory follicles based on the estimated time of death relative to the estimated time of spawning. Postovulatory follicles were, therefore, aged according to their state of degeneration with criteria developed for skipjack tuna, yellowfin tuna, and bigeye tuna, *Thunnus obesus* (Hunter et al., 1986; McPherson, 1988; Nikaido et al., 1991; Schaefer, 1996), all of which spawn in water temperatures above 24°C and resorb their postovulatory follicles within 24 hours of spawning. We assumed that southern bluefin tuna resorb postovulatory follicles at the same rate as other tropical spawning tuna because water temperature appears to be the dominant factor governing resorption rates (Fitzhugh and Hettler, 1995). We recorded postovulatory follicles in histological sections according to methods of Hunter and Macewicz (1985a), Hunter et al. (1986) and Schaefer (1996). Postovulatory follicles were classified as either 0 (absent), 1 (new) (Fig. 2E), 2 (less than 12 hours old), 3 (12 to 24 hours old), or 4 (indistinguishable owing to tissue decay). The incidence of females with postovulatory follicles of any age was used to determine spawning frequency.

Females were classified into one of four spawning states depending on the oocytes, atretic state, and postovulatory follicle class present.

1 Immature: Ovaries contain no advanced yolked oocytes or advanced yolked oocytes in the α stage of atresia. No residual hydrated oocytes present.

2 Spawning: Ovary contains advanced yolked oocytes and evidence of spawning activity (migratory nucleus or hydrated oocytes or postovulatory follicles). Less than 100% of advanced yolked oocytes are in the α stage of atresia. If >50% of advanced yolked oocytes are atretic, early yolked oocytes are considered nonatretic.

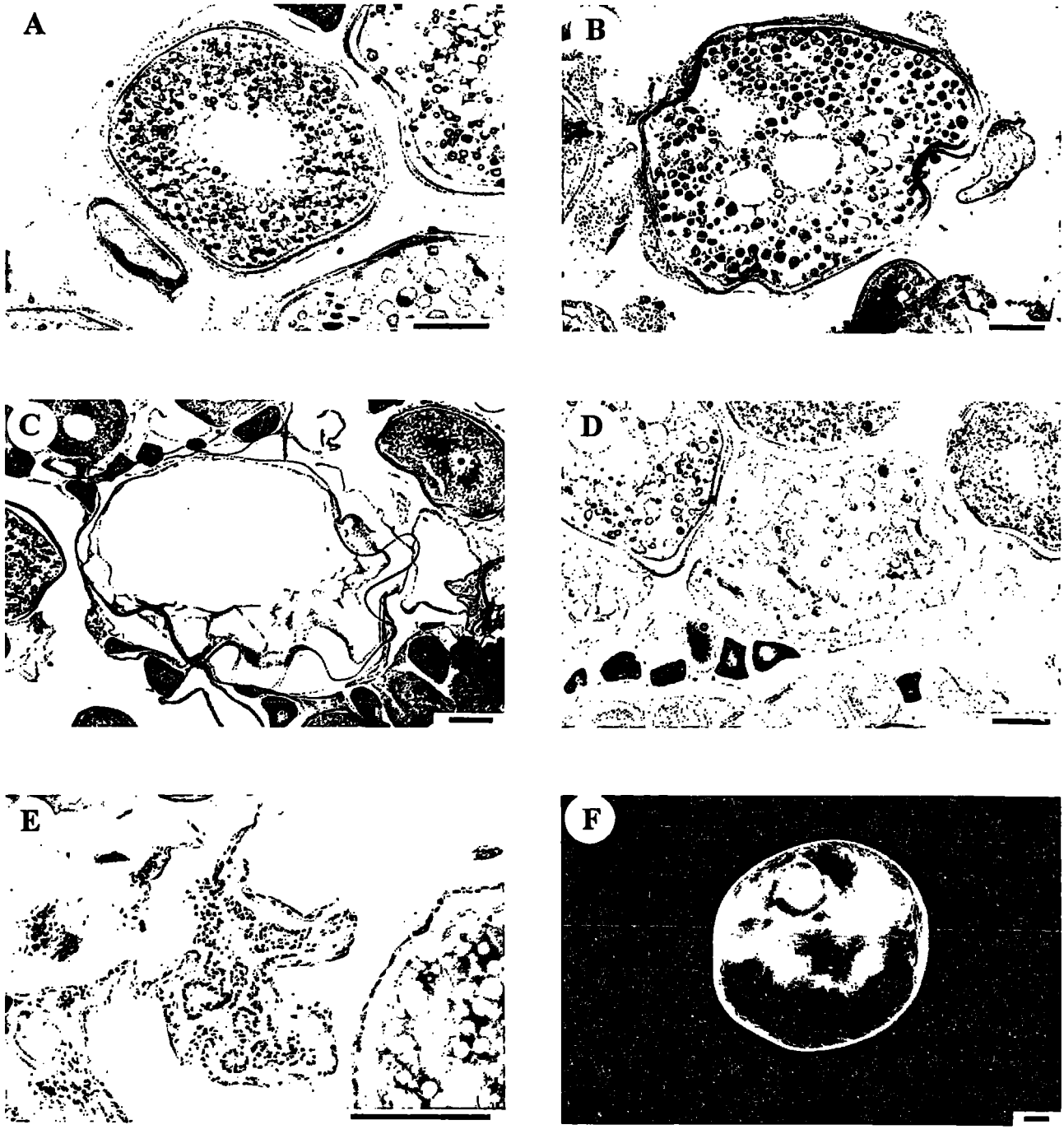


**Figure 2**

Photomicrographs of southern bluefin tuna, *Thunnus maccoyii*, ovarian tissue collected from the spawning ground (northeast Indian Ocean) between October 1992 and June 1995. (A–E) Transverse sections stained with Harris's haematoxylin and eosin. (A) advanced yolked-stage oocyte; (B) migratory-nucleus-stage oocyte; (C) oocyte in the early stages of hydration with some yolk plates still visible; (D) fully yolked oocyte in a stage of α atresia; (E) new postovulatory follicle; (F) hydrated-stage whole oocyte. Bar = 0.1 mm.

3 Nonspawning (mature): Ovary contains advanced yolked oocytes but no evidence of spawning activity (migratory nucleus or hydrated oocytes or postovulatory follicles). Less than 100% of advanced yolked oocytes are in the α stage of atresia. If >50% of advanced yolked oocytes are atretic, early yolked oocytes are considered nonatretic.
4 Postspawning: Ovaries contain either: 1) >50% of both early and advanced yolked oocytes in the α stage of atresia; 2) 100% of advanced yolked oocytes in the α stage of atresia; or 3) no yolked oocytes are present but oocytes in the β stage of atresia are, and residual hydrated oocytes may or may not be present.

### Fecundity

To find out if the annual fecundity of southern bluefin tuna could be determined before spawning began, we measured the distribution of oocyte sizes within ovaries of four females at various stages of maturity. Ovarian subsamples containing at least 1,000 oocytes were removed from each ovary, teased apart, and each oocyte (greater than 100 μm in diameter) was measured in a random orientation to the nearest μm under a stereomicroscope.

We estimated batch fecundity (the number of hydrated oocytes released per spawning) by the gravimetric method (Hunter et al., 1985) for 21 females with unovulated hydrated oocytes (Fig. 2F). A split-plot analysis of variance (ANOVA) was used to determine the appropriate locations to subsample the ovary. The data were structured with 6 fish examined as blocks, ovarian lobe (left or right) as main plots and twelve subsamples as subplot effects. Six subsamples were taken from each ovarian lobe in the anterior, middle, and posterior regions of both lateral sides (Table 1). A significant difference between ovarian lobes was found in the number of hydrated oocytes per gram of total ovary weight and in the lobe × lateral side interaction. Consequently, a subsample of less than 1 g was taken from both sides of each ovarian lobe. Each subsample, consisting of a core from the periphery to the lumen, was weighed to the nearest 0.01 mg and fixed in 10% buffered formalin. Each subsample was teased apart and washed through two sieves, similar to those of Lowerre-Barbieri and Barbieri (1993) to separate out the hydrated oocytes, which were counted under a stereomicroscope. The number of hydrated oocytes per gram of ovary was raised to the weight of both ovaries to give an estimate of batch fecundity for each of the four subsamples.

## Results

### Ovary maturation

Ovaries obtained from fish on the spawning ground (northeast Indian Ocean), the staging ground (southeast Indian Ocean), and the feeding grounds (Southern Ocean) show clear differences in development based on ovary weight (Fig. 3). Females less than 140 cm showed no or minor ovary development; therefore it appears that they would not spawn in the coming season. The majority of ovaries collected from the feeding grounds weighed less than 1 kg and had a gonad index (GI) of <3.2, whereas ovaries from the southeast Indian Ocean weighed up to 2.8 kg and had GI values up to 4.9. Some of the ovaries of females caught between August and December on the feeding grounds showed signs of maturity, because their MAGO's were in advanced yolked stage with diameters greater than 400 μm. Females from the spawning ground had larger ovaries, weighing up to 7.4 kg. All ovaries from fish collected on the spawning ground had a MAGO diameter greater than 400 μm, except three ovaries with MAGO's between

**Table 1**

Split-plot ANOVA of the effect of location of tissue sample from southern bluefin tuna, *Thunnus maccoyii*, ovaries on the number of hydrated oocytes per gram of ovary.

| Source | df | Sum of squares | Mean square | *F*-value | *P*-value |
|---|---|---|---|---|---|
| Blocks | | | | | |
| Fish | 5 | 17,201,897 | 3,440,380 | 279.721 | <0.001 |
| Main plots | | | | | |
| Lobe | 1 | 168,326 | 168,326 | 13.686 | 0.014 |
| Main plot error | 5 | 61,497 | 12,299 | 0.764 | 0.580 |
| Subplot effect | | | | | |
| Lateral side | 1 | 711 | 711 | 0.044 | 0.834 |
| Region | 2 | 34209 | 17,104 | 1.062 | 0.353 |
| Lateral side × region | 2 | 82,599 | 41,300 | 2.565 | 0.087 |
| Lobe × lateral side | 1 | 152,159 | 152,159 | 9.450 | 0.003 |
| Lobe × region | 2 | 12,944 | 6,472 | 0.402 | 0.671 |
| Lobe × region × lateral side | 2 | 58,207 | 29,103 | 1.808 | 0.175 |
| Subplot error | 50 | 805,044 | 16,101 | | |

153 and 207 μm. These three female had recently finished spawning because their ovaries contained either 100% of advanced yolked oocytes in an α atretic state or residual hydrated oocytes but no healthy advanced yolked oocytes.

## Spawning Season

Southern bluefin tuna were caught on the spawning ground during every month, except July. Catch per unit of effort (CPUE), expressed as the number of fish caught per vessel fishing day, showed that abundance was low from May to August (Fig. 4). In the 1993–94 season, abundance peaked in February, and in the following season, abundance peaked in October and February.

Females with high GI values were caught on the spawning ground during all months that ovaries were collected. Gonad index values were variable, however, ranging from 1.3 to 13.1. There were no peaks or trends during this time. These observations suggest that spawning activity is constant throughout the season.

## Histological classification

All ovaries examined histologically from the Southern Ocean were classified as immature, nonspawning (mature), or postspawning. Females greater than 140 cm, with advanced yolked oocytes, collected between August and December were probably prespawners preparing to migrate to the spawning ground. Surprisingly, 78% of these prespawning females had α atresia of advanced yolked oocytes. The level of atresia present was related to ovary weight or GI (Fig. 5). The ovaries of all females with GI's<2 had no or <10% α atresia (atretic states 0 or 1), whereas 80% of females with GI's>2 had 10 to 50% α atresia (atretic state 2). This finding suggests that females begin resorbing yolked oocytes as their ovaries mature. Atresia of unyolked or early yolked oocytes was not observed in these females. Postspawning females were found in the Southern Ocean in all months that ovaries were collected, including both the early and late months of the spawning season (September to December). Ovaries, however, were not collected between January and March from the Southern Ocean.

The ovaries of all females sampled on the spawning ground were classified as mature because they contained either advanced yolked oocytes or oocytes in either an α or β stage of atresia. Of the females, 69.2% were classed as spawning, 30.2% as nonspawning, and the remaining 0.6% as postspawning on the basis of oocyte stage, atretic stage, and postovulatory follicle class present. The mean GI

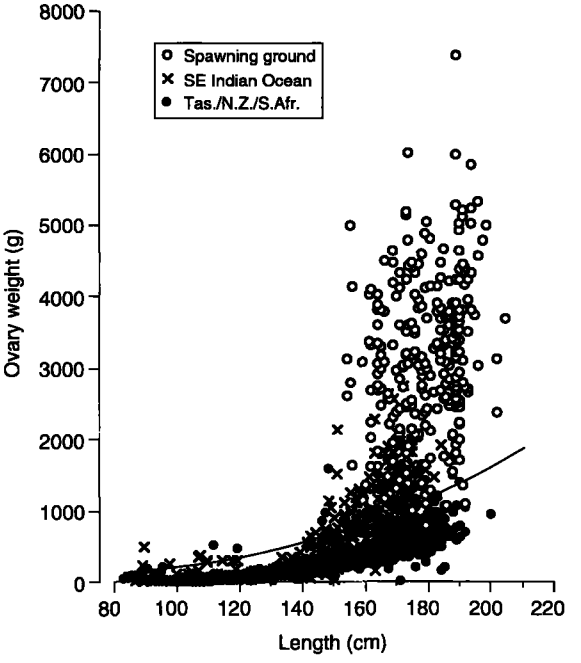


**Figure 3**

The relation between ovary weight and body length for southern bluefin tuna, *Thunnus maccoyii*, caught on the spawning ground in the northeast Indian Ocean, on the staging grounds in the southeast Indian Ocean, and on feeding grounds off Tasmania, New Zealand, and South Africa. The line represents a gonad index of 2.

(±95% CI) of spawning and nonspawning females was similar at 5.4 (0.37) and 5.6 (0.29) but GI was not calculated for postspawning females because the sample size was too small ($n$=3). Spawning and nonspawning females were found on the spawning ground throughout the spawning season. All postspawning females were collected in October. The majority of females identified as spawning (86.1%) had ovaries containing no or less than 10% α atresia. The remaining 13.9% of females identified as spawning contained more than 10% α atresia. Nearly 90% of nonspawning females, however, contained 10–50% of advanced yolked oocytes in an α atretic state. We have used this criterion of <10% α atresia to group fish we considered to be at the height of spawning, which we refer to as "prime spawning condition."

There did not appear to be any seasonal trends in the proportions of each atretic state throughout the spawning season (Fig. 6), suggesting that spawning in southern bluefin tuna is not synchronized. This is confirmed by an absence of an increase in the incidence of postspawning females at the end of the spawning season.

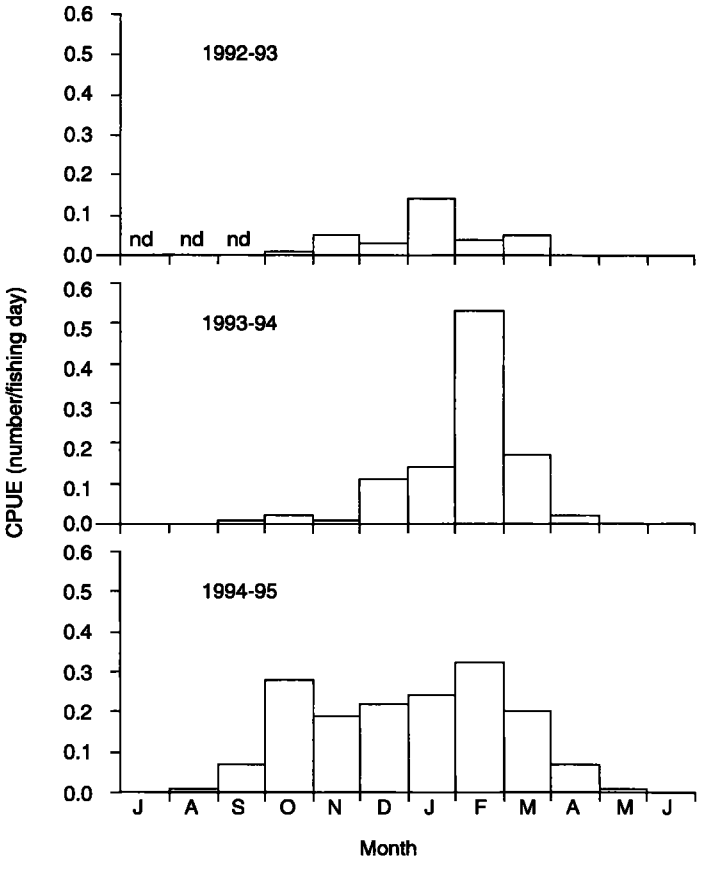


**Figure 4**

CPUE of southern bluefin tuna, *Thunnus maccoyii*, (number caught per vessel per fishing day) by month for three consecutive spawning seasons. From December 1993, additional companies with higher catch rates were monitored causing an increase in CPUE from that date.

## Spawning frequency

The ovaries of 68.7% of females had evidence of recent or imminent spawning activity. The absence of a peak in the percentage of females spawning during the season (Fig. 7) suggests that spawning intensity was constant. The ovaries of 120 females gave evidence of two spawning events, that is, they contained maturing oocytes (either migratory nucleus or hydrated) and postovulatory follicles. The majority of ovaries contained progressively more developed oocytes with progressively older postovulatory follicles. If postovulatory follicles are resorbed within 24 hours of spawning, then southern bluefin tuna are capable of spawning daily.

The fraction of females that spawned per day, measured by the fraction of females with postovulatory follicles, was 0.62 (Table 2). This gave a weighted mean spawning interval of about 1.6 days. If we examine only those females in "prime spawning condition" (<10% α atresia), then the spawning fraction was 0.90 giving a weighted mean interval of 1.1 days. This value suggests that once females start spawning, they spawn daily.

## Batch fecundity

The ovaries of nonspawning females collected from the southeast Indian Ocean contained a large number of unyolked oocytes less than 150 μm in diameter (Fig. 8). This number was reduced as females matured during the season and began spawning. Oocytes of all stages were present in the ovary of spawning females; therefore it appears that southern bluefin tuna have an asynchronous pattern of oocyte development. Unlike species with determinate annual fecundity, a gap in the oocyte size-frequency distribution did not appear between unyolked (<200 μm diameter) and early yolked (200 to 400 μm diameter) oocytes (Fig. 8). This finding indicates that advanced yolked oocytes are continually maturing during the spawning season, from the pool of unyolked oocytes, and are spawned. The ovaries of 86% of females identified as spawning contained no or <10% α atresia, indicating that the majority of advanced yolked oocytes that are matured are spawned. Residual hydrated oocytes were found in the ovaries of only 5.6% of females collected from the spawning ground, which suggests that all hydrated oocytes are released at each spawning.

The mean relative batch fecundity and 95% CI's estimated for 20 females of known weight was 56.5 (±16.1) oocytes per gram of body weight. The relation between length (cm) and batch fecundity (BF) was best described by the equation

$$BF = (4.78242 \times 10^{-17}) \times L^{7.530}$$

($F$=23.9, df=1,18, $P$<0.001) (Fig. 9).

However, the relation was highly variable with only 57% of the variance explained by the regression.

# Discussion

## Spawning ground and season

All female southern bluefin tuna sampled on the spawning ground were mature, and the smallest was

147 cm long. Davis[2] showed that the mean length at which 50% of southern bluefin tuna were mature was around 152 cm based on oocyte diameters>400 μm, and 162 cm based on GI's>2. Warashina and Hisada (1970) considered that southern bluefin tuna caught on the "Oka" grounds (Fig. 1) in the 1960's reached maturity at 130 cm, although reanalysis of these data showed that this was the smallest size at which they matured and that 50% maturity was not reached until 146 cm (Anonymous[3]). Size at maturity appears to have increased progressively since then, being 154 cm in the period 1985–89. The increase in length at maturity can be attributed, in part, to an increase in the growth rate of southern bluefin tuna between the 1960's and 1980's reported by Hearn,[4] because maturity appears to be determined by age rather than length.

[2] Davis, T. L. O. 1995. Size at first maturity of southern bluefin tuna. Council for the conservation of southern bluefin tuna scientific meeting; 10–19 July 1995, Shimizu, Japan. Far Seas Fisheries Res. Lab., Shimizu, Japan, Rep. CCSBT/95/9, 9 p.

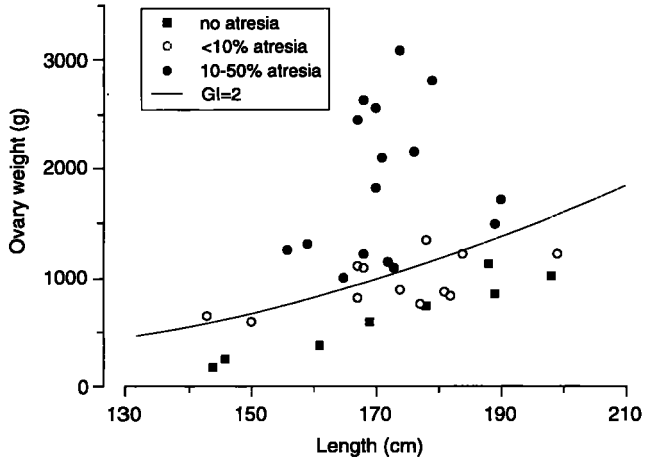


**Figure 5**

Levels of atresia by length of southern bluefin tuna, *Thunnus maccoyii*, caught off the spawning ground in the northeast Indian Ocean.

The abundance of southern bluefin tuna on the spawning ground was not constant throughout the spawning season. Catch-per-unit-of-effort data indicated that a peak in catches occurred in October for the 1993–94 season and in October and February for the 1994–95 season. Japanese CPUE data also indicate there were two peaks in abundance on the spawning ground in the early years of the fishery; the first in September and October and the second in February and March (Davis and Farley[5]). The reason for two peaks is unknown but could be linked to the widespread distribution of southern bluefin tuna along the feeding grounds of the West Wind Drift. It is possible that the cues for migration to the spawning grounds take place at different times depending on where the fish are prior to spawning. Fish may reach spawning condition earlier in some areas than in others. Also the time needed to migrate to the spawning grounds would differ between areas.

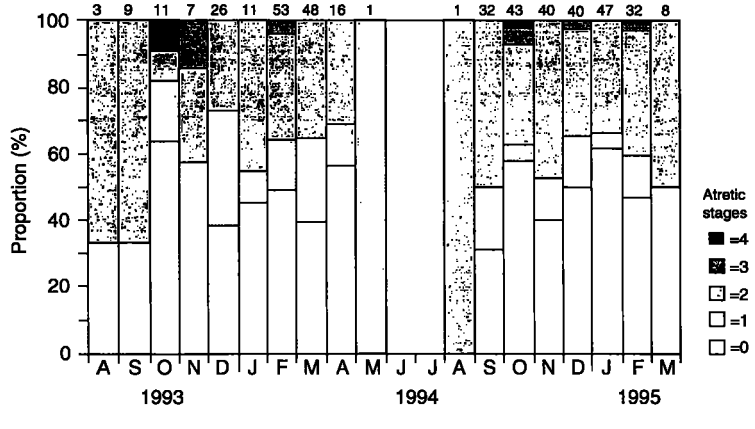


**Figure 6**

The proportion of each atretic stage by month recorded in southern bluefin tuna, *Thunnus maccoyii*, caught on the spawning ground.

## Spawning duration

This study extends the known duration of the spawning season of southern bluefin tuna. Females were caught on the spawning ground in

[3] Anonymous. 1994b. Report of the southern bluefin tuna trilateral workshop, 17 January–4 February 1994, CSIRO, Hobart, Australia, 172 p.

[4] Hearn, W. S. 1994. Models for estimating SBT age at length during the transition period. 13th SBT trilaterial scientific meeting; 19–29 April 1994, Wellington, New Zealand. Ministry of Agriculture and Fisheries, Wellington, New Zealand, Rep. SBFWS/94913, 16 p.

[5] Davis, T. L. O., and J. H. Farley. 1995. Catch monitoring of fresh tuna caught by the Bali-based Indonesian/Taiwanese longline fishery. Council for the conservation of southern bluefin tuna scientific meeting; 10–19 July 1995, Shimizu, Japan. Far Seas Fisheries Res. Lab., Shimizu, Japan, Rep. CCSBT/95/2, 18 p.

**Table 2**

Spawning fraction and spawning interval of southern bluefin tuna, *Thunnus maccoyii*, by month for all females and females in prime spawning condition collected from the spawning ground between October 1992 and March 1995. POF = postovulatory follicles. *n* = no. of fish in sample.

| | | All females | | | | Females in prime spawning condition (<10% atresia) | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | *n* | *n* with POF's | Spawning fraction | Spawning interval (days) | *n* | *n* with POF's | Spawning fraction | Spawning interval (days) |
| 1992 | Oct | 3 | 1 | 0.3 | 3.0 | 1 | 1 | 1.0 | 1.0 |
| | Nov | 1 | 1 | 1.0 | 1.0 | 1 | 1 | 1.0 | 1.0 |
| | Dec | 1 | 1 | 1.0 | 1.0 | 1 | 1 | 1.0 | 1.0 |
| 1993 | Jan | 9 | 8 | 0.9 | 1.1 | 7 | 7 | 1.0 | 1.0 |
| | Feb | 3 | 1 | 0.3 | 3.0 | 2 | 1 | 0.5 | 2.0 |
| | Mar | 4 | 4 | 1.0 | 1.0 | 4 | 4 | 1.0 | 1.0 |
| | Apr | 2 | 0 | 0.0 | | | | | |
| | Aug | 3 | 3 | 1.0 | 1.0 | 1 | 1 | 1.0 | 1.0 |
| | Sep | 9 | 4 | 0.4 | 2.3 | 3 | 3 | 1.0 | 1.0 |
| | Oct | 11 | 8 | 0.7 | 1.4 | 9 | 8 | 0.9 | 1.1 |
| | Nov | 7 | 4 | 0.6 | 1.8 | 4 | 4 | 1.0 | 1.0 |
| | Dec | 26 | 20 | 0.9 | 1.1 | 19 | 19 | 1.0 | 1.0 |
| 1994 | Jan | 11 | 6 | 0.5 | 1.8 | 6 | 6 | 1.0 | 1.0 |
| | Feb | 53 | 36 | 0.7 | 1.5 | 34 | 31 | 0.9 | 1.1 |
| | Mar | 48 | 31 | 0.6 | 1.5 | 31 | 28 | 0.9 | 1.1 |
| | Apr | 16 | 13 | 0.8 | 1.2 | 11 | 11 | 1.0 | 1.0 |
| | May | 1 | 0 | 1 | 0 | | | | |
| | Aug | 1 | 1 | 1.0 | 1.0 | | | | |
| | Sep | 32 | 12 | 0.4 | 2.7 | 16 | 11 | 0.7 | 1.5 |
| | Oct | 43 | 26 | 0.6 | 1.7 | 26 | 22 | 0.8 | 1.2 |
| | Nov | 40 | 22 | 0.6 | 1.8 | 21 | 19 | 0.9 | 1.1 |
| | Dec | 40 | 23 | 0.6 | 1.7 | 26 | 22 | 0.8 | 1.2 |
| 1995 | Jan | 47 | 30 | 0.6 | 1.6 | 31 | 28 | 0.9 | 1.1 |
| | Feb | 32 | 20 | 0.6 | 1.6 | 19 | 19 | 1.0 | 1.0 |
| | Mar | 8 | 3 | 0.4 | 2.7 | 4 | 3 | 0.8 | 1.3 |
| Unknown | | 16 | 11 | 0.7 | 1.5 | 8 | 8 | 1.0 | 1.0 |
| Total | | 467 | 289 | 0.62 | 1.62 | 287 | 259 | 0.90 | 1.11 |

all months except July, although the main spawning season appeared to be from September to April when CPUE was highest. Previously, the spawning period was reported to be limited to the months of September to March (Mimura, 1958; Kikawa, 1964a). Our study included fish from areas north of that traditionally fished by Japanese vessels, which may explain the extended spawning season. An increase in the length of the spawning season towards equatorial waters has been suggested for many species including black skipjack, *Euthynnus lineatus* (Schaefer, 1987), yellowfin tuna, *Thunnus albacares* (McPherson, 1991), blue marlin, *Makaira nigricans* (Hopper, 1990), and other multiple spawning fish (Qasim, 1955).

The actual duration of spawning in individual southern bluefin tuna could not be de-

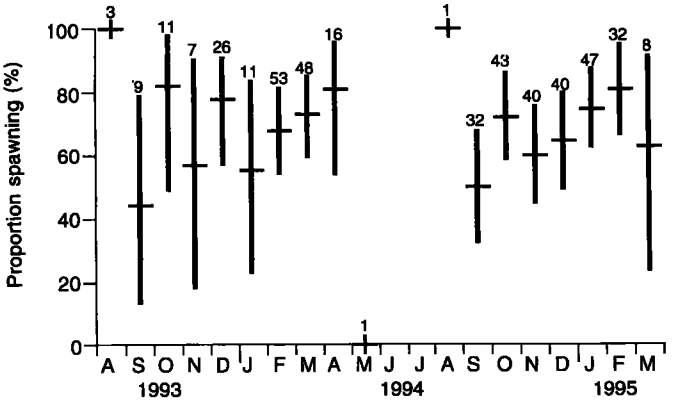


**Figure 7**

The proportion of southern bluefin tuna, *Thunnus maccoyii*, spawning by month. The vertical bars indicate 95% confidence limits of the mean for samples sizes >5. The numbers indicate sample sizes.

termined. However, the prevalence of females in different phases of spawning activity (nonspawning, spawning, or postspawning) on the spawning ground should be in direct proportion to the duration of that phase, if females in each phase are equally catchable. The ratio of nonspawners:spawners:postspawners for females caught on the spawning ground was estimated to be 0.30:0.69:0.01 or 0.44:1:0.01 if spawners are set as 1. In other words, spawning females were 2.3 times more prevalent than nonspawning females and 108 times more prevalent than postspawning females on the spawning ground. This finding indicates that the duration of the nonspawning phase is less than half, and the postspawning phase one onehundredth, of the duration of the spawning phase.

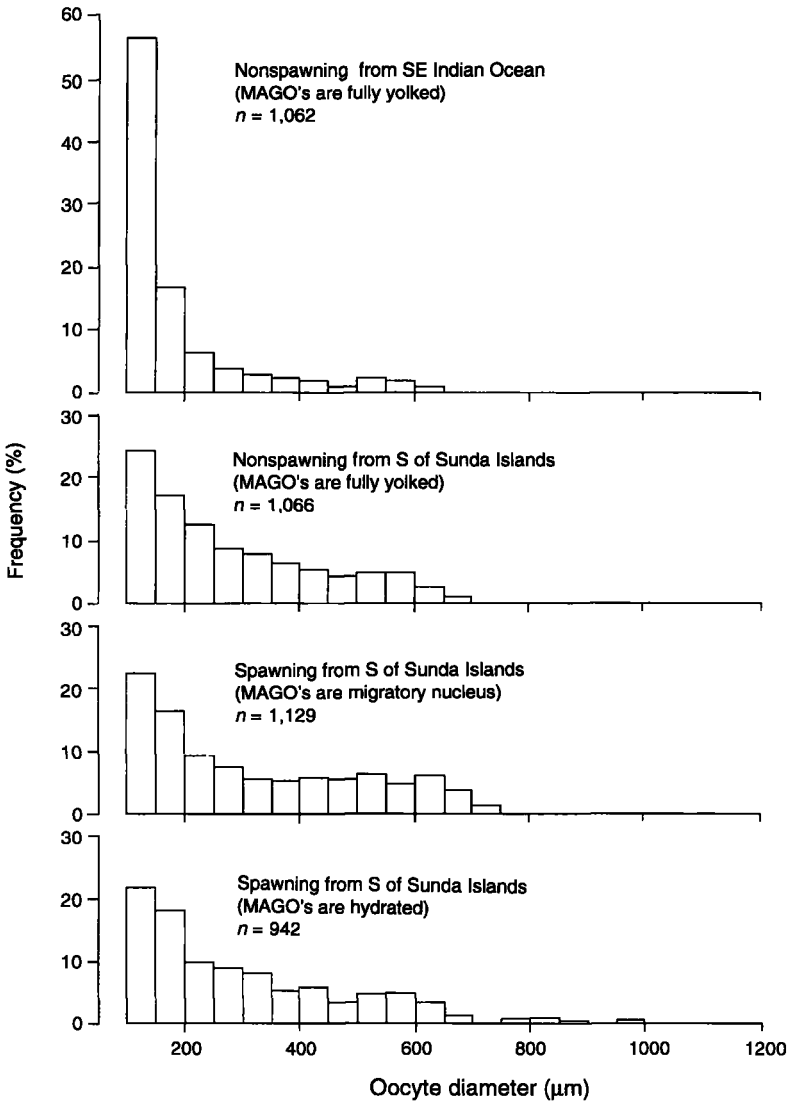


**Figure 8**

Size-frequency distribution of oocytes representing the advanced stages of maturation, by 50-µm intervals, in southern bluefin tuna, *Thunnus maccoyii*, ovaries. Only oocytes >100 µm were measured.

## Spawning frequency and fecundity

The potential annual fecundity of southern bluefin tuna is indeterminate (not fixed prior to spawning) because unyolked oocytes are continually matured and spawned during the season. Annual fecundity is indeterminate in many tuna species such as black skipjack (Schaefer, 1987), skipjack tuna (Hunter et al., 1986), and yellowfin tuna (Schaefer, 1996). The fecundity of southern bluefin tuna was estimated by Kikawa (1964b) as the number of advanced yolked oocytes in the ovary, and by Thorogood (1986) as the number of oocytes >300 µm in diameter in the ovary. These estimations of fecundity were not potential annual fecundity because southern bluefin tuna are capable of continuously maturing and spawning oocytes from a pool of unyolked oocytes (<300 µm).

Southern bluefin tuna can spawn many times during a season. The ovaries of 25% of the females collected from the spawning ground contained evidence that they had all recently spawned (postovulatory follicles) and were about to do so again (migratory nucleus or hydrated oocytes). We assume that postovulatory follicles persist in the ovaries of southern bluefin tuna for about 24 hours as has been found in other tropical spawning tunas (Hunter et al., 1986; McPherson, 1988; Nikaido et al., 1991; Schaefer, 1996). The average interval between spawning in southern bluefin tuna, estimated from the proportion of ovaries containing postovulatory follicles, was 1.1 days for females in "prime spawning condition." Similar spawning rates have been reported in other tuna species that spawn in tropical waters: 1.54 and 1.27 days for yellowfin tuna (McPherson, 1991; Schaefer, 1996); 1.1 days for bigeye tuna (Nikaido et al, 1991) and 1.18 days for skipjack tuna (Hunter et

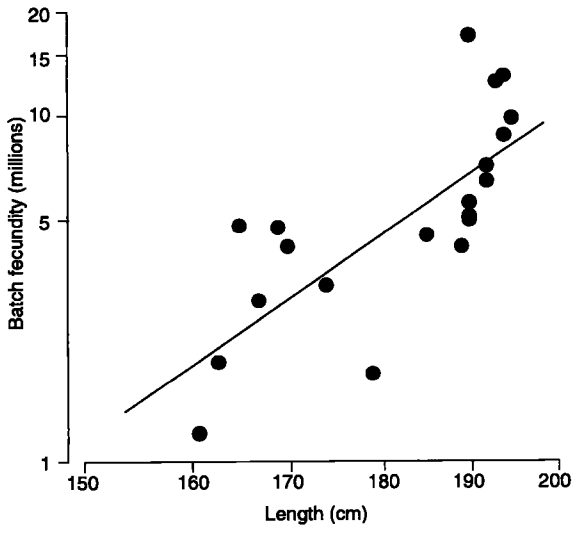


**Figure 9**

The relation between batch fecundity and length of southern bluefin tuna, *Thunnus maccoyii*, (both scales are logged).

al., 1986). The mean spawning interval of reproductively active yellowfin tuna (those whose ovaries contain advanced yolked oocytes and may or may not contain postovulatory follicles and contain no or less than 50% α atresia) was 1.14 days (Schaefer, 1996). Histological sections indicated that slight variations in the lengths of individual spawning intervals exist in southern bluefin tuna, which may be normal or the result of external stresses such as decreased food availability or the stress of capture (Hunter et al., 1986).

Our estimate of mean relative batch fecundity for southern bluefin tuna (57 oocytes per gram of body weight) is similar to that found in yellowfin tuna (68 oocytes per gram of body weight) (Schaefer, 1996) but less than that for black skipjack tuna (81 to 153 oocytes per gram of body weight) (Schaefer, 1987) and skipjack tuna (40 to 130 oocytes per gram of body weight) (Stéquert and Ramcharrum, 1995). Hunter et al. (1985) reported that the minimum number of females needed for a reliable batch fecundity estimate in northern anchovy was 50. We, however, found only 21 southern bluefin tuna ovaries with unovulated hydrated oocytes from the 475 ovaries collected from the spawning ground. There could be several reasons for this. Oocytes in the hydrated stage may be very short-lived in southern bluefin tuna, which would reduce the chance of sampling females with hydrated ovaries. Spawning may occur during a specific time of the day, and if sampling was not conducted just prior to this, fewer females with hydrated ovaries would be collected. Spawning in many tuna species is known to occur in the late evening or early morning (Hunter, et al., 1986; Schaefer, 1987; McPherson, 1991; Nikaido et al., 1991; Schaefer, 1996). Because our ovaries were sampled from females caught on Indonesian-based longlining vessels, which generally operate during daylight hours (Ishida et al., 1994), the chances of catching females that were about to spawn would be reduced. Further, if spontaneous spawning occurred while southern bluefin tuna were on the longlines, then fewer females with unovulated hydrated oocytes would be sampled. Spontaneous spawning has been observed in skipjack tuna soon after capture (Kaya et al., 1982).

Batch fecundity in southern bluefin tuna increased with body length. The variation in estimates for females of similar size may be normal because females were collected in different years and at different times in their spawning cycles. Hunter et al. (1985) suggested that the relation between batch fecundity and fish weight should be estimated annually in northern anchovy because batch fecundity can vary by a factor of 2 between years. Batch fecundity is also known to vary significantly during the spawning season in many fish species (Conover, 1985). A decrease in batch fecundity during the spawning season was found in Atlantic mackerel, *Scomber scombrus* (Watson et al., 1992), as individuals moved northwards. Batch fecundity can also peak during the middle of the spawning season if conditions are suitable, or it can remain constant if conditions are unpredictable (Conover, 1985).

## Spawning strategies

We found that many southern bluefin tuna ovaries, collected both on and off the spawning ground, contained moderate levels of α atresia (10–50% of advanced yolked oocytes). High levels of α atresia are thought to indicate a decline in the spawning rate (Hunter and Macewicz, 1985a) and would normally occur towards the end of an individual's spawning season. Hunter and Macewicz (1980) classified northern anchovy as early postspawning if their ovaries contained less than 50% of advanced yolked oocytes in an α atretic state and postspawning if their ovaries contained more that 50% α atresia. Because we found that ovarian atresia increased with gonad index in the ovaries of prespawning females from the Southern Oceans, it appears that increased α atresia will not always mark the cessation of spawning in southern bluefin tuna. This ovarian atresia found in prespawning females could be a normal hormonal process that occurs during ovary maturation, as suggested by Macer (1974) for horse mackerel (*Trachurus*

*trachurus*). Atresia can also be caused by starvation as Scott (1962) found in maturing rainbow trout (*Salmo gairdneri*). It is not known if prespawning southern bluefin tuna are resorbing developing oocytes to gain the energy required for migration to the spawning grounds or because the ovary can only accommodate a certain volume of oocytes.

Many ovaries from nonspawning southern bluefin tuna ovaries collected from the spawning ground contained 10–50% atresia of their advanced yolked oocytes. The precise reproductive stage of these females is unclear. The similarity in atretic levels between these females and the prespawning females from the southern oceans, and in their high mean GI values, suggests that these females may have only just arrived on the spawning ground or were in the early stages of their spawning cycle. If this is the case, the relatively large numbers of nonspawning females (30% of females sampled) indicates that southern bluefin tuna may delay the onset of spawning possibly to recover from the energetic costs of migration. Their presence on the spawning ground throughout the spawning season suggests that there is a continual supply of new spawners onto the ground. Alternatively, southern bluefin tuna may not spawn continuously while on the spawning ground, but in pulses. The nonspawning females may be experiencing a lull in spawning activity between spawning episodes. The presence of many nonatretic yolked oocytes in their ovaries suggests that they could recommence spawning in the current season. Lunar spawning cycles have been documented in many tropical spawning fishes (see reviews by Johannes, 1978; Taylor, 1984; Robertson et al., 1990), however, we detected no evidence of a lunar cycle.

Spawning in southern bluefin tuna is not synchronized for the stock as a whole. There are several lines of evidence to support this statement: the presence of prespawning females both on and off the spawning ground throughout the spawning season; the absence of a peak in GI during the spawning season; the constant level of spawning intensity (percentage of females spawning) during the spawning season; the absence of any increase in the incidence of oocyte atresia towards the end of the spawning season; and the presence of postspawning females off the spawning ground both early and late in the spawning season. Thus it appears that there is a turnover of new spawners replacing old spawners on the spawning ground throughout the season. A similar turnover of pre- and postspawning southern bluefin tuna has been reported on the "Oki" fishing ground (Fig. 1) south of the spawning ground (Kikawa, 1964b). Nonsynchronized spawning has been found in other multiple spawning species such as skipjack tuna (Cayré and Farrugio, 1986), chub mackerel, *Scomber japonicus* (Dickerson et al., 1992), and Atlantic croaker, *Micropogonias undulatus* (Barbieri et al., 1994). Cayré and Farrugio (1986) reported that spawning in skipjack tuna in the Atlantic is synchronized within schools. Individuals in a school can mature rapidly and spawn batches of oocytes simultaneously when conditions become favourable. It is unclear if southern bluefin tuna can do this, or to what extent the long spawning season is the result of individual fish or schools arriving on the spawning ground and maturing at different times. It is also unclear if the spawning period is constant for all individuals. In many species, including jack mackerel, *Trachurus symmetricus*, and chub mackerel, *Scomber japonicus*, older spawners are reported to have a longer spawning period than younger spawners (Knaggs and Parrish, 1973; MacCall et al., 1980).

The low number of postspawning female southern bluefin tuna (3) found on the spawning ground suggests that as soon as individuals have finished spawning they quickly move off the ground. The reasons for this departure are uncertain, but it may be due to decreased food availability through increased competition because many fish are gathering to spawn in a relatively small area, or to an inability to withstand the warmer water temperatures on the spawning ground for extended periods of time. Adult bluefin tuna are unique among the tunas because they live predominantly in cold water (as low as 5°C) and only move into warmer waters to spawn (Olson, 1980). Their ability to maintain their body temperature above ambient water temperature, through the development of an increased lateral blood supply and heat exchangers, has enabled them to occupy higher latitudes than many tuna species can tolerate. This adaptation to cold water, however, may preclude them from extended stays in warm water, resulting in a rapid migration off the spawning ground after spawning.

After spawning, southern bluefin tuna migrate south from the spawning ground into the West Wind Drift (Mimura, 1962) to feed and gain condition over the southern winter months. The minimum time for an individual to travel to the Southern Ocean however, is unknown. The maximum sustained swimming speeds of small yellowfin and skipjack tunas are predicted to be between 2 and 4 body lengths/s (Brill, 1996), and these values are thought to be similar in other active fish species. Southern bluefin tuna are unlikely to travel at their maximum sustained swimming speed in a straight line from the spawning grounds to the southern oceans because they will be feeding on the way south. If a 180-cm fish travelled at between 1 and 2 body lengths/s, from the spawning ground to Tasmania (6,000 km), it would take

between 19 and 39 days. Warashina and Hisada (1970) reported that lean fish with brownish meat have been caught in the Tasman Sea as early in the spawning season as November. These lean fish are believed to be postspawning females who have recently migrated from the spawning ground. The earliest that postspawning females were observed on the spawning ground was in October of both the 1993–94 and 1994–95 spawning seasons. The appearance of these postspawning fish on the spawning ground in October and again around Tasmania in November supports the idea that southern bluefin tuna are capable of travelling that distance in approximately one month. It also supports the idea that individuals spawn for a relatively short time in contrast to the whole season.

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# Dolphin prey abundance determined from acoustic backscatter data in eastern Pacific surveys

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**Abstract.**—Acoustic backscatter data from a 38-kHz echo sounder and a 150-kHz acoustic Doppler current profiler (ADCP) were collected during Southwest Fisheries Science Center marine mammal surveys in the eastern Pacific aboard the NOAA ship *David Starr Jordan* in 1992 and 1993. These data were processed to give profiles of volume scattering strength. A deep scattering layer dominated the time-depth patterns of backscatter. This layer migrated from a depth of 300–400 m during the day to 0–100 m at night, when it was located just above the thermocline. The source of backscatter was primarily small fish and squid, which are dolphin prey. Dolphin sighting rates were correlated positively with nighttime volume scattering strength above the thermocline. Spatial and temporal variability of prey biomass in the surface layer, as indexed by volume scattering strength, may have important consequences for dolphin feeding, as well as for distributional responses to habitat variability by dolphins.

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Acoustic data, consisting of the returns of pulses of sound from targets in the water column, are routinely used to assess fish distribution and abundance (Forbes and Nakken, 1972; Johannesson and Mitson, 1983; MacLennan and Simmonds, 1992). Such data are now also being used to quantify the biomass and distribution of zooplankton and micronekton (Greene and Wiebe, 1990; Hewitt and Demer, 1993). Innovative techniques using multifrequency amplitude and phase information can give estimates of size, movement, and acoustic properties of individual planktonic organisms (Farmer and Huston, 1988; Holliday et al., 1989). Another approach in acoustic studies of zooplankton and micronekton has been to employ instrumentation that is used routinely, notably the acoustic Doppler current profiler (ADCP, Roe and Griffiths, 1993). Several studies have used uncalibrated ADCP echo intensity data, with various levels of processing, to estimate relative patterns of plankton biomass distribution in space and time (Flagg and Smith, 1989; Plueddemann and Pinkel, 1989; Smith et al., 1989; Heywood et al., 1991).

We have been collecting echo intensity data from a 38-kHz echo sounder since 1986 and from a 150-kHz ADCP since 1992 on Southwest Fisheries Science Center marine mammal surveys. This report describes data collection and processing and presents results from two cruises during which nearly complete data sets were obtained (population of *Delphinus* stocks 1992 [PODS92] and 1993 [PODS93]) (Fig. 1). Other data collected on these surveys provide a context for these results in terms of predators and habitat. Line-transect data were collected for dolphin abundance estimates (Mangels and Gerrodette, 1994a, 1994b). We use sighting rate here as an index of dolphin abundance. Physical and biological oceanographic data were also collected to characterize habitat variability (Philbrick et al., 1993).

## Materials and methods

A 38-kHz Simrad EK-400 scientific sounder was used on NOAA ship *David Starr Jordan* beginning in 1986. Rather than a commercial echo integrator, we used an acoustic data acquisition (ADA) system, consisting of an analog-to-digital converter and a personal computer. A 150-kHz ADCP was installed on the *Jordan* in 1991. We collected nearly complete sets of 38- and 150-kHz acoustic data in 1992 and 1993.

A sonar equation relating volume backscattering strength per $m^3$ ($S_v$,

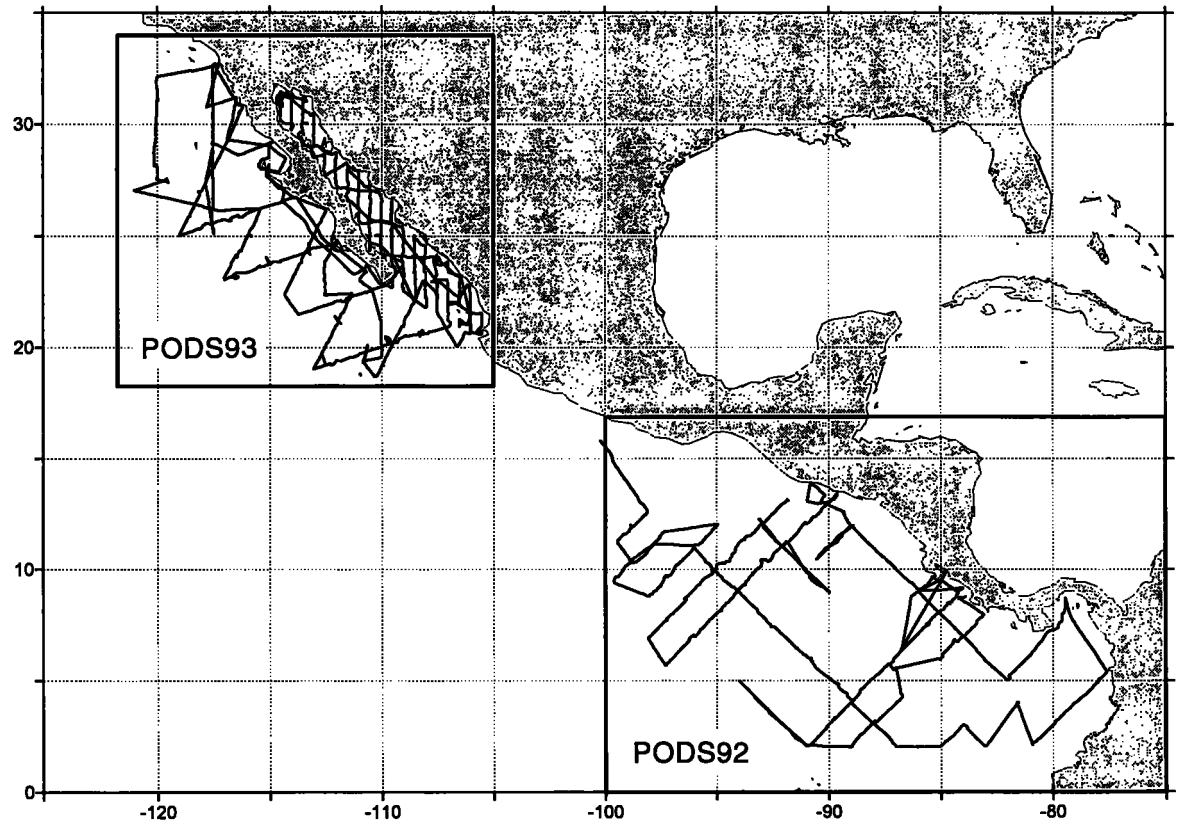


**Figure 1**

Cruise tracks of NOAA ship *David Starr Jordan* during Population of *Delphinus* Stocks (PODS) cruises (28 July–2 November 1992) and (28 July–6 November 1993).

dB // 1μ*Pa* at 1 m) to the echo level (EL), integrated and recorded after 20logR TVG amplification in the transceiver, was formulated as follows (Simmonds, 1990):

$$S_v = EL - (SL + RR) - 10 \log \psi - 10 \log c\tau/2, \quad (1)$$

where $EL$ = 20 log $V_0$ (dB) ($V_0$="gain-controlled envelope" signal, volts);
$SL$ = source level (dB);
$RR$ = receiver response (including receiver gain and transducer on-axis voltage response), dB;
10 log $\psi$ = equivalent beam angle;
$c$ = speed of sound (m/s);
$\tau$ = pulse length (1 × 1/1,000 per millisecond).

Transmission loss does not appear in this equation because it was corrected by a 20log$R$ time-varied gain (TVG) function applied to $V_0$ in the transceiver. The TVG was checked with a transceiver test mode that input a constant voltage signal. The recorded 20log$R$ TVG output did not differ significantly from the theoretical function ($TVG = 20 \log R + 2\alpha R$, where $\alpha$ is the nominal sound absorption coefficient of 0.008 dB/m and $R$ is range in meters). The range ($R$) was based on a sound velocity entered into the control unit at the start of the cruise.

On-axis sensitivity ($SL$+$RR$) was estimated by measuring the system response ($EL$) to a standard calibration sphere (38.1-mm diameter tungsten carbide with 6% cobalt binder, target strength $TS$ = –42.3 dB; Foote, 1990) suspended 7 m below the transducer. In this case, Equation 1 reduces to

$$EL = TS + (SL + RR), \quad (2)$$

where $EL = 20 \log V_0 + 20 \log R$.

The "gain-controlled envelope" signal ($V_0$) represents a peak voltage and was converted to a root-mean-square (rms) voltage by multiplying by $1/\sqrt{2}$. The additional 20log$R$ term was added to the system's 20logR TVG, used during the echo-integration surveys, to correct for the spherical spreading of the return from the point calibration target. Solving Equa-

tion 2 for the on-axis sensitivity gave ($SL+RR$) = 74.2 dB.

Operationally, the ADA program squared $V_o$, which is proportional to pressure at the face of the transducer, to give an echo intensity value (Eq. 1) proportional to power or energy flux per unit of area. The intensity values were then binned in 50 10-m bins between 10-m and 510-m depth. The binned intensities were averaged at 10-sec intervals over ten minutes (60 pings), equivalent to an interval of 3 km at the typical ship speed of 18 km/h. Recorded intensities were converted to units of decibels (dB=10 log $I/I_r$, where $I_r$ represents the standard reference of 1μPa at a 1-m distance from the face of the transducer). Then, a correction to the TVG function was formulated by using depth-dependent sound velocities and attenuation coefficients calculated from CTD data taken once or twice daily with the algorithms of Francois and Garrison (1982). Finally, a constant 53.4 dB was subtracted to account for the combined source level, transducer response, receiver gain, and beam pattern terms ($-SL - RR - 10 \log \psi - 10 \log \tau/2$) in Equation 1. The equivalent beam angle is very difficult to measure directly without special apparatus; therefore we used the manufacturer's nominal value (10 log $\psi$=–19.6 dB; Simrad EK400 Scientific Sounder Instruction Manual).

Acoustic Doppler current profilers have been used since the early 1980's to estimate current velocity from the Doppler shift of acoustic signals backscattered from suspended matter (plankton and sediments) in the water column. Echo intensity is calculated and recorded during data-processing. RD Instruments has developed instrument modifications and an algorithm to calibrate these values and to estimate volume backscattering strength ($S_v$, dB). The algorithm is based on the following working version of a sonar equation (RD Instruments, 1990):

$$S_v = 10 \log \left[ \begin{array}{c} 4.47 \times 10^{-20} K_2 K_s (T_t + 273) \\ \left(10^{k(E-E_r)/10} - 1\right) R^2 / \\ \left(c P K_1 10^{-2\alpha R/10}\right) \end{array} \right], \quad (3)$$

where $K_2$ = system noise factor = 4.3;
$K_s$ = system constant = $4.17 \times 10^5$;
$T_t$ = transducer temperature (°C);
$k$ = conversion factor = 0.435 dB/count;
$E$ = echo intensity (counts);
$E_r$ = reference level for echo intensity (counts);
$R$ = slant range (m);
$c$ = sound velocity (m/s);
$P$ = transmit pulse length = 8 m;
$K_1$ = power into the water, $W$;
$\alpha$ = sound absorption coefficient (dB/m).

Although this equation was formulated to be applied to individual beams of the ADCP, we used average amplitude data for $E$ because we were using an empirical reference level ($E_r$). The reference level for echo intensity, $E_r$, represents thermal noise in the system electronics plus ship noise. $E_r$ was assumed equal to the minimum value of $E$ (<40 counts) observed in each average profile or ensemble (~740 pings in 10 minutes). The manufacturer states that this in-situ method of estimating $E_r$ is preferable to calculating $E_r$ from measured system temperatures. Because ship temperature was relatively constant and water temperature ranged over only 4°C in 1992 and 10°C in 1993, $E_r$ varied by only (±7–8 counts. Values of $E$ < 10 counts were not used (RD Instruments, 1990) and appear as blank areas at depth in 150 kHz time-depth sections (Fig. 2).

Values for $c$ and $\alpha$ were calculated from CTD data taken once or twice daily according to Francois and Garrison (1982). Transducer temperature, $T_t$, was assumed equal to observed surface temperature. Slant range, $R$, was corrected for estimated sound velocity in relation to the value assumed by the ADCP software (1,475 m/s). The conversion factor, $k$ (dB/count), depends on the temperature of the system electronics. However, the deck unit was located in a temperature-controlled room (18–21°C) so that the range of $k$ was 0.433 to 0.437 (<1 dB). Power into the water, $K_1$, was assumed constant and estimated to be 53.4 $W$ (RD Instruments, 1990). The ADCP was set up with 50 bins of length 8 m, starting at 4 m from the transducers.

In both the 38- and 150-kHz data sets, the depth bin representing the bottom was identified initially by an algorithm searching for strong gradients of $S_v(z)$. These results were modified by visual inspection of time-depth sections. Data from the bottom depth bin and below were excluded from subsequent analysis. Some 1992 and 1993 profiles of $S_v$ appeared to be biased low on account of sound attenuation due to bubbles beneath the ship during stationkeeping and during very rough weather (cf. Fig. 2, 20 August, at the first tick marking the morning CTD station). We identified biased profiles from anomalously low $S_v$ in bins below the top depth bin. The problem was more prevalent in the 150-kHz data (2.5% of 1992 profiles and 1.0% of 1993 profiles) than in the 38-kHz data (0.5% of 1992 profiles and 0.1% of 1993 profiles). We excluded the biased profiles from statistical analyses.

Dolphin sightings were recorded during daylight hours from the flying bridge of the vessel by a team

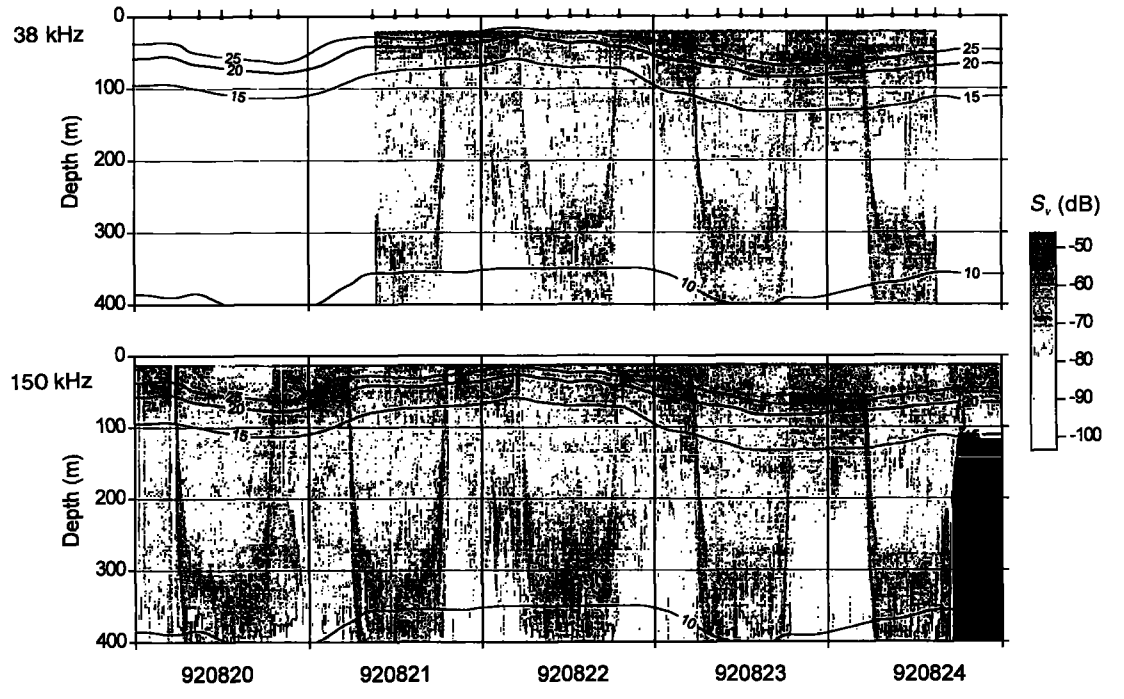


**Figure 2**

Time-depth sections of 38-kHz and 150-kHz volume scattering strength ($S_v$, dB) and temperature during five days of PODS92 surveys. Contour lines are isotherms (°C), from XBT (expendable bathythermograph) profiles at tick marks along top of section.

of three observers using 25-power binoculars (Mangels and Gerrodette, 1994a, 1994b). Local dolphin abundance was indexed by the number of sightings of spotted (*Stenella attenuata*), spinner (*S. longirostris*), striped (*S. coeruleoalba*), common (*Delphinus delphis* and *D. capensis*), bottlenose (*Tursiops truncatus*), Risso's (*Grampus griseus*), rough-toothed (*Steno bredanensis*), Fraser's (*Lagenodelphis hosei*), Pacific white-sided (*Lagenorhynchus obliquidens*), and unidentified dolphins. Daily numbers of sightings were standardized to sighting rates of schools or individuals per 100 km in optimum sea-state conditions (Gerrodette[1]). Sighting rates were log-transformed to normalize distributions before testing correlation with various time and depth means of $S_v(z,t)$. We report correlations with 150 kHz $\overline{S}_v$ here because data were collected on about 25% more days than those for 38kHz $\overline{S}_v$.

Acoustic and other data were gridded by kriging with the software SURFER (Golden Software, 1995). Variogram models were fitted to the data and the best fit was selected by using the original code based on Pannatier (1996). Contour maps were also generated with SURFER .

## Results

The five-day time-depth sections in Figure 2 illustrate features observed in all sections: 1) data at one or both frequencies were occasionally missing; 2) the 150-kHz signal was lost in the noise at depths >200 m; and 3) bottom depth was <400 m as on 24 August after about 1700 hours. All time-depth sections of $S_v$ were dominated by a deep-scattering layer (DSL) at 300–400 m depth during daylight hours and 0–100 m during the night. The DSL migrated about 200 m in 1–2 hours near dawn and dusk. Morning descent was generally more rapid than evening ascent. During some days, the DSL was split into two distinct layers at depth, separated by up to 100 m (cf. Fig. 2, 38 kHz section on 22 and 23 August).

The DSL was detected at both 38 and 150 kHz. However, the 150-kHz return from the DSL at its daytime depth was barely above background noise levels. The smaller effective depth range of the ADCP was due to 1) greater attenuation of sound at the higher frequency ($\alpha$=0.039 dB/m at 150 kHz com-

[1] Gerrodette, T. 1996. On estimating relative abundance. Unpubl. manuscript.

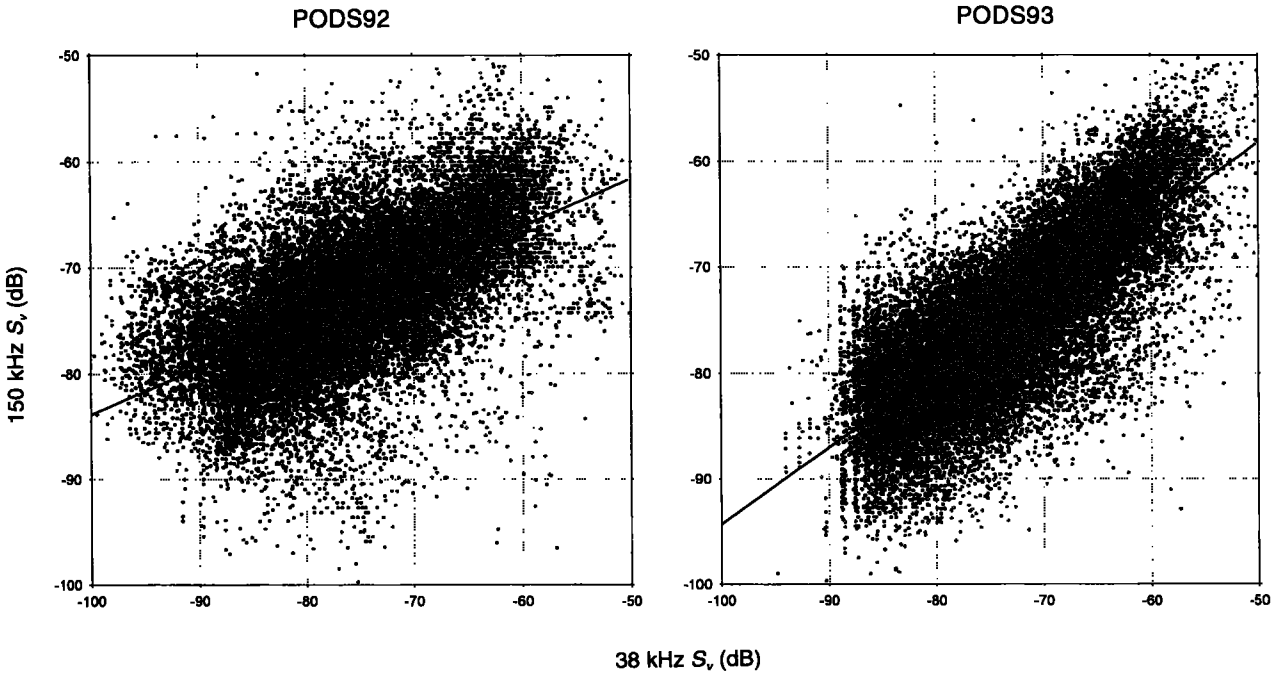


**Figure 3**

Relationships between 38-kHz and 150-kHz volume scattering strength ($S_v$, dB) in corresponding 10-and 8-m depth bins (centered at 25, 65, 105, 145, 185, 225, 265, and 305 m) at all times of day or night during PODS92 ($n$=24,193) and PODS93 ($n$=26,963) surveys.

pared with 0.008 dB/m at 38 kHz) and 2) transducer orientation 30° off the vertical, resulting in a slant range 15% greater than depth.

Volume scattering strengths at 38 and 150 kHz were significantly correlated (Fig. 3, $r$=0.58 in 1992 and $r$=0.77 in 1993). Some error in this relation is due to the different sizes and inexact depth matching of bins between frequencies. The ADCP samples echo intensity only in the last quarter of each depth bin, so that scattering is averaged over only 2 m, compared with 10 m for the 38-kHz echo sounder. Correlation decreased at depth (e.g. in 1993, $r$=0.83 at 25 m and $r$=0.53 at 185 m). This could have been due simply to the low signal to noise ratio at depth in the 150-kHz data. However, it probably also reflects changes in species and size composition, and thus spectral response, of scatterers at depth. The mean difference between 38- and 150-kHz volume scattering strength in Figure 3 was –2.9 dB in 1992 and 0.0 dB in 1993.

Spatial patterns of mean day and night volume scattering strength ($\overline{S}_v$) in the surface layer (0–100 m) were very similar at the two frequencies; therefore only the 38-kHz patterns are illustrated here (Figs. 4 and 5). On average, night values exceeded day values by 6.4 dB in 1992 and 11.0 dB in 1993 (Table 1). Thus, near-surface $\overline{S}_v$ was 4 and 13 times greater at night than during the day, indicating that 77–92% of the scatterers left the surface layer during the day. Mean surface $\overline{S}_v$ values (daily or nightly, 38 or 150 kHz) varied by 11.5 to 20.6 dB during the cruises, representing ranges of 14 to 115 times.

In 1992, low $\overline{S}_v$ was observed along 8–9°N both night and day (Fig. 4). $\overline{S}_v$ increased to the south towards the equator and to the north and east towards

**Table 1**

Mean day (0800–1600) and night (2000–0400) volume scattering strengths ($S_v$, dB) in the surface layer (0–100 m) in 1992 and 1993. Values are cruise means, with range in parentheses. PODS92 = Population of *Delphinus* Stocks 1992 cruise; PODS93 = Population of *Delphinus* Stocks 1993 cruise.

| | | Day | Night |
|---|---|---|---|
| PODS92 | 38 kHz | –75.1 (–82.2 to –70.7) | –68.6 (–77.1 to –62.0) |
| | 150 kHz | –73.9 (–83.7 to –69.0) | –67.5 (–76.8 to –57.3) |
| PODS93 | 38 kHz | –76.3 (–85.8 to –69.4) | –65.3 (–73.5 to –60.2) |
| | 150 kHz | –79.2 (–90.2 to –70.1) | –68.2 (–80.3 to –59.7) |

the coast. The highest $\overline{S}_v$ values were observed along the coast of Costa Rica and the coast of Mexico south of the Gulf of Tehuantepec (16°N, 95°W).

In 1993, $\overline{S}_v$ was high in the Gulf of California and along the Pacific coast of southern Baja California (Fig. 5). $\overline{S}_v$ was generally low in the northern and

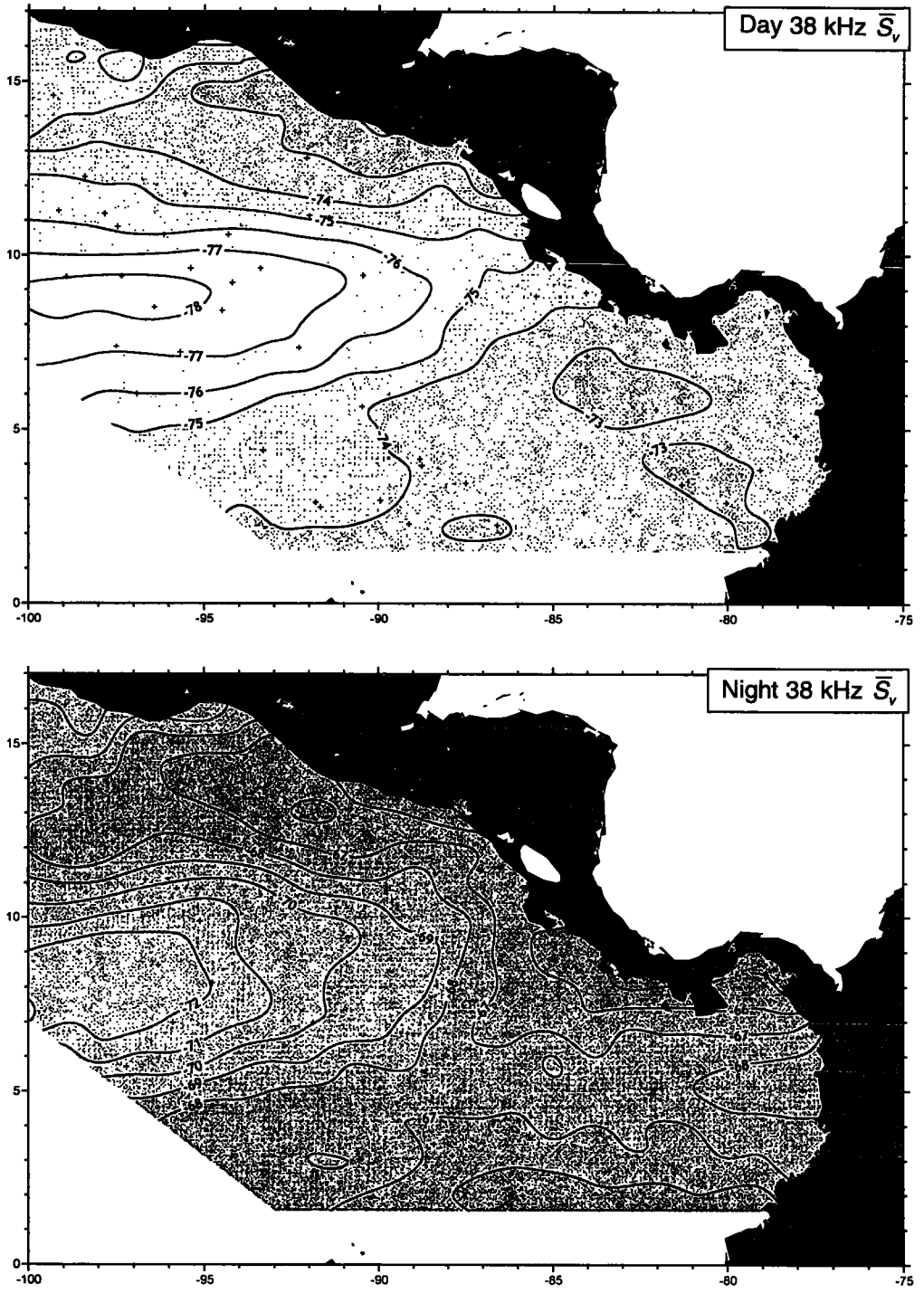


**Figure 4**

Maps of daily (0800–1600) and nightly (2000–0400) 38-kHz mean volume scattering strength ($S_v$, dB) in the surface layer (0–100 m) during PODS92 surveys, 28 July –2 November 1992.

offshore part of the study area and increased towards the southeast corner near Cabo Corrientes (20°N, 105°W).

Time-depth sections (Fig. 2) show a close relation between the deep scattering layer and the thermocline at night. The DSL ascended through the thermocline in the evening, then remained just above the thermocline until it descended in the early morning. The DSL followed changes in the depth of the thermocline during some nights (cf. 22–23 August, Fig. 2). Where the thermocline is deep, $S_v$ is maximum at 10–20 m above the thermocline and then declines closer to the surface. Where the thermocline is shallow, $S_v$ is maximum at, or very close to, the surface. The nighttime depth of the DSL was significantly correlated with thermocline depth, except for the 38-kHz DSL in 1993 (Table 2). Mean $\overline{S}_v$ above the thermocline was slightly, but not significantly, greater above more shallow thermoclines 1992.

Dolphin abundance, as indexed by sighting rates of schools or individuals per 100 km, was significantly correlated with nighttime mean $\overline{S}_v$ above the thermocline in 1992 and with 0–400 m mean $\overline{S}_v$ in 1993 (Table 3, the 150-kHz results are shown here owing to larger sample sizes but the 38-kHz results were similar). In 1992, both mean $\overline{S}_v$ above the thermocline and dolphin abundance were high near the countercurrent thermocline ridge along 9°N (Fig. 6). In 1993, mean $\overline{S}_v$ above the thermocline and dolphin abundance were relatively high near the mouth of the Gulf of California, at intermediate thermocline depths.

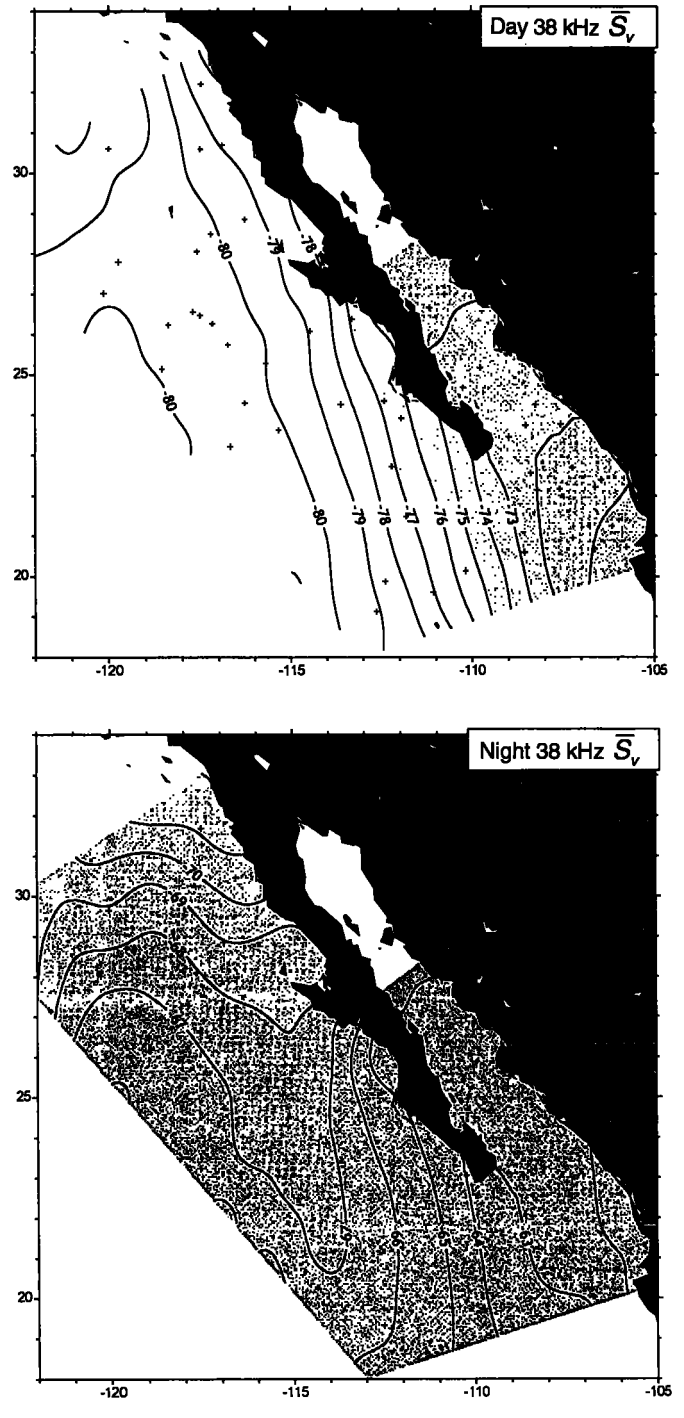


**Figure 5**

Maps of daily (0800–1600) and nightly (2000–0400) 38-kHz mean volume scattering strength ($S_v$, dB) in the surface layer (0–100 m) during the PODS93 survey, 28 July–6 November 1993.

## Discussion

Deep scattering layers have been observed throughout the Pacific with low-frequency depth sounders (<30 kHz). Tont (1976) reported mean daytime depths of 319 m in the eastern tropical Pacific and 282 m in the California Current, similar to the depths observed here (Fig. 2). Small mesopelagic fish with gas-filled swimbladders are now recognized to be the most important low-frequency backscatterers in the open ocean (Chapman, 1947; Marshall, 1951; Brooks, 1977), although early reports attributed DSL's to cephalopods (Lyman, 1948) or euphausiids (Hersey and Moore, 1948).

What do our acoustic observations represent? Volume scattering strength (dB) represents a sum of individual target strengths (TS), except at very high target densities where shadowing and multiple scat-

tering occur (MacLennan and Simmonds, 1992). Target strength is a nonlinear function of sound frequency and the cross-sectional area of the target (Demer and Martin, 1995) and TS per unit of area is typically expressed as a function of the dimensionless number ($ka$), where $k$ is the acoustic wavenumber ($k=2\pi/\lambda$) and $a$ is a characteristic dimension of the target (Chu et al., 1992). At low sound frequencies ($ka<1$, "Rayleigh" scattering), TS drops off rapidly. Thus, scattering of relatively low frequency sound by small targets is weak. At high frequencies ($ka>1$, "geometric" scattering), early models predicted TS to be approximately constant (Love, 1977). Most other models of geometric scattering are highly nonlinear, with deep nulls in individual TS versus ($ka$) curves. However, Chu et al. (1992) suggested that averaging over pings and individuals in field studies of volume backscattering should "smear out" these nonlinearities.

The wavelengths of 38-and 150-kHz sound correspond to target dimensions of approximately 4 and 1 cm, respectively. This is the effective size of macrozooplankton and micronekton organisms, such as euphausiids, siphonophores, small fish, and squid. Targets <4 cm, such as copepods, will scatter sound strongly at 150 kHz. Scattering of 38-kHz sound will be relatively weak Rayleigh scattering and may be undetectable over system noise. These smaller targets may have weakened the correlation between backscattering at the two frequencies (Fig. 3).

We were unable to make net tows to identify acoustic targets, owing to time constraints on the cetacean survey cruises. Therefore, we can make only an educated guess about the composition of the observed deep-scattering layers. Roe et al. (1984), in a uniquely comprehensive study of a community of vertically migrating organisms in the temperate northeast Atlantic, considered fish, decapod crustaceans, mysids, euphausiids, amphipods, copepods, ostracods, siphonophores, medusae, ctenophores, and chaetognaths. Ignoring small or weak scatterers, we must consider fish, crustaceans (decapods, mysids, and euphausiids), and siphonophores, as well as cephalopods, as possible components of the observed DSL's.

Average biomass densities of mesopelagic fish (primarily myctophids) and cephalopods are equal to, or slightly greater than, those of crustaceans in the eastern tropical Pacific (Blackburn, 1968; Blackburn et al., 1970) and subtropical Pacific (Maynard et al., 1975). Target strength depends on the composition, shape, and orientation of the target, as well as on relative size. At 38–120 kHz, small fish with gas-filled swim bladders (e.g. clupeoids) and squid have target strengths 5–10 dB greater than those for crustaceans of the same size (Tables 6.3 and 6.4 in MacLennan and Simmonds, 1992; Marchal et al., 1993). Siphonophores have a gas bladder that scatters sound and have been observed migrating with myctophids in a DSL off Baja California (Barham, 1966). However, myctophids, flying fish, and squid were much more abundant than siphonophores at night dipnet stations on our cruises.[2] Therefore, mesopelagic fish and

**Table 2**

Pearson product-moment correlations between properties of the nighttime (2000–0400) deep-scattering layer and the thermocline depth observed in 1992 and 1993. $S_v$ = volume scattering strength (dB). Thermocline depth = depth of maximum 10-m temperature gradient. ***=$P<0.001$, **=$P<0.01$. PODS92 = Population of *Delphinus* Stocks 1992 cruise; PODS93 = Population of *Delphinus* Stocks 1993 cruise.

| | | Correlations with thermocline depth | |
|---|---|---|---|
| | | Depth of maximum $S_v$ | Mean $S_v$ above thermocline |
| PODS92 | 38 kHz | +0.86*** | –0.15 |
| | 150 kHz | +0.84*** | –0.23 |
| PODS93 | 38 kHz | +0.25 | –0.01 |
| | 150 kHz | +0.43** | +0.15 |

**Table 3**

Correlations between dolphin sighting rates (schools and individuals per 100 nautical miles of effort, log-transformed) and mean 150-kHz volume scattering strength ($S_v$, dB) above the thermocline at night (2000–0400), and 0 to 400 m night and day (0800–1600). *** = $P<0.001$, ** = $P<0.01$, * = $P<0.05$. PODS92 = Population of *Delphinus* Stocks 1992 cruise; PODS93 = Population of *Delphinus* Stocks 1993 cruise.

| | Dolphin sighting rates | |
|---|---|---|
| | Schools | Individuals |
| PODS92 | | |
| Night $S_v$ above thermocline | +0.35* | +0.38** |
| Night $S_v$ 0–400m | +0.05 | +0.02 |
| Day $S_v$ 0–400m | –0.01 | –0.02 |
| PODS93 | | |
| Night $S_v$ above thermocline | +0.27 | +0.15 |
| Night $S_v$ 0–400m | +0.36** | +0.20 |
| Day $S_v$ 0–400m | +0.38** | +0.18 |

[2] Pitman, R. 1996. Southwest Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, Box 271, La Jolla, CA 92038. Personal commun.

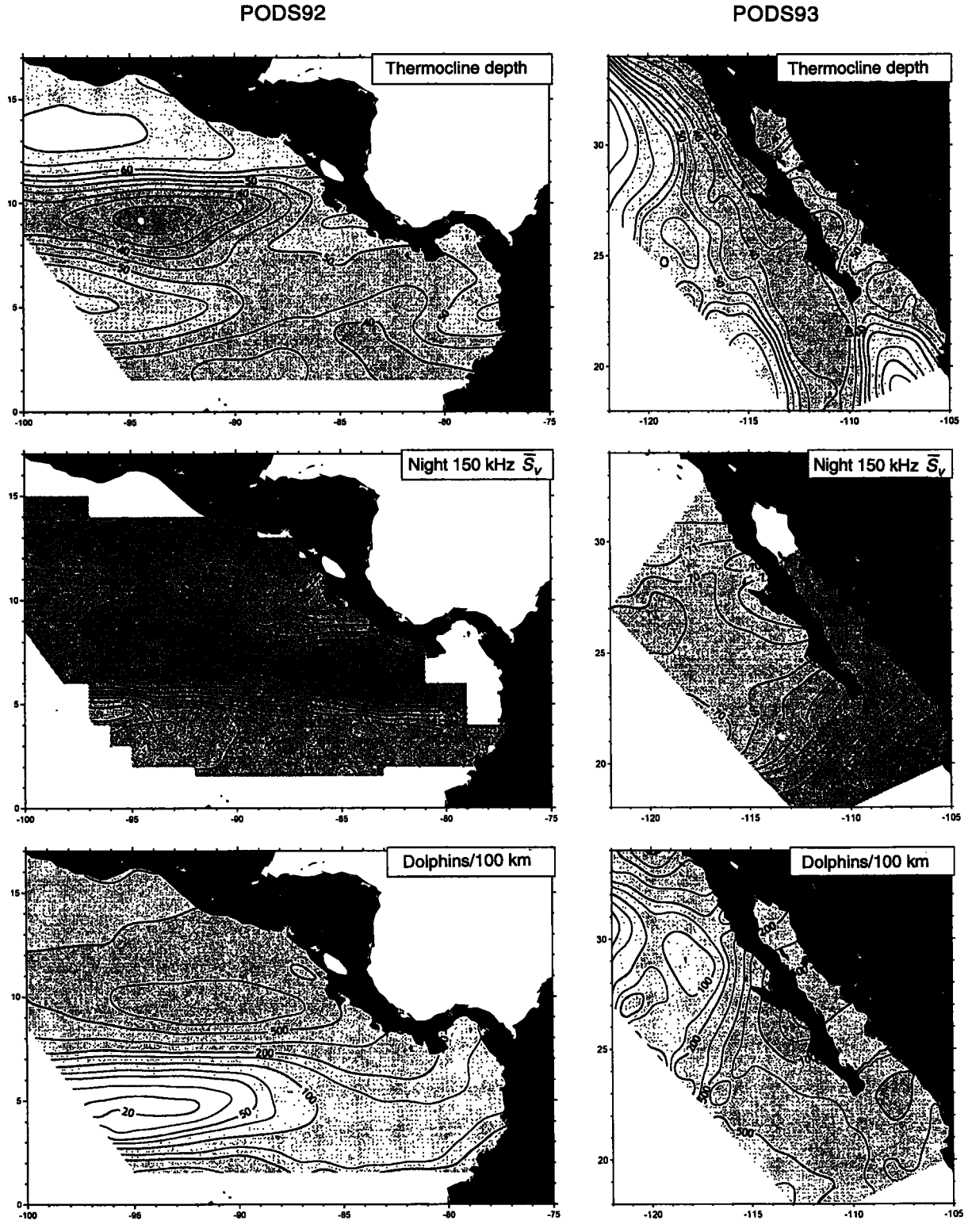


**Figure 6**

Thermocline depth (m), average nighttime backscatter above the thermocline (dB), and dolphin sighting rate observed in 1992 and 1993.

squid were most likely the major component of the observed DSL's, although a variety of crustaceans were undoubtedly present in the survey areas. Nonmigrating, epipelagic fish and squid are likely represented by near-surface backscattering during the day.

The small fish and squid that we argue were detected by our acoustic systems are dolphin prey (Fitch and Brownell, 1968; Miyazaki et al., 1973; Perrin et al., 1973; Robison and Craddock, 1983; Robertson and Chivers, 1997). The ranges of volume scattering strength we observed—more than three orders of magnitude among bins (Fig. 2), up to 10× variation between night and day and 500× variation among daily means—must be important factors in dolphin feeding strategies and habitat choices. Thermocline depth, which influences prey distribution, is an important component in dolphin habitat variability (Reilly and Fiedler, 1994).

We observed a positive correlation between the abundance of dolphins (observed during daylight) and the abundance of prey at night, when spotted and spinner dolphins are known to feed on mesopelagic prey near the surface (Perrin et al., 1973; Robertson and Chivers, 1997). Over 90% of the dolphins identified in both surveys were common, spotted, spinner, and striped dolphins. In the eastern tropical Pacific (PODS92), a region characterized by a strong and shallow thermocline (Wyrtki, 1967), nighttime prey abundance was more closely related to thermocline depth. Off Baja California (PODS93), the thermocline had less influence on distribution of prey. Dolphin community structure was also different: common dolphins represented 61% of the identified dolphins in this region, compared with only 37% in the PODS92 survey area.

Our results indicate that dolphin distribution can be related to prey abundance measured acoustically and that the physical environment influences the abundance of dolphin prey. Marchal et al. (1993) observed a similar DSL in the eastern tropical Atlantic that was related both to thermal structure and to tuna abundance. Simple and readily available sonar systems can yield useful results when survey time or resources are limited. Monitoring long-term changes in zooplankton or micronekton biomass, as Roemmich and McGowan (1995) did with net samples off southern California, could be facilitated by the application of such acoustic methods. However, in present and future studies of cetacean feeding and cetacean responses to habitat variability, we will use multispectral acoustic systems and validation by net samples to quantify availability and distribution of specific prey types.

## Acknowledgments

We thank Valerie Philbrick for collecting these data; Denny Sutton and Jim Anthony of NOAA's Pacific Marine Center for support in maintaining the acoustic systems; Roger Hewitt and Dave Demer for assistance in the calibration of the EK-400 echo sounder; Ken Richter, Dave Demer, and Paul Smith for comments on an earlier draft of this manuscript; and Steve Reilly for continued support of environmental studies during marine mammal surveys.

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# Feeding habits of pelagic summer flounder, *Paralichthys dentatus*, larvae in oceanic and estuarine habitats

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**Abstract.**—Pelagic larval summer flounder, *Paralichthys dentatus*, were collected in the NW Atlantic Ocean from 1985 to 1993, and their feeding habits were examined in relation to larval stage. Collections included preflexion, flexion, premetamorphic, and metamorphic larvae, although preflexion larvae composed the bulk of the specimens. Incidence of feeding and gut-fullness data indicated that larvae began feeding near sunrise and continued feeding throughout daylight hours. Incidence of feeding reached its lowest point, 8.3%, at 0400–0559 hours, then dramatically increased to 54.6% at 0600–0759. Maximum gut fullness was seen between 1200 and 1559. The only time during which all larvae contained prey in their guts was 0800–0959. Immature copepodites were the primary prey for all oceanic larval stages. In addition, small prey, such as tintinnids and copepod nauplii, made major contributions to the preflexion diet, and large prey, such as calanoid copepods and appendicularians, made major contributions to the diets of premetamorphic and metamorphic larvae. Metamorphic larvae were also collected as they entered a New Jersey estuary, at night, and their diet was examined. At 1800–1959 and 2000–2159 hours, the incidence of feeding in estuarine larvae was significantly lower than in oceanic larvae. The estuarine diet was dominated by the calanoid copepod, *Temora longicornis*. Incidence of feeding was observed to decline as metamorphosis progressed, from 19.1% at stage G to 2.9% at stage H. However, this apparent cessation in feeding, when the right eye was at the midpoint of migration, may not bring about undue ecological peril to summer flounder larvae.

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Fishery Bulletin 96:248–257 (1998).

The summer flounder, *Paralichthys dentatus*, an important component of recreational and commercial fisheries over the continental shelf and in estuaries of the Middle Atlantic Bight (United States), is currently overexploited. Evidence of this includes a drastic reduction in both commercial and recreational landings, in relation to peak years, and compressed age structure (Able and Kaiser, 1994). Both the fishery's decline and efforts to culture summer flounder (Bengtson et al., 1994; Bengtson and Nardi, 1995) are reviving interest in the basic biology of this species. Although much is known about the early life history of summer flounder, beginning with a description of eggs and larvae (Smith and Fahay, 1970) and including the timing of spawning, offshore distribution of eggs and larvae (Smith, 1973; Able et al., 1990), inshore occurrence of larvae and juveniles (Able et al., 1990), patterns of metamorphosis (Keefe and Able, 1993), and settlement processes (Burke et al., 1991; Keefe and Able, 1994; Norcross and Wyanski, 1994), many gaps still exist in our collective knowledge of larval and early-juvenile ecology.

Because survival beyond the early life history stages is based on an "eat and not be eaten" strategy (Keenleyside, 1979; Olla and Davis, 1988; Olla et al., 1994), feeding habits clearly define much of larval and early-juvenile ecology. Recently, larval summer flounder studies have focused on the effects of delayed feeding on survival and growth (Bisbal and Bengtson, 1995a), describing the starving condition (Bisbal and Bengtson, 1995b) and the development of the digestive tract (Bisbal and Bengtson, 1995c). Although these studies examined natural rates and processes, they were all conducted on larvae that were reared in a laboratory. Most of what is known about the early feeding ecology of wild summer flounder has been derived from metamorphosing larvae and early juveniles that were captured with benthic trawls in estuarine nursery habitats (Burke, 1995). Beyond the patent inference that planktonic larvae ingest plankton (e.g. Morse, 1981), very little is known regarding the early pelagic feeding ecology of this species (Rogers and Van Den Avyle, 1983; Grimes et al., 1989).

This study considers feeding ecology of larval summer flounder collected in pelagic habitats in the NW Atlantic Ocean from 1985 to 1993. Feeding habits were examined in relation to larval stage. Metamorphic larvae were also collected as they entered an estuarine habitat in New Jersey, and their diet was examined.

## Materials and methods

During fall and winter, pelagic larval summer flounder were collected in the NW Atlantic Ocean from 1985 to 1993 by the National Marine Fisheries Service (NMFS) Marine Resources Monitoring, Assessment, and Prediction (MARMAP) surveys (Able et. al., 1990). These monthly to bimonthly surveys were conducted over the continental shelf from Cape Lookout, North Carolina, to Cape Sable, Nova Scotia, by the RV *Albatross IV* and the RV *Delaware II*. The vast majority (96.4%) of oceanic specimens were collected during October and November, and a few were collected in December, January, and March. Surveys used 61-cm diameter bongo frames fitted with 0.333- and 0.505-mm mesh nets (Sherman, 1980). The nets were towed obliquely through the water from the surface to depths of 22–75 m and back to the surface at a speed between 1.5 and 3.5 knots. Samples from 50 stations were the focus of this study (Fig. 1). Collections were chosen for analysis on the basis of number of summer flounder larvae that were present. All collections with 10 or more summer flounder larvae were examined. Additional stations with fewer specimens were examined to balance time blocks so that each 2-h block included at least 10 specimens and at least 2 collections, and to include the full size range of larvae.

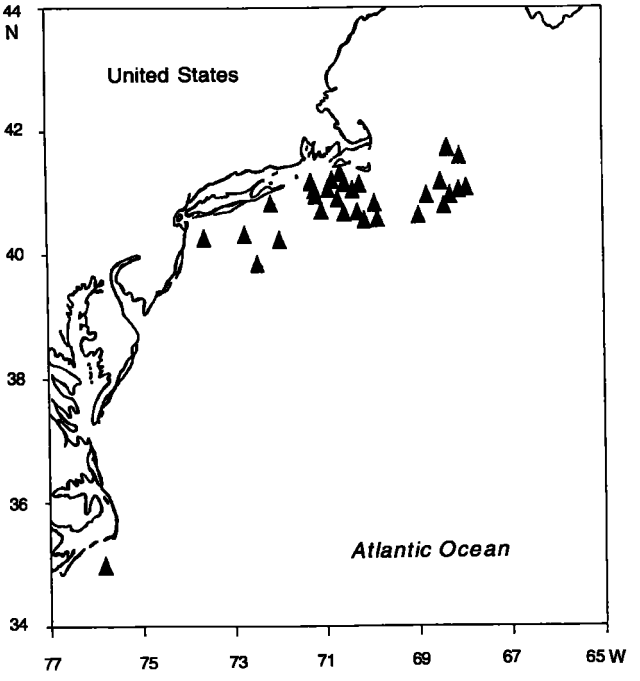


**Figure 1**

Location of the oceanic sites in the NW Atlantic Ocean, off the NE United States, where pelagic larval summer flounder, *P. dentatus*, were collected.

Specimens were preserved in 10% formalin at sea and remained in formalin for approximately 12 months. They were then transferred to 70% ethanol. Specimen shrinkage clearly occurred as a result of fixation. Within 24 hours of examination specimens were soaked in glycerin where they remained throughout their dissection (see Arthur, 1976; Gadomski and Boehlert, 1984).

After standard length (SL) (snout to notochord tip until full flexion, then to posterior edge of hypurals, Gadomski and Boehlert, 1984) of each larva was measured and morphological stage was determined, the digestive tract was removed. Contents of the entire digestive tract were evaluated. Gut contents were teased out and prey items were identified to the lowest possible taxon.

Diet was analyzed in terms of numerical percentage composition (%N), volumetric percentage composition (%Vol), and percent frequency of occurrence (%FO). Prey that comprised <1% of the diet by number and by volume were pooled into the "other" prey category. Prey volumes were estimated, generally by assuming a spheroidical geometry, from prey dimensions. The three analyses (%N, %Vol, and %FO) were combined to yield a more comprehensive assessment of prey importance, the index of relative importance (IRI = (%N + %Vol) × %FO) (Pinkas et al., 1971).

A comparison of larval sizes with established definitions of length at yolk absorption and length at flexion (Smith and Fahay, 1970; Martin and Drewry, 1978) revealed that considerable shrinkage had occurred prior to the examination of these specimens. As a result, data were pooled across stations for analysis by morphological stage, rather than by size class. Morphological stages were defined as preflexion (PF): straight notochord and no indication of caudal-fin ray development; flexion (FLX): beginning of caudal-fin ray development (i.e. ossification), accompanied or not by an upturn of the notochord tip and ossification of ural bones (hypurals, epurals, parahypurals); postflexion, premetamorph (PM): completion of caudal-fin ray ossification, upturn of notochord, and ossification of the ural bones, accompanied by resorption of the notochord tip, such that it no longer extends beyond the edge of the hypural bones (Fahay[1]); and metamorph (M): metamorphic

[1] Fahay, M. 1995. Northeast Fisheries Science Center, Howard Marine Sciences Laboratory, Natl. Mar. Fish. Serv., NOAA, Highlands, NJ 07732. Personal commun.

stages F– through I (Keefe and Able, 1993), based on degree of eye migration.

Incidence of feeding and gut fullness were also examined, as a function of 2-h time blocks. Gut fullness (F) was recorded as 0 = empty, 1 = 1–25%, 2 = 26–50%, 3 = 51–75%, and 4 = 76–100% full. Incidence of feeding was recorded as the percent frequency of larvae that had prey in their guts (i.e. $F > 0$), in relation to the total number of specimens examined in a time block.

A total of 550 oceanic larvae were examined. Of these, 18 were excluded from analysis because large portions of their guts were missing, and 11 were excluded because their primitive condition likely impaired their ability to ingest prey (Blaxter, 1986; Gadomski[2]). Primitive characteristics included presence of yolk sac, absence of eye pigment, and undeveloped mouth. Evidence of prey ingestion was lacking in the 29 excluded larvae. This study was based on 521 oceanic larvae that were deemed to be functionally intact.

A second series of collections were examined to determine the feeding ecology of summer flounder larvae as they enter an estuarine nursery habitat. Metamorphic larvae were collected from plankton entering the Great Bay–Little Egg Harbor (New Jersey) estuary (Fig. 2) during fall, winter, and spring from 1989 to 1995. Most estuarine specimens (71.4%) were collected between November and January. The remainder were collected between February and June, and in October. Stationary plankton nets (1-m diameter, 1.0-mm mesh) were set for 30 min, at the surface and just off the bottom, on nocturnal flood tides, from a bridge across Little Sheepshead Creek (Szedlmayer et al., 1992; Keefe and Able, 1993). This site is characterized by Atlantic Ocean water on flood tides (Charlesworth, 1968, cited in Szedlmayer et al., 1992); thus larvae were likely captured as they entered the estuary from the ocean, or soon after.

Estuarine specimens were preserved in 95% ethanol, and they remained in ethanol until their examination. Specimens were processed as above. Because all estuarine specimens were metamorphic (ME), morphological stages were recorded in terms of Keefe and Able's (1993) metamorphic stages: F– through I. The estuarine portion of this study was based on 119 specimens.

## Results

Preflexion (PF) larvae were the dominant morphological stage in oceanic collections, accounting for 84.3% of the specimens (Table 1). Later morphological stages were progressively rarer, with flexion (FLX) larvae accounting for 12.5%, postflexion, premetamorphic (PM) larvae accounting for 1.7%, and metamorphic (M) larvae accounting for 1.5% of the oceanic specimens in this study. Although greater than 33% of the larvae in each morphological stage contained prey in their guts, stages PM and M were combined for dietary analyses because of their small representation in these collections and similarity in diet.

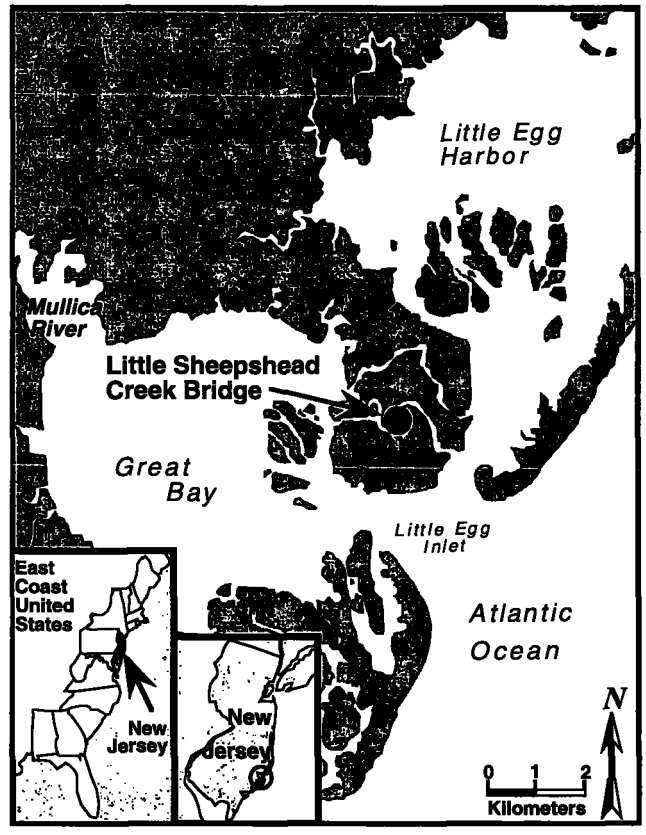


**Figure 2**

Location of the estuarine site in Little Sheepshead Creek, New Jersey, where metamorphic summer flounder, *P. dentatus*, were collected. (Figure by K. W. Able, Rutgers University.)

Larval lengths that were recorded at the time samples were sorted (usually within 12 months of collection) were compared with lengths at the time of examination in order to estimate shrinkage. Comparisons based on 329 specimens defined mean shrinkage as 13.7% (SD=5.83).

### Diet of preflexion (PF) larvae

The dominant stage in this study, PF, was represented by a total of 439 specimens: 56.9% contained recognizable prey, and 43.1% had empty guts. Lengths at the time of examination ranged from 1.9 to 6.9 mm SL (Table 1).

[2] Gadomski, D. 1995. Columbia River Research Laboratory, National Biological Service, 5501A Cook-Underwood Road, Cook, WA 98605. Personal commun.

**Table 1**

Feeding incidence and number of prey ingested by summer flounder, *P. dentatus*, larvae by time block, habitat, and larval stage. OC = oceanic, ES = estuarine, PF = preflexion, FLX = flexion, PM = premetamorphic, and M = metamorphic (oceanic). Estuarine metamorphic stages are as defined by Keefe and Able (1993). Numeric data exclude copepod eggs that appeared to have been ingested incidentally by metamorphic larvae.

| | Habitat type | No. larvae examined | Standard length (mm) mean | SD | range | No. larvae with food | Percentage feeding | Total no. food items | No. food items per feeding larvae |
|---|---|---|---|---|---|---|---|---|---|
| **Time block (h)** | | | | | | | | | |
| 0000–0159 | OC | 67 | 3.8 | 1.22 | 2.3–7.5 | 11 | 16.4 | 40 | 3.6 |
| | ES | 15 | 11.4 | 1.29 | 8.6–13.4 | 1 | 6.7 | 1 | 1.0 |
| 0200–0359 | OC | 18 | 4.5 | 1.04 | 3.4–6.7 | 2 | 11.1 | 3 | 1.5 |
| | ES | 11 | 12.3 | 1.91 | 8.8–14.6 | 1 | 9.1 | 1 | 1.0 |
| 0400–0559 | OC | 60 | 4.8 | 1.35 | 2.2–7.2 | 5 | 8.3 | 7 | 1.4 |
| | ES | 11 | 11.3 | 0.97 | 9.5–12.9 | 2 | 18.2 | 3 | 1.5 |
| 0600–0759 | OC | 44 | 4.3 | 1.39 | 2.6–7.6 | 24 | 54.5 | 104 | 4.3 |
| | ES | 2 | 10.3 | 0.44 | 10.0–10.6 | 0 | 0.0 | 0 | 0.0 |
| 0800–0959 | OC | 10 | 4.1 | 0.76 | 3.2–5.3 | 10 | 100.0 | 46 | 4.6 |
| 1000–1159 | OC | 33 | 3.8 | 0.96 | 2.7–5.8 | 27 | 81.8 | 107 | 4.0 |
| 1200–1359 | OC | 39 | 3.7 | 1.23 | 2.1–8.0 | 38 | 97.4 | 259 | 6.8 |
| 1400–1559 | OC | 41 | 3.6 | 1.16 | 2.1–8.3 | 36 | 87.8 | 256 | 7.1 |
| 1600–1759 | OC | 67 | 3.6 | 0.70 | 2.6–6.2 | 47 | 70.1 | 168 | 3.6 |
| 1800–1959 | OC | 32 | 3.8 | 1.12 | 1.9–7.9 | 27 | 84.4 | 106 | 3.9 |
| | ES | 36 | 12.4 | 1.62 | 8.8–14.5 | 5 | 13.9 | 13 | 2.6 |
| 2000–2159 | OC | 60 | 3.9 | 1.37 | 2.3–9.0 | 42 | 70.0 | 258 | 6.1 |
| | ES | 39 | 11.9 | 1.48 | 8.1–13.9 | 5 | 12.8 | 12 | 2.4 |
| 2200–2359 | OC | 50 | 4.1 | 1.25 | 2.1–8.3 | 11 | 22.0 | 31 | 2.8 |
| | ES | 5 | 11.3 | 1.76 | 8.8–13.5 | 1 | 20.0 | 2 | 2.0 |
| **Larval stage** | | | | | | | | | |
| PF | OC | 439 | 3.6 | 0.85 | 1.9–6.9 | 250 | 56.9 | 1276 | 5.1 |
| FLX | OC | 65 | 5.6 | 0.75 | 3.7–7.2 | 22 | 33.8 | 86 | 3.9 |
| PM | OC | 9 | 6.6 | 0.92 | 4.8–7.6 | 4 | 44.4 | 17 | 4.3 |
| M | OC | 8 | 7.7 | 0.97 | 5.8–9.0 | 3 | 37.5 | 6 | 2.0 |
| G | ES | 47 | 11.9 | 1.74 | 8.1–14.4 | 9 | 19.1 | 19 | 2.1 |
| H– | ES | 34 | 12.0 | 1.51 | 8.8–14.6 | 3 | 8.8 | 7 | 2.3 |
| H | ES | 35 | 11.8 | 1.35 | 8.8–14.5 | 1 | 2.9 | 2 | 2.0 |
| H+ | ES | 1 | 12.6 | | 12.6 | 1 | 100.0 | 1 | 1.0 |
| I | ES | 2 | 13.3 | 0.71 | 12.8–13.8 | 1 | 50.0 | 3 | 3.0 |

Immature copepodites composed the bulk of the diet (61.4% Vol, 37.3% IRI; Table 2) of PF larvae. Copepod nauplii, the second most important prey, composed 20.0% (N and IRI) of the diet. Tintinnids, despite being the most abundantly ingested prey (28.7% N), ranked third in importance at 19.3% (IRI). Bivalve larvae and copepod eggs were the only other prey that accounted for >1% of the diet, and together they composed 21.7% (IRI).

The size of ingested prey was directly related to larval size. Only PF larvae, the smallest larvae, abundantly ingested small prey, i.e. tintinnids, copepod nauplii, copepod eggs, and bivalve larvae. Diatoms and dinoflagellates were also occasionally ingested (4.4% FO), although both were of such minor importance in the total diet that they were pooled into the "other" prey category. The mean number of prey found in the guts of PF larvae was 5.1 (SD=4.47, range: 1–25). For PF larvae, the ingestion of copepod eggs and invertebrate eggs was clearly independent of the ingestion of berried females. Visual cues of prey may be important for feeding larvae because grains of sand that visually "mimicked" bivalve larvae, in size, shape, and color, were ingested along with bivalve larvae by 4.4% of PF larvae.

## Diet of flexion (FLX) larvae

A total of 65 FLX specimens were represented in this study: 33.8% contained recognizable prey, and 66.2% had empty guts. Lengths at the time of examination ranged from 3.7 to 7.2 mm SL (Table 1).

Immature copepodites dominated the diet of FLX larvae, regardless of method of analysis (Table 3).

**Table 2**

Diet of pelagic preflexion (PF) summer flounder, *P. dentatus*, larvae collected from the NW Atlantic, in terms of numerical percentage composition (%N), volumetric percentage composition (%Vol), percentage frequency of occurrence (%FO), and percentage index of relative importance (*IRI* = (*%N* + *%Vol*) × *%FO*). All values are based on a sample size, with prey, of 250 larvae.

| Prey | %N | %Vol | %FO | %IRI |
|---|---|---|---|---|
| Tintinnids | 28.7 | 3.3 | 37.6 | 19.3 |
| Copepod nauplii | 20.0 | 10.2 | 41.2 | 20.0 |
| Copepodites | 16.0 | 61.4 | 30.0 | 37.3 |
| Calanoids | 0.6 | 4.9 | 2.0 | 0.2 |
| Cyclopoids | 0.6 | 2.0 | 2.4 | 0.1 |
| Copepod eggs | 16.0 | 1.2 | 34.8 | 9.6 |
| Bivalve larvae | 12.1 | 14.8 | 28.0 | 12.1 |
| Invertebrate eggs | 3.7 | 0.9 | 11.6 | 0.9 |
| Other | 2.3 | 1.3 | 9.2 | 0.5 |

**Table 3**

Diet of pelagic flexion (FLX) summer flounder, *P. dentatus*, larvae collected from the NW Atlantic, in terms of numerical percentage composition (%N), volumetric percentage composition (%Vol), percentage frequency of occurrence (%FO), and percentage index of relative importance (*IRI* = (*%N* + *%Vol*) × *%FO*). All values are based on a sample size, with prey, of 22 larvae.

| Prey | %N | %Vol | %FO | %IRI |
|---|---|---|---|---|
| Polychaete larvae | 1.2 | 0.5 | 4.5 | 0.1 |
| Copepod nauplii | 2.3 | 0.2 | 9.1 | 0.2 |
| Copepodites | 68.6 | 66.7 | 86.4 | 92.8 |
| Calanoids | 13.9 | 27.5 | 18.2 | 6.0 |
| Cyclopoids | 3.5 | 1.9 | 9.1 | 0.4 |
| Copepod eggs | 3.5 | <0.1 | 9.1 | 0.3 |
| Bivalve larvae | 5.8 | 2.8 | 4.5 | 0.3 |
| Invertebrate eggs | 1.2 | 0.4 | 4.5 | 0.1 |

The well-digested condition of copepodites precluded specific identifications, but most appeared to be calanoids. The only other prey category to represent more than 10% of the diet by any analysis was adult calanoid copepods, which despite accounting for 27.5% of dietary volume, composed only 6.0% IRI.

Tintinnids were not observed in the FLX larval diet, and other small prey items (copepod nauplii, copepod eggs, bivalve larvae, and invertebrate eggs) contributed little to the diet. The mean number of prey ingested by FLX larvae was 3.9 (SD=2.33, range=1–9).

## Diet of oceanic premetamorphic and metamorphic (PM+M) larvae

A total of 9 PM and 8 M specimens were represented in this study: 44.4% of PM larvae and 37.5% of M larvae contained recognizable prey, and 55.6% of PM larvae and 62.5% of M larvae had empty guts. Lengths at the time of examination ranged from 4.8 to 7.6 mm SL for PM larvae and 5.8 to 9.0 mm SL for M larvae (Table 1). Combining the two stages (PM+M): 41.2% contained prey, and 58.8% had empty guts.

As with earlier morphological stages, immature copepodites were the primary prey for PM and M larvae, accounting for 50.1% of the diet (IRI). However, adult calanoid copepods and appendicularians, the secondary and tertiary prey (in terms of IRI), together contributed more than twice as much as copepodites to dietary volume (Table 4). Although it was not always possible to identify copepods to species, the most frequently ingested calanoid copepod appeared to be *Centropages typicus*. *Temora longicornis* and *Pseudocalanus* spp. also contributed to the diet. Appendicularians were only observed in the diet of PM and M larvae.

**Table 4**

Diet of pelagic postflexion, premetamorphic (PM), and metamorphic (M) summer flounder, *P. dentatus*, larvae collected from the NW Atlantic, in terms of numerical percentage composition (%N), volumetric percentage composition (%Vol), percentage frequency of occurrence (%FO), and percentage index of relative importance (*IRI* = (*%N* + *%Vol*) × *%FO*). All values are based on a sample size, with prey, of 7 larvae. Data exclude copepod eggs that appeared to have been ingested incidentally.

| Prey | %N | %Vol | %FO | %IRI |
|---|---|---|---|---|
| Copepod nauplii | 8.7 | 0.5 | 28.6 | 1.7 |
| Copepodites | 60.9 | 27.1 | 42.9 | 50.1 |
| Calanoids | 13.0 | 34.6 | 42.9 | 27.2 |
| Appendicularians | 17.4 | 37.8 | 28.6 | 21.0 |

The mean number of prey ingested by PM and M larvae was 3.3 (SD=2.14, range=1–6). Copepod eggs that were abundant in the gut of a single M-stage larva were excluded because they were probably ingested incidentally.

## Incidence of feeding

An examination of incidence of feeding (defined as the percentage frequency of larvae with prey in their guts) in relation to 2-h time blocks over the course of

24 h (Table 1) revealed that pelagic larvae began feeding near sunrise in oceanic habitats. The presence of prey in larval guts reached its lowest point, 8.3%, at 0400–0559 hours, then dramatically increased to 54.5% at 0600–0759 hours, the time block of sunrise for all collections. The only time during which incidence of feeding was 100% was 0800–0959. Throughout hours of full daylight, incidence of feeding remained high, ≥70%. Late afternoon or early-evening feeding may have buoyed the feeding incidence at 2000–2159, but evidence of recent feeding decreased sharply from 2000–2159 to 2200–2359 hours. During late night hours, the percentage of larvae that had prey in their guts gradually decreased from 22.0% at 2200–2359 to 8.3% at 0400–0559.

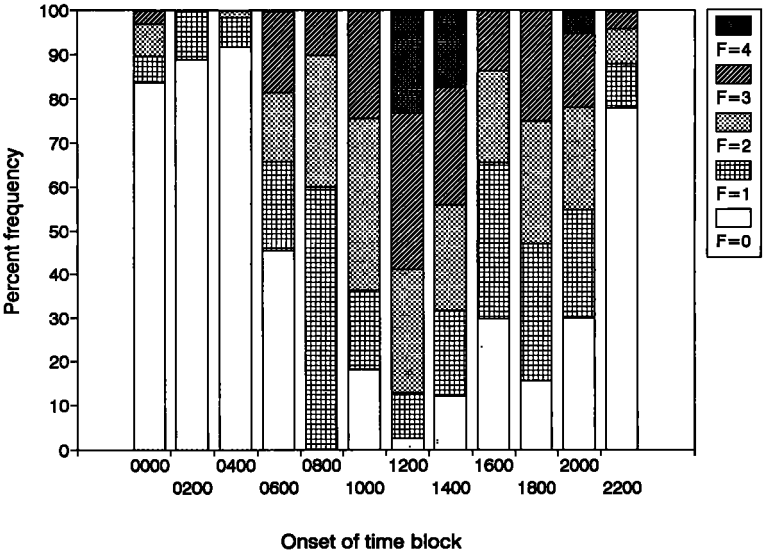


**Figure 3**

Gut fullness (F) of pelagic larval summer flounder *P. dentatus*, in the NW Atlantic Ocean, as a function of time of day (EST), where 0 = empty, 1 = 1–25%, 2 = 26–50%, 3 = 51–75%, and 4 = 76–100% full.

## Gut fullness

Because incidence of feeding data were generated from gut-fullness data (i.e. $F>0$), they provide a qualitative measure of gut fullness; however, gut-fullness data also provide direct estimates of the volume of prey in the gut over the course of 24 h (Fig. 3). Although larvae appeared to begin feeding at 0600–0759, full guts were not observed until 1200–1359. Maximum gut fullness ($F=4$) was only seen at 1200–1559 and 2000–2159. The only time block during which all larvae contained prey in their guts was 0800–0959.

## Diet of metamorphic (ME) larvae in estuaries

The estuarine portion of this study was based on 119 metamorphic larvae (ME), representing metamorphic stages G through I (Keefe and Able, 1993) (with $n=47$ at stage G, $n=34$ at stage H–, $n=35$ at stage H, $n=1$ at stage H+, and $n=2$ at stage I, Table 1). The guts of 15 (12.6%) ME larvae contained recognizable prey, and 87.4% had empty guts. At the time of examination, larval lengths ranged from 8.1 to 14.6 mm SL.

Pelagic feeding was clearly demonstrated by > 85% of ME larvae. The primary prey of pelagic ME larvae was the calanoid copepod *Temora longicornis*, regardless of the method of analysis (Table 5).

The mean number of prey found in the guts of ME larvae was 2.1 (SD=0.99, range=1–4). The relatively good condition of some prey items in the guts of fish collected late at night suggests that some prey were likely ingested after dark.

**Table 5**

Diet of metamorphic (ME) summer flounder, *P. dentatus*, larvae collected from a New Jersey estuary, in terms of numerical percentage composition (%N), volumetric percentage composition (%Vol), percentage frequency of occurrence (%FO), and percentage index of relative importance ($IRI = (\%N + \%Vol) \times \%FO$). All values are based on a sample size, with prey, of 15 larvae. Prey were pelagic unless otherwise indicated.

| Prey | %N | %Vol | %FO | %IRI |
|---|---|---|---|---|
| Polychaete larvae | 3.1 | 0.7 | 6.7 | 0.4 |
| Polychaete tentacles (benthic) | 3.1 | 12.0 | 6.7 | 1.6 |
| Cirripede larvae | 3.1 | 0.2 | 6.7 | 0.3 |
| *Paracalanus parvus* | 3.1 | 2.0 | 6.7 | 0.5 |
| *Centropages typicus* | 6.3 | 13.6 | 6.7 | 2.1 |
| *Temora longicornis* | 46.8 | 55.3 | 53.3 | 86.2 |
| *Acartia* sp. | 3.1 | 2.9 | 6.7 | 0.6 |
| Unidentified calanoids | 6.3 | 3.7 | 13.3 | 2.1 |
| Harpacticoids (benthic) | 6.3 | 1.5 | 6.7 | 0.8 |
| Mysids (diurnal migrants) | 9.4 | 6.1 | 13.3 | 3.3 |
| *Oikopleura* sp. | 6.3 | 1.8 | 13.3 | 1.7 |
| Unidentified prey remnants | 3.1 | 0.2 | 6.7 | 0.4 |

Evidence of benthic feeding was observed only in late-stage metamorphic larvae (H+ and I). Of two late-stage larvae that had prey in their guts, one

single larva (stage I, 13.8 mm SL) clearly demonstrated benthic feeding, having ingested polychaete tentacles and harpacticoid copepods, and the other larva had ingested a mysid, a taxon noted for diurnal migrations (Newell and Newell, 1977). All late-stage larvae in estuarine collections displayed noticeably darker pigmentation than was observed in earlier stages.

### Incidence of feeding in estuaries

A comparison of the incidence of feeding of oceanic and estuarine summer flounder larvae was limited to nocturnal collections and revealed strikingly different patterns (Table 1; Fig. 4). Between 1800 and 0759 hours the incidence of feeding of estuarine larvae never exceeded 20.0%, whereas values for oceanic larvae ranged from 8.3% to 84.4%. The greatest differences between oceanic and estuarine larvae were observed early in the night: at 1800–1959 and 2000–2159 the incidence of feeding in estuarine collections was significantly lower than in oceanic collections ($P<0.01$, $\chi^2=33.78$, 1 df, at 1800–1959; $P<0.01$, $\chi^2=30.99$, 1 df, at 2000–2159) (Fig. 4). Because most (63.0%) larvae in estuarine samples were collected between 1800 and 2159 (Table 1), these comparisons were not biased by low sample size.

Within estuarine habitats, incidence of feeding declined with metamorphic stage, from 19.1% at stage G to 2.9% at stage H (Table 1). Time was not a factor in this decline because the distribution of larvae of stages G, H–, and H was the same across early- (1800–2159), mid- (2200–0159), and late-night (0200–0559) collections ($P=0.18$, $\chi^2=6.22$, 4 df).

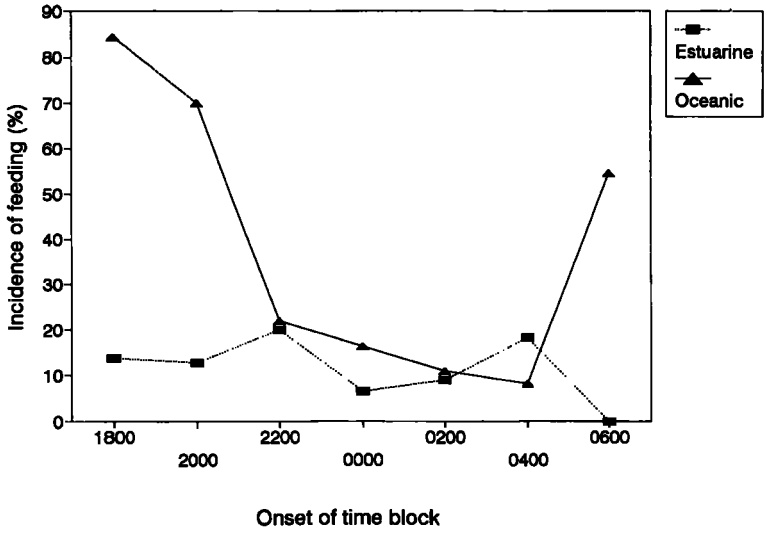


**Figure 4**

Incidence of feeding of larval summer flounder, *P. dentatus*, in the NW Atlantic Ocean and in a New Jersey estuary, as a function of time of day (EST) through the night. Data are based on a total of 331 oceanic and 119 estuarine specimens.

## Discussion

The diet of all stages of oceanic summer flounder larvae was dominated by immature copepodites in the NW Atlantic Ocean. The size of other ingested prey was directly related to larval size. Small prey items such as copepod nauplii, tintinnids, and bivalve larvae, were important only in the diet of early (PF) stage larvae. Large prey items, such as adult calanoid copepods and appendicularians were important only in the diet of later (PM and M) stage larvae.

The diet of metamorphosing (ME) larvae that were collected in a New Jersey estuary was dominated by the calanoid copepod *Temora longicornis*.

These observations differ sharply from the diet of metamorphosing larval summer flounder in a North Carolina estuary (Burke, 1995). Burke (1995) reported that the larval diet was dominated by polychaetes and mysids. However, all larvae in the North Carolina study (Burke, 1995) were caught in estuarine nursery areas with benthic trawls, whereas in the present study oceanic larvae were caught with bongo nets, and estuarine larvae were caught with stationary plankton nets. Clearly these two studies captured metamorphosing larvae during different ecological phases of the transition from pelagic to benthic ecology. The diet of late-stage metamorphic larvae that demonstrated benthic feeding in an estuarine habitat in the present study was similar to the diet of comparable size larvae in Burke's (1995) study. The darker pigmentation of benthic-feeding, late-stage larvae suggests that this pigmentation may be a valid marker of adaptation to the benthic habitat in summer flounder, as has been observed in other species (Grover et al., in press).

The pelagic diet of a congener, the olive flounder,[3] *Paralichthys olivaceus*, may represent a more cogent comparison. In Wakasa Bay in the Japan Sea, Minami (1982) reported that

[3] The common and scientific names of fish species used in *Fishery Bulletin* are those recommended by the American Fisheries Society (Am. Fish. Soc. Spec. Publ. 20, 5th ed., 1991). The following names have been changed accordingly: Japanese flounder to olive flounder; *Parophrys vetulus* to *Pleuronectes vetulus*; *Isopsetta isolepis* to *Pleuronectes isolepis*; and *Limanda ferruginea* to *Pleuronectes ferrugineus*.

copepod nauplii were the most important prey in the diet of all premetamorphic stages of Japanese flounder larvae. However, Ikewaki and Tanaka (1993) later reported that olive flounder diet, in Wakasa Bay, was dominated by copepod nauplii only for first-feeding larvae and by appendicularians, *Oikopleura* spp., for later stages through early-metamorphic-phase larvae. Minami (1982) reported that appendicularians, copepods, and mysids were the dominant prey of early-, mid-, and late-metamorphic larvae, respectively. The sizable contribution of copepod nauplii to the diet of preflexion (PF) summer flounder larvae resembled the contribution observed in the diet of first-feeding (Ikewaki and Tanaka, 1993) and early stage olive flounder larvae (Minami, 1982). However, appendicularians, the dominant prey item for early-metamorphic larvae (Minami, 1982), and for all larval stages beyond first-feeding in olive flounder (Ikewaki and Tanaka, 1993), occurred only in the diet of premetamorphic and metamorphic (PM+M) summer flounder larvae.

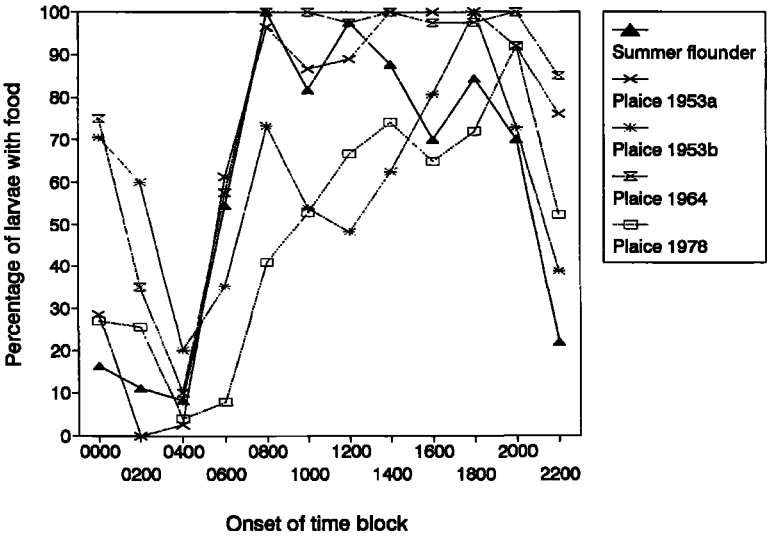


**Figure 5**

Incidence of feeding of pelagic larval summer flounder, *P. dentatus*, in the NW Atlantic Ocean and of pelagic larval plaice, *P. platessa*, in the Southern Bight of the North Sea and the English Channel, as a function of time of day. Sources of plaice data are as follows: 1953a = 48-h station, Shelbourne, 1953; 1953b = other stations (Shelbourne, 1953); 1964 = Ryland, 1964; 1978 = Last, 1978.

Pelagic summer flounder larvae that were collected in the NW Atlantic Ocean displayed a diurnal feeding pattern similar to that reported for several other flatfish larvae (e.g. plaice, *Pleuronectes platessa*: Shelbourne, 1953; Ryland, 1964; Last, 1978; dab, *Limanda limanda*: Last, 1978; English sole, *Pleuronectes vetulus*, and butter sole, *Pleuronectes isolepis*: Gadomski and Boehlert, 1984). Both incidence of feeding and gut-fullness data (Figs. 3 and 4) appear to confirm the visual nature of larval summer flounder feeding in oceanic collections. This is not surprising, because marine fish larvae are mostly visual feeders (Hunter, 1981; Blaxter, 1986; Huse, 1994). However, the optimal illumination level for feeding varies with species (Huse, 1994). For example, Atlantic cod, *Gadus morhua*, larvae feed preferentially at very low light levels, and turbot, *Scophthalmus maximus*, larvae feed preferentially at high levels of illumination, whereas plaice larvae feed over a wide range of illumination levels (Huse, 1994).

Within the flatfishes, additional relationships between illumination and larval feeding have been demonstrated. For example, sole, *Solea solea*, larvae can feed in the dark from the early posthatching stage (Blaxter, 1969). Oceanic collections of yellowtail flounder, *Pleuronectes ferrugineus*, larvae have shown that the highest incidence of feeding occurred between 1600 and 0100 (Smith et al., 1978). The near absence of feeding between 0700 and 1300 suggests that onset of feeding in yellowtail flounder larvae is triggered by something other than, or in addition to, illumination (Smith et al., 1978).

Data from oceanic collections in the present study suggest that the relationship between illumination and feeding of summer flounder larvae is much like that observed in one of the two flatfish species studied by Huse (1994). Laboratory observations are required to ascertain whether summer flounder larvae feed preferentially at high illumination levels or over a wide illumination range. However, an examination of incidence of feeding of pelagic plaice larvae (Shelbourne, 1953; Ryland, 1964; Last, 1978) in relation to comparable summer flounder data (Fig. 5) reveals similar patterns of feeding periodicity. From this, a similarity in optimal illumination levels for feeding for summer flounder and plaice larvae is suggested. To wit, pelagic summer flounder larvae would be expected to feed well over a wide range of illumination levels.

If the ecological analogy between plaice larvae and summer flounder larvae extends through metamorphosis, then a dramatic increase in light sensitivity (and a lower threshold light intensity for feeding) at metamorphosis (Blaxter, 1968) would be predicted for summer flounder. Limited field evidence supports this. A comparison of the incidence of feeding of oce-

anic and estuarine summer flounder larvae revealed strikingly different patterns (Fig. 4). Early in the night, incidence of feeding was much lower in estuarine collections. Fasting during metamorphosis, as has been noted in plaice (Riley, 1966; Lockwood 1984; Hamerlynck et al., 1989), may have contributed to this pattern. Plaice and sole have shown marked decreases in food-searching behaviors (distance covered per minute and time spent in feeding activity) at metamorphosis (Blaxter and Staines, 1971). Late at night, at 0400–0559, incidence of feeding in estuarine collections was double the rate seen in oceanic summer flounder collections (Fig. 4). A lower threshold light intensity for feeding at metamorphosis may have contributed to this, although small sample sizes of late-night estuarine collections preclude overreaching conclusions. Resolution of the threshold of light intensity for feeding of metamorphic summer flounder in a controlled laboratory setting could result in determination of optimal illumination levels at metamorphosis in aquaculture.

Metamorphosis has been considered a critical interval in the early life of some marine fishes (Thorisson, 1994). In the present study, the incidence of feeding of summer flounder larvae was observed to decline with metamorphic development to stage H. This suggests that the midpoint in the migration of the right eye (Keefe and Able, 1993) may be a critical period for summer flounder. In a laboratory study, a cessation of feeding was observed at stage G (Keefe and Able, 1993). However, cessation of feeding at metamorphosis may not place flatfish in any real danger of starvation (Lockwood, 1984). Metamorphic plaice larvae are capable of surviving without food for 7–25 d, without reaching the "point of no return" (Wyatt, 1972). Blaxter and Hempel (1963) have defined the "point of no return" as the point at which starved larvae become too weak to feed. Midmetamorphic summer flounder larvae are capable of surviving 56 d without reaching the "point of no return" (Keefe and Able, 1993). At metamorphosis and shortly thereafter flatfish may be more vulnerable to predation (van der Veer and Bergman, 1987; Witting and Able, 1993, 1995) than to starvation (Thorisson, 1994).

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# Age composition, growth, reproductive biology, and recruitment of King George whiting, *Sillaginodes punctata*, in coastal waters of southwestern Australia

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**Abstract.**—The age structure, growth and reproductive biology have been determined for the recreationally and commercially important King George whiting, *Sillaginodes punctata*, off southwestern Australia. The maximum lengths and ages, asymptotic lengths ($L_\infty$), and growth coefficients ($K$) were 596 mm, 14 years, 532 mm, and 0.47, respectively, for females, and 555 mm, 13 years, 500 mm and 0.53, respectively, for males. Sexual maturity is attained by 50% of female *S. punctata* by ca. 410 mm in length, and by the majority of both female and male fish at the end of their fourth year of life. The monthly trends in the proportions of mature gonads and the prevalence of different oocyte stages and postovulatory follicles indicated that, in southwestern Australia, *S. punctata* spawns from June to September. Spawning is thus initiated when water temperatures are declining from their maxima. During the spawning period, many of the ovaries of large fish contained yolk vesicle and yolk granule oocytes, as well as hydrated oocytes or postovulatory follicles (or both), indicating that *S. punctata* is a multiple spawner. Furthermore, because hydrated oocytes or postovulatory follicles were often found together with large numbers of yolk granule oocytes, *S. punctata* presumably releases eggs in batches during the spawning period. Recruitment of *S. punctata* into sheltered nearshore waters (<1.5 m) commences in late September, three months after the onset of spawning, and continues until early November. When juvenile *S. punctata* reach ca. 1.5 years of age and ca. 250 mm, the legal minimum length for capture, they move out into slightly deeper waters (2–6 m) in marine embayments and estuaries. After attaining ages of ca. 4 years and lengths of ca. 370 mm, they then migrate from these waters, where fishing pressure is greatest, into regions near or around reefs at depths of 6–50 m, where spawning occurs. In contrast to *S. punctata*, the five other whiting species in southwestern Australian waters, which all belong to the genus *Sillago*, spawn between late spring and early autumn. In the case of the three *Sillago* species that undergo an offshore migration, this movement occurs at a relatively small size and young age and leads to their occupying open sandy areas. The implications of *S. punctata* habitat and biological data for fishery management are discussed.

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The King George whiting, *Sillaginodes punctata*, which is the largest of the 31 species belonging to the Sillaginidae, occurs along the lower west and southern coasts of Australia (McKay, 1992), where it is a very important recreational and commercial species (see Kailola et al., 1993). Although a number of studies have been carried out on the biology of *S. punctata* (Scott, 1954; Thomson, 1957a; Gilmour, 1969; Robertson, 1977; Caton[1]; Cockrum and Jones[2]), these have concentrated mainly on fish caught in shallow waters, in which mature fish tend not to be found. Although Cockrum and Jones[2] obtained *S. punctata* from deeper waters, where spawning presumably occurs, data on the pattern of gonadal development, which is required to determine precisely the peak time and duration of spawning of this species, are very limited. Indeed, estimates of the timing and duration of spawning of *S. punctata* have been derived predominantly from backcalculations of daily growth increments of recently settled juveniles (Bruce, 1989; Bruce and Short, 1992; Jenkins and May, 1994; Fowler and Short, 1996). These latter studies, which were carried out off southeastern Australia, indicate that *S. punctata* spawns between early autumn and early winter. However, *S. punctata* is recruited into nearshore waters far earlier off South Australia than off southwestern Australia, which suggests that this species spawns later in the latter region (cf. Fowler and Short, 1996; Hyndes et al., 1996a).

Although age structures and growth parameters have been estimated for populations of *S. punctata* off southeastern Australia, the ages

[1] Caton, A. E. 1966. Preliminary synopsis of biological data on the Australian (spotted or King George) whiting (*Sillaginodes punctatus*) (Cuv. and Val.) 1829. CSIRO Technical Session, Department of Fisheries and Fauna Conservation Agenda Item 5, 43 p.

[2] Cockrum, K. S., and G. K. Jones. 1992. The reproductive biology and fecundity of King George whiting (*Sillaginodes punctata*) in South Australian waters, 1953–1988. South Australian Research and Development Institute Fisheries Research Paper 25, 18 p.

of fish in those studies were determined by the growth zones on scales or whole otoliths, which in neither case had been validated as being formed annually (Scott, 1954; Gilmour, 1969; Caton[1]; Jones et al.[3]). The present study demonstrates that, in the case of the populations of *S. punctata* in southwestern Australian waters, the growth zones on scales are difficult to discern and all of those on the otoliths of larger fish are only revealed after the otoliths have been sectioned. Data obtained from sectioned otoliths have thus been used to determine the age structure and growth rate of *S. punctata* on the lower west coast of Australia. Emphasis has then been placed on determining the length and age at first maturity, the location and period of spawning, and the period during which *S. punctata* is recruited into its nearshore nursery grounds. The implications of these biological data for managing this important species are then considered. Our results have been compared with those obtained for populations of *S. punctata* elsewhere in Australia. We have also compared aspects of the biology of *S. punctata* with those of the five other whiting species in the same region, all of which belong to the genus *Sillago* and, in the case of *S. schomburgkii* and *S. bassensis*, are fished both recreationally and commercially. This comparison enabled us to elucidate the extent to which age composition, growth, spawning period, and size-related shifts in habitat vary among the species comprising this abundant family.

## Materials and methods

Small *S. punctata*, i.e. <300 mm, were collected from sites in nearshore marine waters (<1.5 m depth) between latitudes 32°00'S and 32°31'S on the lower west coast of Australia between June 1991 and May 1993 (see map in Hyndes et al., 1996a). Sampling was undertaken with a 21.5 m long seine net, which had a mesh size of 3 mm in the pocket. Large *S. punctata*, i.e. >300 mm, were obtained from recreational anglers, who were fishing between February 1993 and August 1996 in waters <50 m in depth between 31°55'S and 32°45'S. These anglers kindly supplied frozen carcasses, including gonads, after they had been filleted, together with a record of the date, location, and depth at which each fish had been captured.

The total length (TL) of each fish was measured to the nearest 1 mm. When a gonad could be identified as either an ovary or a testis, it was assigned to one of eight developmental stages, according to the criteria of Laevastu (1965): I = virgin; II = maturing virgin; III = developing; IV = maturing; V = mature; VI = spawning; VII = spent; and VIII = recovering or spent. However, multiple spawning by representatives of this species in each spawning season (see "Results" section) meant that it was often difficult to ascertain whether certain gonads should be recorded as stages V, VI, or VII. The data for these three stages, subsequently referred to collectively as mature gonads, were therefore pooled. It was not possible to recognize stage VIII gonads in males. Ovaries of the large female *S. punctata* collected in each month of the study were placed for 24 h in Bouin's fixative and then dehydrated in a series of ethanols. The midregion of each of these ovaries was embedded in paraffin wax, cut transversely (6 µm) and stained with Mallory's trichrome. The circumferences of 30 oocytes, where the section passed through the nucleus, were recorded to the nearest 5 µm by using the OPTIMAS (OPTIMAS Corp., 1994) computer imaging package. This enabled the diameters of these oocytes to be calculated. Because hydrated oocytes had collapsed as a result of freezing, their circumferences could not be measured. The oocyte measurements for fish in each calendar month during the three years of this study were pooled in order to provide histological data for up to 10 ovaries from each of those months. The terminology for the oocyte stages was adapted from that given in Khoo (1979).

The length at which 50% of female *S. punctata* first attained maturity ($L_{50}$) was calculated by fitting a logistic function to the proportion of mature fish in each 50-mm length interval in the spawning period of June to September (see "Results" section) by a nonlinear technique (Saila et al., 1988) with a nonlinear subroutine in SPSS (SPSS Inc., 1994). The logistic equation is

$$P_L = \left[1 + e^{(a+bL)}\right]^{-1}$$

where $P_L$ = the proportion of fish with mature gonads at length interval $L$; and
$a$ and $b$ = constants.

The $L_{50}$ was then derived from the equation

$$L_{50} = -ab^{-1}.$$

Preliminary examination of scales and sagittal otoliths collected from large *S. punctata* caught during the initial stages of the study showed that growth zones were often difficult to detect in scales, whereas at least some growth zones could be clearly discerned

[3] Jones, G. K., D. A. Hall, K. L. Hill, and A. J. Staniford. 1990. The South Australian marine scalefish fishery stock assessment; economics; management. South Australian Department of Fisheries Green Paper, January 1990, 186 p.

in whole otoliths. For this reason, sagittal otoliths were subsequently removed from each fish, cleaned, dried, stored, and used to estimate the ages of fish. In order to determine whether it was necessary to section otoliths to reveal all translucent zones, the number of translucent zones in the otoliths of 100 randomly selected *S. punctata*, in which whole otoliths displayed at least one such zone, were counted prior to and after sectioning. Of the otoliths that showed two to six translucent zones after sectioning, 19% exhibited one less zone prior to sectioning. Furthermore, in those otoliths that displayed seven or more translucent zones after sectioning, over 50% exhibited one less zone and 30% displayed between two and four fewer zones prior to sectioning. Thus, the otoliths of *S. punctata* had to be sectioned in order to discern all the translucent zones in those structures, a procedure that is also required for ageing several other fish species (e.g. Campana, 1984; Beamish and McFarlane, 1987; Casselman, 1987; Hyndes et al., 1992a). Otoliths were mounted and embedded in black epoxy resin and cut into approximately 0.8-mm transverse sections with a diamond saw. Sections were mounted on glass slides and their surface ground on sequentially finer grades of carborundum paper , with particle sizes ranging between ca. 30–10 μm. They were then coated with clear nail polish and examined microscopically under reflected light. The distance between the outer edge of the outermost translucent zone and the periphery of each otolith (marginal increment) was measured. This was expressed either as a proportion of the distance between the focus and the outer edge of the translucent zone, when only one translucent zone was present, or as a proportion of the distance between the outer edges of the two outermost translucent zones, when two or more translucent zones were present. Measurements were always made along the longest axis of each sectioned otolith and recorded to the nearest 0.05 mm. The number of translucent zones on each otolith was recorded. The birth date was designated as the midpoint of the main spawning period, based on the trends shown by gonadal and oocyte development (see "Results" section). Von Bertalanffy growth curves were fitted to the individual lengths of females and males at the estimated age at capture by a nonlinear technique (Gallucci and Quinn, 1979) with a nonlinear subroutine in SPSS (SPSS Inc., 1994). The von Bertalanffy equation is

$$L_t = L_\infty\left[1-e^{-K(t-t_0)}\right],$$

where $L_t$ = the length at age $t$ (years);
$L_\infty$ = the mean of the asymptote predicted by the equation;
$K$ = the growth coefficient; and
$t_0$ = the hypothetical age at which fish would have zero length if growth followed that predicted by the equation.

The growth curves derived for females and males were compared by using a maximum-likelihood test (Kimura, 1980).

A fine mesh seine net, which was 5.5 m long and consisted of 1-mm mesh, was used in alternate weeks between late July and late December 1994 to collect recently settled *S. punctata* from sheltered nearshore sites in regions similar to those sampled by the 21.5-m seine net. The standard length (SL) of each of these fish on each sampling occasion was measured to the nearest 0.1 mm, except when the sample size was large, in which case measurements were made on a subsample of 100 fish.

## Results

### Age and growth

The mean marginal increment in sectioned otoliths with one translucent zone ranged from 0.42 to 0.54 between May and October, but then fell precipitously to 0.09 in November, before gradually increasing to 0.39 by April (Fig. 1). The marginal increments in otoliths with 2, 3, and 4–13 translucent zones also declined markedly between October and November and followed similar trends (Fig. 1). Thus, irrespective of the number of translucent zones in the otoliths, the marginal increment declined markedly and then rose progressively only once during a 12-month period, demonstrating that the translucent zones are formed annually.

In order to determine the size and age composition of *S. punctata* at different times of the year, the total lengths of fish caught in nearshore waters by seine net and in more offshore waters by anglers were pooled (Fig. 2A). Small *S. punctata* were first caught with seine nets in nearshore waters in early November, in which month their lengths ranged from 25 to 50 mm. By late December, the maximum length had increased to 68 mm (data not shown). The length range of the corresponding cohort, which comprised fish with otoliths that did not possess a translucent zone, increased to between 122 and 298 mm by August to October (Fig. 2A). Because the birth date of *S. punctata* was designated as 1 August (see below), the members of this cohort represent early 1+ fish. By November, a translucent zone had become discernible at the edge of the otoliths of these 1+ fish. The length range of this cohort ranged from 158 to

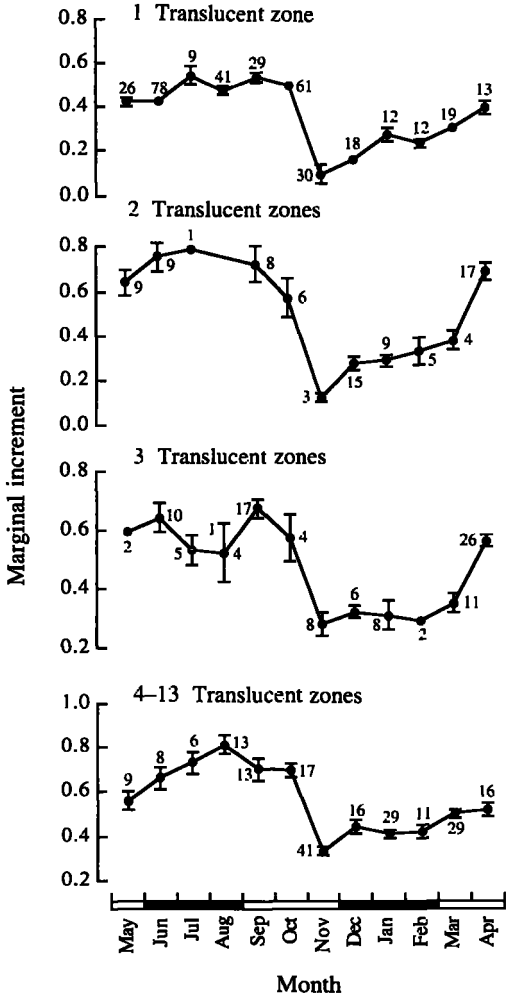


**Figure 1**

Mean monthly marginal increments ±1SE for sagittal otoliths of *Sillaginodes punctata*. Sample sizes are given for each month. In this Figure and Figure 5, the filled bars on the x-axis refer to winter and summer months, and the open bars to autumn and spring months.

282 mm from November to January, and from 251 to 403 mm from August to October, when this group of fish had just commenced their third year of life, and thus represents early 2+ fish (Fig. 2A). Between August and October, the lengths of 3+, 4+, and 5+ fish ranged from 340 to 425, from 403 to 480, and from 431 to 495 mm, respectively. *Sillaginodes punctata* attained maximum ages of 14+ and lengths of 596 mm in the case of females and maximum ages of 13+ and lengths of 555 mm with males.

Growth curves derived for female and male *S. punctata* (Fig. 3) differed significantly ($P<0.05$). The asymptotic length ($L_\infty$) and growth coefficient ($K$) for females were 532 mm and 0.47, respectively, whereas for males they were 500 mm and 0.53, respectively (Table 1).

**Table 1**

Von Bertalanffy growth parameters (±95% CL) derived from length at age data for *Sillaginodes punctata* caught on the lower west coast of Australia. $L_\infty$ is the asymptotic length, $K$ is the growth coefficient, $t_0$ is the hypothetical age at which fish would have zero length, $r^2$ is the regression coefficient, $n$ is the sample size.

| | von Bertalanffy parameters | | | | |
|---|---|---|---|---|---|
| | $L_\infty$ | $K$ | $t_0$ | $r^2$ | $n$ |
| Females | 532.4 ±6.9 | 0.47 ±0.02 | 0.13 ±0.02 | 0.97 | 760 |
| Males | 500.1 ±7.7 | 0.53 ±0.02 | 0.16 ±0.02 | 0.96 | 637 |

## Age and length at sexual maturity

For determining the length and age at maturity of female *S. punctata*, the data for mature (stages V–VII) and recovering or spent (stage VIII) ovaries were combined (Fig. 4). During the spawning period, which was determined as occurring from June to September (see below), the proportion of female fish with mature and recovering or spent ovaries increased sharply from 4% in the 350–399 mm length class to 71% in the 400–449 mm length class, and 100% in fish >500 mm (Fig. 4A). The length at which 50% of female *S. punctata* were mature, represented by the $L_{50}$, was 413 mm. Maturity was first attained by females at the end of their third year of life, when ca. 15% of fish possessed mature ovaries (Fig. 4B). However, by the end of the fourth year of life, the proportion of mature females had increased markedly to 72% and in subsequent years to 100%. A similar pattern was shown by the maturity stages for male fish (data not shown).

## Gonadal and oocyte development

Because the vast majority of *S. punctata* did not reach maturity until the end of their fourth year of life, the following monthly trends shown by gonadal stages were derived from fish that were ≥3.4 years old and thus these fish were expected to reach maturity in the following spawning period. Between January and May, the ovaries of all female *S. punctata* ≥3.4 years old were at either stages III or IV (Fig. 5). Mature ovaries were found in over 70% of females by June and in 90 and 100% by July and August, respectively. The proportion of mature ovaries declined markedly to 43% in September, whereas the contribution of

recovering or spent ovaries (stage VIII) increased from 9 to 48% between August and September (Fig. 5). Female fish with mature ovaries were virtually absent by November, and those with stage-VIII ovaries represented only ca. 8% of the fish caught both in this month and in December. The gonadal development of males followed a similar trend to that of females (Fig. 5).

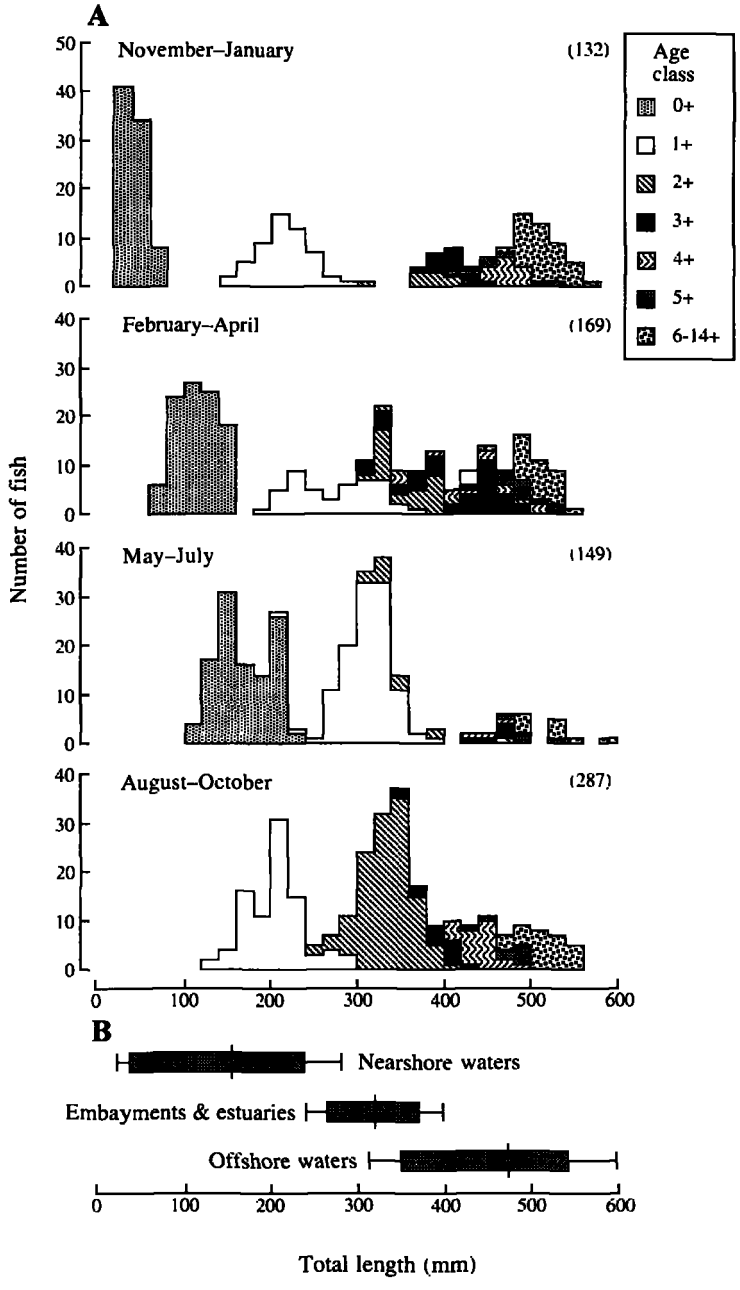


**Figure 2**

(**A**) Frequency histograms for total lengths of the different age classes of *Sillaginodes punctata*, from data obtained from samples collected by the 21.5-m seine net in nearshore marine waters and from anglers in deeper waters. Sample sizes are given in parentheses. (**B**) Median, 90 percentiles, and range of lengths for fish caught in shallow nearshore marine waters, deeper waters in marine embayments and estuaries, and in deeper and more offshore marine waters around reefs.

In each month, the oocyte diameters for *S. punctata* exhibited a well-defined mode between 50 and 80 μm (Fig. 6), which represents the perinuclear oocytes. Yolk vesicle and yolk granule oocytes first appeared in ovaries in April, when the diameters of these larger oocytes ranged between 255 and 430 μm. However, many other yolk vesicle and yolk granule oocytes were undergoing atresia. In the following month, the maximum oocyte diameter declined to 150 μm, reflecting the fact that no yolk vesicle or yolk granule oocytes were present. In June, the maximum diameter increased to 465 μm (Fig. 6), as a result of the development of yolk vesicle and yolk granule oocytes. These large oocytes were abundant between June and August, and many ovaries were dominated by yolk granule oocytes. The proportion of yolk vesicle and yolk granule oocytes declined in September, and the few remaining yolk vesicle and yolk granule oocytes that were present in October were at an advanced stage of atresia.

Hydrated oocytes that had collapsed during sectioning were found in large numbers in some ovaries between June and August. Because the ovaries in those months sometimes contained large numbers of postovulatory follicles, they had already discharged hydrated oocytes. Furthermore, hydrated oocytes and postovulatory follicles were occasionally found in the same ovary.

## Juvenile recruitment and depth distribution

The new 0+ recruits of *S. punctata* were first caught in late September 1994. The minimum standard length of these fish remained at ca. 14 mm between 23 September and 3 November, before increasing to ca. 30 mm between mid-November and mid-December (Fig. 7). The maximum length of these new recruits increased progressively from 26 mm in late September to 64 mm by mid-December (Fig. 7).

Although the vast majority of *S. punctata* caught by anglers in embayments and estuaries at depths of 2–6 m were <370 mm in length and <4 years of age, those that were collected outside embayments and estuaries and in the vicinity of reefs at depths of 6–50 m were predominantly greater than this length and age (Fig. 8, A and B). Furthermore, *S. punctata* that contained mature (stages V–VII) or recovering or spent (stage VIII) gonads were caught predominantly in and around reefs and at the edges of seagrass beds adjacent to these areas, where water depths exceeded 6 m (Fig. 8).

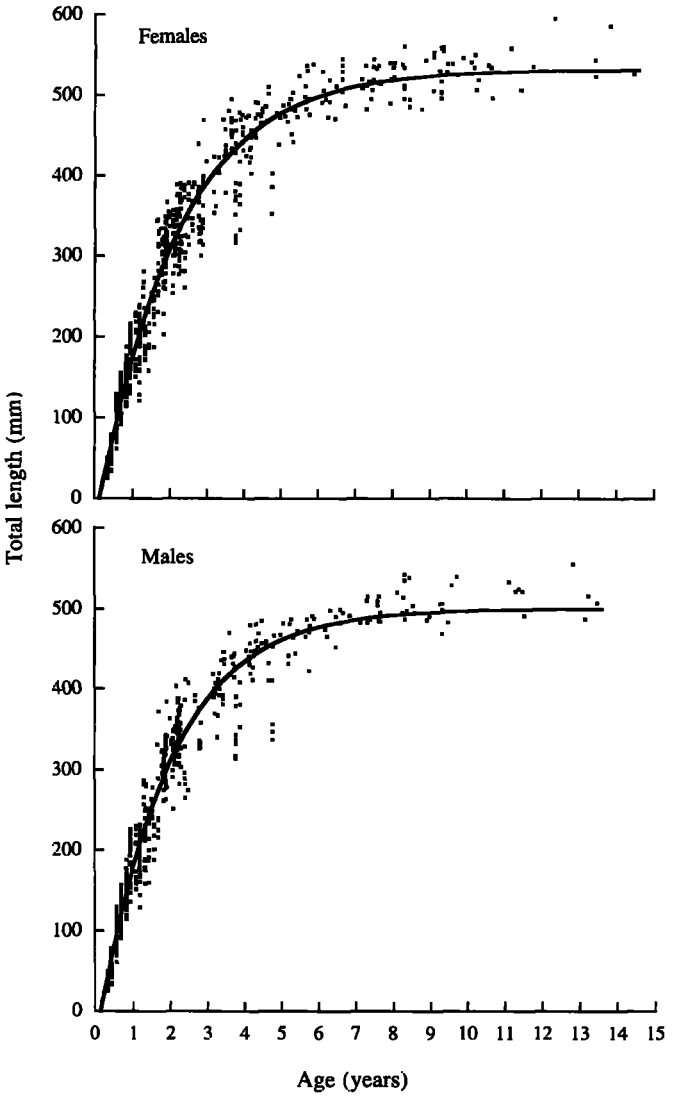


**Figure 3**

Von Bertalanffy growth curves fitted to total length-at-age data derived from sagittal otoliths of female and male *Sillaginodes punctata*.

## Discussion

### Sexual maturity and spawning period

Gonadal data indicate that, in southwestern Australia, female *S. punctata* reach maturity at the end of their fourth year of life or when they have attained a length of ca. 410 mm. This length far exceeds the 350 mm at which 50% of the members of this species reach maturity in southeastern Australian waters (see Cockrum and Jones[2]). However, the data of Cockrum and Jones[2] suggest that the length at maturity of *S. punctata* in southeastern Australia has declined since the 1950's as a result of fishing pressure, a trend that has been observed with increased fishing pressure in other species of teleosts (Wootton, 1990). Such a conclusion would be consistent with the fact that in southwestern Australia, where *S. punctata* is not at present as heavily exploited, the length at maturity (ca. 410 mm) is similar to that recorded in South Australia in the 1950's (Scott, 1954; Cockrum and Jones[2]).

Because large numbers of yolk granule and hydrated oocytes and postovulatory follicles were first found in the ovaries of large female *S. punctata* in June and were prevalent in ovaries through September, we conclude that this species spawns during this four-month period between early winter and early spring. Because the advanced oocytes present in ovaries in October and November were usually undergoing atresia, the spawning period of *S. punctata* rarely extends beyond September. The spawning of *S. punctata* during winter to early spring in southwestern Australia contrasts with the autumn and early winter spawning period found for *S. punctata* in southeastern Australia (Bruce, 1989; Jenkins and May, 1994; Fowler and Short, 1996; Cockrum and Jones[2]). Thus, although the duration of the spawning period of *S. punctata* is similar in both regions, it is initiated three months later on the lower west coast of Australia. It may thus be relevant that, in both regions, this species spawns when water temperatures are declining from their maxima and that this decline occurs more rapidly in southeastern Australia than on the lower west coast of Australia (Fig. 1 in Hyndes and Potter, 1996; Fowler[4]). The above

[4] Fowler, A. 1995. SARDI (South Australian Research and Development Institute), PO Box 120, Henley Beach, Adelaide, South Australia 5022, Australia.

spawning periods for *S. punctata* contrast with those of the majority of other temperate marine teleost species, including other whiting species, which typically breed at some period between late spring and early autumn (Morton, 1985; Vouglitois et al., 1987; Conover, 1992; Hyndes and Potter, 1996, 1997; Hyndes et al., 1996b). Because some of the estuaries of southwestern Australia often become closed from the sea by a sand bar in summer, a winter spawning period would allow the juveniles to become recruited into those estuaries (see "Nursery and spawning grounds" heading).

The presence in some ovaries of *S. punctata* of large numbers of yolk granule oocytes, together with either hydrated oocytes or postovulatory follicles, suggests that this species releases its eggs in batches. Furthermore, the presence of hydrated oocytes or postovulatory follicles, or both, in many of those ovaries which also contained advanced oocytes indicates that, although many oocytes were close to being released from those ovaries, others had recently been discharged. There is thus strong circumstantial evidence that *S. punctata* spawns on more than one occasion and possibly frequently during each breeding period. The conclusion that *S. punctata* is a multiple spawner (sensu de Vlaming, 1983) supports the conclusions of Cockrum and Jones[2] and parallels the situation recorded for several other sillaginid species (Morton, 1985; Hyndes and Potter, 1996, 1997; Hyndes et al., 1996b) and other teleosts in marine and estuarine waters in southwestern Australia (e.g. Hyndes et al., 1992b; Sarre et al., 1997).

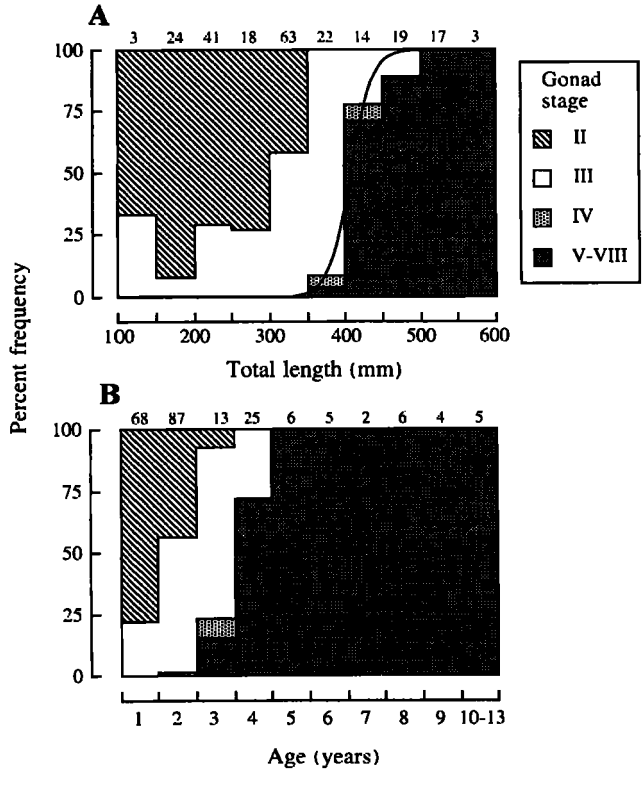


**Figure 4**

Percent frequency of occurrence of sequential stages in gonadal development in (**A**) each sequential 50-mm length class, and at (**B**) each age of female *Sillaginodes punctata* caught between June and September. The logistic curve, derived from the percentage of mature gonads for each length class, is also shown. Sample sizes are given above each length and age class.

## Age and growth

The asymptotic lengths ($L_\infty$) and growth coefficients ($K$) of female and male *S. punctata* in southwestern Australia, i.e. 532 and 0.47, and 500 mm and 0.53, respectively, lie within the range calculated for this species in southeastern Australia. However, these two parameters varied markedly in different localities within that latter region, i.e. 444 to 715 mm and 0.15 to 0.45 (Scott, 1954; Gilmour, 1969; Jones, 1980; Caton[1]; Jones et al.[3]). Such variation reflects either differences in the patterns of growth of this species in different locations or errors associated with deriving the age of fish from growth zones in scales or whole otoliths.

*Sillaginodes punctata* reaches a far greater size and age than the five other sillaginid species in southwestern Australia, all of which belong to the genus *Sillago* (Table 2). Furthermore, *S. punctata* does not attain maturity until it is four years old, which is far older than the age at which most of those *Sillago* species first spawn (Table 2). Because size and age at maturity are usually related to the length and age attained by teleosts (e.g. Beverton, 1992; Hyndes and Potter, 1997), this difference presumably reflects the greater size and age attained by *S. punctata*.

## Nursery and spawning grounds

0+ *S. punctata* were first caught in the sheltered nearshore waters of marine embayments of southwestern Australia in late September, when their lengths ranged from 14 to 24 mm. Because this length range approximates that at which this species settles to a benthic habit (Jenkins and May, 1994; Bruce, 1995), these early juvenile fish would only recently have moved into those nearshore waters. The fact

**Table 2**

Asymptotic total length (mm), growth coefficient, maximum age (years), length at maturity (mm), age at maturity (years), and location of the nursery and spawning areas for *Sillaginodes punctata* and the *Sillago* species found in southwestern Australian waters. F = females; M = males.

| Species | Asymptotic length ($L_\infty$) | | Growth coefficient ($K$) | | Maximum age ($T_{max}$) | | Length at maturity ($L_m$) | | Age at maturity ($T_m$) | | Nursery grounds | Spawning grounds |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | F | M | F | M | F | M | F | M | F | M | | |
| *Sillaginodes punctata* | 532 | 500 | 0.47 | 0.53 | 14 | 13 | 400 | 400 | 4 | 4 | Sheltered nearshore | Reefs |
| *Sillago bassensis* | 329 | 307 | 0.26 | 0.29 | 7 | 9 | 200 | 200 | 3 | 3 | Exposed nearshore | Deep offshore |
| *Sillago burrus* | 188 | 179 | 2.37 | 2.44 | 4 | 4 | 130 | 120 | 1 | 1 | Sheltered nearshore | Shallow offshore |
| *Sillago robusta* | 169 | 172 | 1.03 | 0.98 | 6 | 5 | 150 | 140 | 2 | 2 | Offshore | Deep offshore |
| *Sillago schomburgkii* | 333 | 325 | 0.52 | 0.53 | 7 | 7 | 200 | 180 | 2 | 2 | Sheltered nearshore | Nearshore |
| *Sillago vittata* | 331 | 312 | 0.43 | 0.45 | 7 | 6 | 140 | 130 | 1 | 1 | Sheltered nearshore | Shallow offshore |

that this size range of *S. punctata* was consistently observed in its specimens from nearshore waters between late September and early November (midspring), indicates that this species settles in its nearshore nursery grounds predominantly during this period. Thus, the first recruits of *S. punctata* enter those nearshore waters approximately three months after spawning is initiated, a time that corresponds to the time that the larvae of this species take to recruit into their nursery areas in South Australia (Bruce, 1989; Bruce and Short, 1992; Fowler and Short, 1996). Recruitment of juvenile *S. punctata* into the shallows commences far earlier in South Australian than in southwestern Australian waters, i.e. June vs. September, reflecting an earlier start to the spawning period, i.e. March vs. June (cf. Bruce, 1989; Fowler and Short, 1996). However, because the juveniles that are recruited into nursery habitats much farther east in Victoria are derived from a spawning that occurs in South Australia (Jenkins and Black, 1994; Jenkins and May, 1994), their larvae have to travel a far longer distance towards their nursery grounds than those recruited into nearshore waters of South Australia; thus recruitment commences far later in Victoria, i.e. September vs. June (Bruce, 1989; Jenkins and May, 1994; Fowler and Short, 1996).

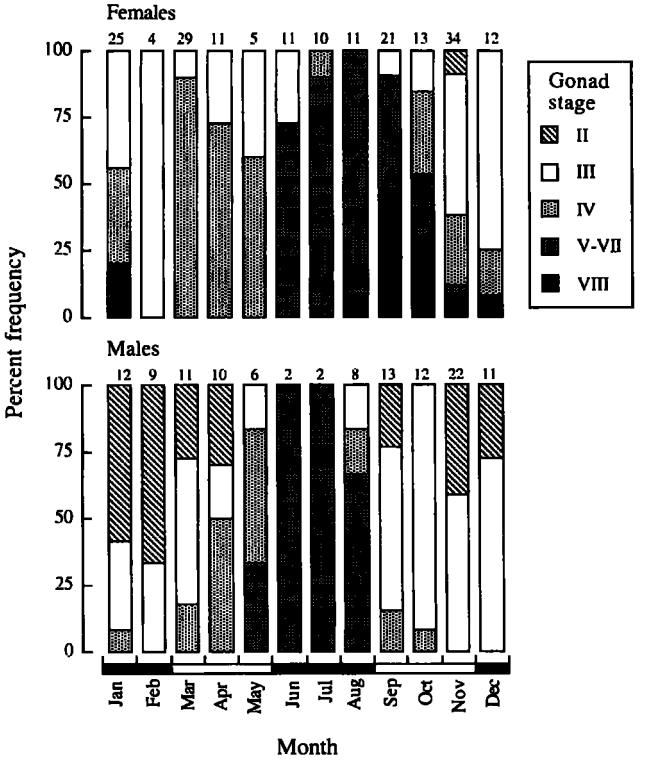


**Figure 5**

Monthly percent frequencies of occurrence of sequential gonadal development stages in female and male *Sillaginodes punctata* ≥3.4 years old. Numbers indicate sample sizes.

After settlement, large numbers of *S. punctata* remain in the sheltered nearshore marine waters of the lower west coast for about 1.5 years (Hyndes et al., 1996a). The fact that the densities of juveniles were far higher in these waters than in nearby exposed waters and even the shallows of estuaries (Hyndes et al., 1996a) indicates that the juveniles of this species prefer sheltered nearshore marine habitats. This conclusion is sup-

ported by the fact that juveniles of *S. punctata* are absent in nearshore waters along the southern coastline of southwestern Australia (Lenanton, 1982; Ayvazian and Hyndes, 1995), where the shoreline is more exposed to rough sea conditions (Hegge et al., 1996). The relative paucity of sheltered nearshore marine habitats on this coastline would account for the relatively high densities of juvenile *S. punctata* that are found in the relatively protected waters of estuaries in this region (Potter et al., 1993; Potter and Hyndes, 1994).

Estuaries along the southern coast of southwestern Australia, where the adjacent marine waters are exposed to wave and swell activity, may thus provide particularly important nursery habitats for *S. punctata*. Many estuaries in this region, however, become closed off from the sea during the summer and autumn, when, as a result of low freshwater discharge, a sand bar forms at their mouths (Lenanton and Hodgkin, 1985). It is thus relevant that *S. punctata* spawns during winter, because this would enable juveniles to enter those estuaries before their mouths become closed. This event parallels the situation with the mugilids *Mugil cephalus* and

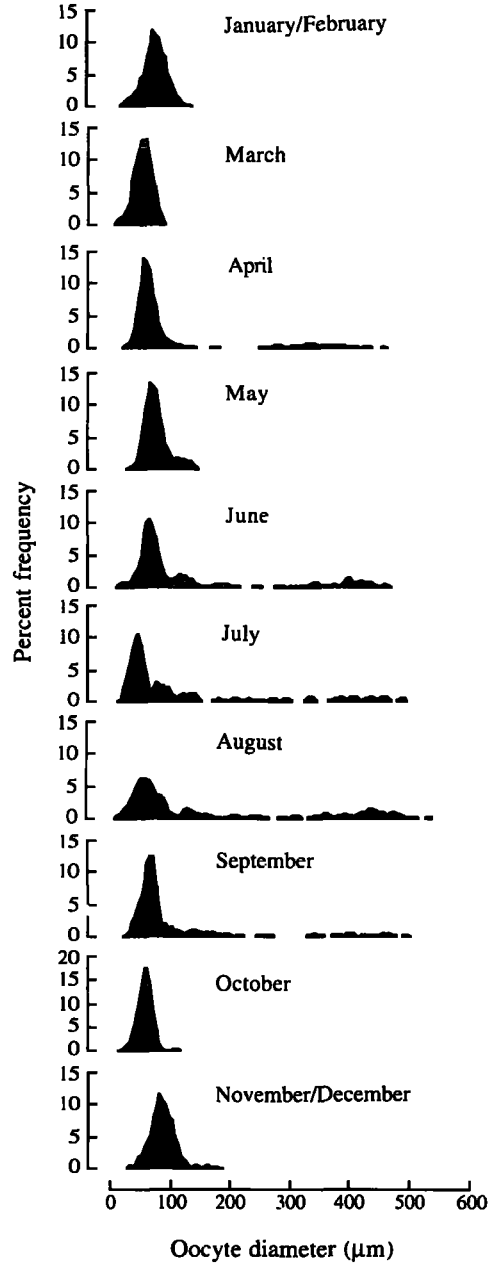


**Figure 6**

Monthly percent frequencies for oocyte diameters in ovaries of *Sillaginodes punctata*. Sample size in each month was 7–10 fish.

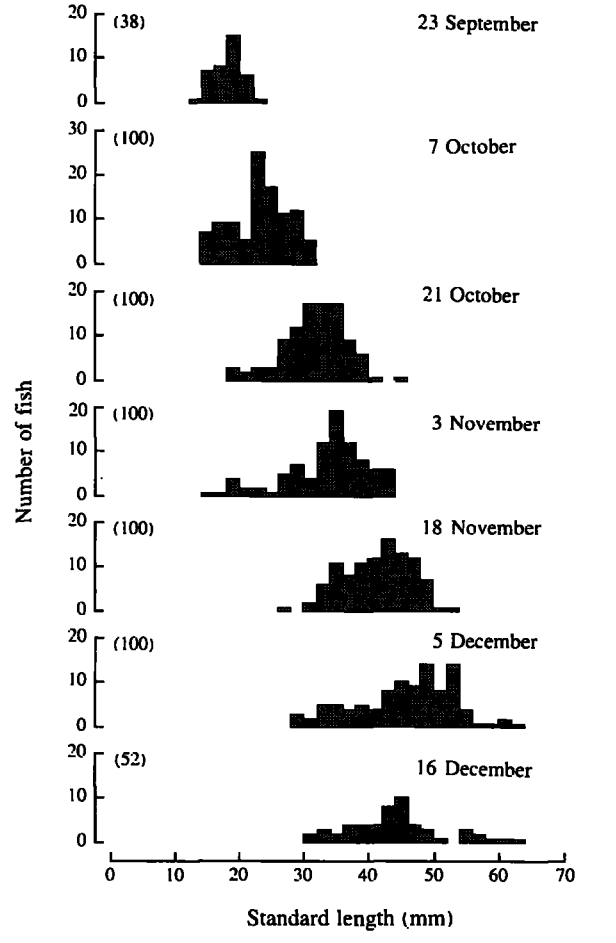


**Figure 7**

Frequency histograms for standard lengths of *Sillaginodes punctata* caught at two weekly intervals by the 5.5-m seine net in sheltered nearshore marine waters between September and December 1994. The numbers in parentheses represent the number of fish measured.

*Aldrichetta forsteri*, which also both spawn in winter in southwestern Australia and whose juveniles soon after enter estuaries in large numbers (Thomson, 1957b; Chubb et al., 1981).

*Sillaginodes punctata* typically remains in sheltered nearshore marine and estuarine waters until it reaches ca. 250 mm in length and ca. 1.5 years of age (Robertson, 1977; Potter et al., 1983; Loneragan et al., 1989; Potter et al., 1993; Potter and Hyndes, 1994; Hyndes et al., 1996a). Thus, unlike smaller species of whiting, such as *Sillago burrus* and *Sillago vittata*, which typically move offshore at lengths of ca. 100 mm and at ages of three to nine months (Hyndes et al., 1996a, 1996b), *S. punctata* remains in its nursery habitats for a far longer period. Because *S. burrus* and *S. vittata* reach maturity at the end of their first year of life, whereas most *S. punctata* first attain maturity at the end of their fourth year of life, this last species takes advantage of the productive waters of marine embayments or estuaries for a longer period before migrating out into spawning grounds in deeper marine waters.

Because the nursery areas of *S. punctata* are located initially in nearshore waters and subsequently in the deeper waters of marine embayments and estuaries, whereas adults occupy areas in and around reefs where water depths are generally greater, this species migrates offshore from shallow nursery grounds as it approaches the size and age at which it will become mature. A movement offshore as body size increases parallels that recorded for populations of *S. punctata* in southeastern Australia and for other whiting species (Scott, 1954; Gilmour, 1969; Robertson, 1977; Weng, 1986; Burchmore et al., 1988; Hyndes et al., 1996a; Caton[1]). Although anglers often caught *S. punctata* in deeper waters near reefs or at the edges of adjacent seagrass beds, they rarely caught them during extensive trawling over the expansive open, sandy areas of the same region where large numbers of other whiting species were caught (Hyndes et al., 1996a). The presence of mature and recovering or spent gonads in the larger members of *S. punctata* caught in areas around reefs also suggests that, unlike the three whiting species *Sillago burrus*, *S. vittata*, and *S. bassensis*, which migrate out into the more open and sandy areas of the inner shelf to spawn (Table 2; Hyndes et al., 1996b; Hyndes and Potter, 1996), *S. punctata* spawns in areas in and around reefs or at the edges of adjacent seagrass beds. Furthermore, whereas *S. burrus* and *S. vittata* move into spawning grounds ranging from 5–15 m in depth, and *S. bassensis* migrates into more offshore waters where the depth is 20–35 m deep (Hyndes et al., 1996a, 1996b; Hyndes and Potter, 1996), *S. punctata* spawns at depths that range from six to at least 50 m.

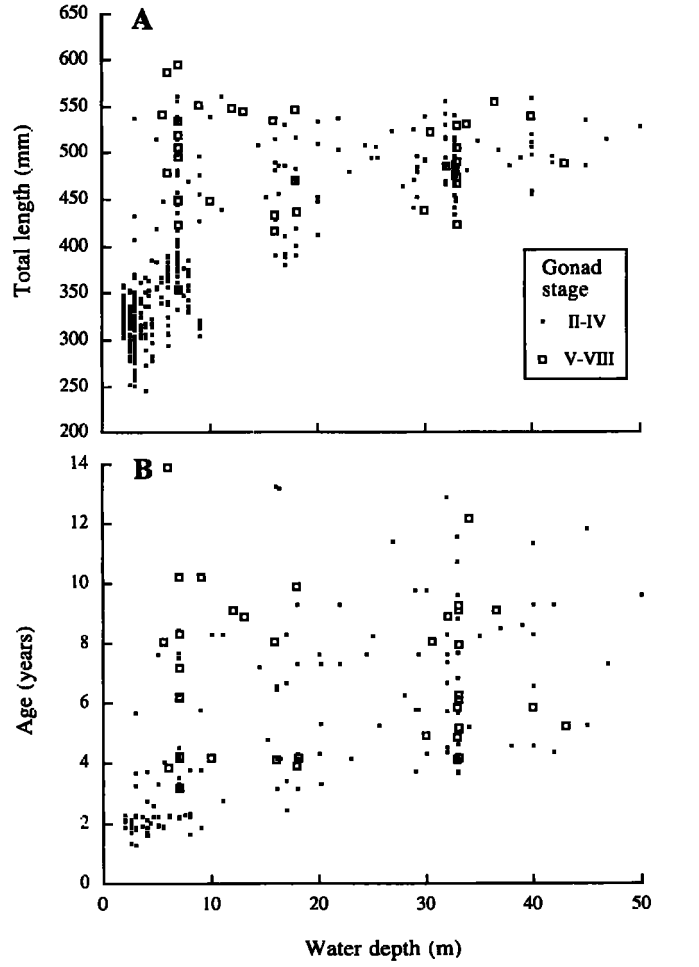


**Figure 8**

(**A**) Total lengths and (**B**) ages at capture, of female and male *Sillaginodes punctata* with immature (stages II–IV) and mature or recovering or spent (or both) (stages V–VIII) gonads collected at different depths by recreational fishers in the inner-shelf waters of the lower west coast of Australia.

## Implications for management

Because *S. punctata* exhibits size-related offshore movements, that involve firstly a movement from nearshore nursery areas to deeper waters in marine embayments and estuaries and subsequently a move-

ment into areas around reefs farther offshore (Fig. 2B), this species essentially occupies three different habitats during the course of its life cycle. Any management plans for *S. punctata* must therefore take into account the need both to protect these habitats and to ensure that fishing pressure in those habitats where fishing occurs does not have a deleterious effect on the stock of this species.

The postlarvae of *S. punctata* settle predominantly in very sheltered nearshore waters of marine embayments and estuaries (Jenkins and May, 1994; Fowler and Short, 1996; Hyndes et al., 1996a; Hyndes, unpubl. data). However, *S. punctata* moves out into slightly deeper waters (2–10 m) in marine embayments and estuaries at ca. 1.5 years in age and at a total length of 250 mm (Fig. 2B). Because this latter length corresponds to the legal minimum length for capture (LML) of *S. punctata* on the lower west coast and approaches the LML of 280 mm on the south coast, this species does not become commercially and recreationally exploited until it has left its very shallow nursery areas and has entered deeper waters. This species remains in these slightly deeper waters until it reaches 350–400 mm (Fig. 2B) and is thus available for capture in marine embayments and estuaries when it is predominantly between 1.5 and 2.5 years in age. Because this species is most heavily exploited when it is in the deeper waters of marine embayments and estuaries, it is fished mainly during this relatively restricted period of its life cycle. From a management point of view, it is also relevant that the fishery in marine embayments and estuaries is based on fish that have not yet reached 410 mm, the length at which they typically first become mature. Subsequently, those *S. punctata* that have run the "gauntlet" of numerous fishermen in marine embayments and estuaries move farther out into areas in and around reefs in deeper waters where they attain maturity and where the reduced number of fishermen targeting this species makes it less susceptible to capture. Furthermore, the catches of *S. punctata* in the more offshore waters are further reduced in winter, when sea conditions are far less favorable for fishing and when, according to fishermen, *S. punctata* are less likely to take bait. Thus, because *S. punctata* spawns during winter, fishing pressure on this species is relatively low during the spawning period.

Because catch and effort statistics for the commercial fishery in southwestern Australia do not suggest that the catch rate for *S. punctata* is declining, this species would not appear currently to be overexploited in this region. However, the number of sheltered nearshore areas that act as nursery areas for *S. punctata* are limited and are often located in the type of region where marinas and other developments are likely to be proposed. Furthermore, recreational fishing effort is rising markedly, and the increasing use of larger vessels and more sophisticated equipment, such as global positioning systems (GPS), means that, particularly in deeper waters, fish are now beginning to be exploited to a greater extent. The resultant advances in fishing efficiency also mean that more sophisticated measures of effort are required to obtain reliable and comparable catch-per-unit-of-effort data for *S. punctata* from the recreational sector, which is ultimately expected to become the main exploiter of this resource.

## Acknowledgments

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# Estimates of marine mammal, turtle, and seabird mortality for two California gillnet fisheries: 1990–1995

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**Abstract.**—Incidental kills of marine mammals, turtles, and seabirds are estimated for the California drift gillnet fishery for broadbill swordfish, *Xiphias gladius*, common thresher shark, *Alopias vulpinus*, and shortfin mako shark, *Isurus oxyrinchus*, and the set gillnet fishery for California halibut, *Paralichthys californicus*, and Pacific angel shark, *Squatina californica*, for the period July 1990 through December 1995. Estimates were based on observations made by National Marine Fisheries Service observers placed aboard commercial fishing vessels. Yearly observer coverage varied between 4% and 18% of estimated total effort. Total fishing effort-days per California Department of Fish and Game fishing block was used as the measure of effort for the drift and set gillnet fisheries. Incidental kill was estimated from observed data and estimates of total effort by using mean-per-unit and ratio estimators. Additional bycatch data collected by NMFS observers were used to derive kill estimates of marine turtles and seabirds.

In the drift gillnet fishery, seven out of 387 mammals observed entangled were released alive. In the set gillnet fishery, five out of 1,263 mammals observed entangled were released alive. Estimates of incidental kill are presented along with estimates of entanglement for species that were observed to be released alive. For the period under consideration, the estimated mortality for the drift gillnet fishery was over 450 marine mammals each year. A total of 20 turtles and 3 seabirds were observed entangled during the entire period. The most frequently entangled species in this fishery were common dolphins, *Delphinus* spp., and northern elephant seals, *Mirounga angustirostris*. Estimated cetacean mortality in the driftnet fishery decreased from 650 in 1991 to 417 in 1995; pinniped mortality decreased from 173 in 1991 to 116 in 1995. Estimated cetacean mortality in the set gillnet fishery ranged from a high of 38 in 1991 to a low 14 in 1993; pinniped mortality rose to a high of 4,777 in 1992 and then decreased to 1,016 in 1995. We postulate that there has been a decline in the number of pinnipeds and cetaceans in the setnet fishery owing to area closure. No similar proposal can be made for the driftnet fishery. The most frequently entangled mammals in the setnet fishery were California sea lions, *Zalophus californianus*, and harbor seals, *Phoca vitulina*. Six turtles and 1,018 seabirds were estimated entangled in this fishery during the NMFS Observer Program from July 1990 to December 1995.

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Fishery Bulletin 96:271–284 (1998).

Two major gillnet fisheries in California are known to kill marine mammals, turtles, and seabirds incidentally: the drift gillnet fishery for broadbill swordfish, *Xiphias gladius*, common thresher shark, *Alopias vulpinus*, and shortfin mako shark, *Isurus oxyrinchus*, and the set gillnet fishery for California halibut, *Paralichthys californicus*, and Pacific angel shark, *Squatina californica*. Historically, concern was focused on incidental kill of seabirds, sea otters, *Enhydra lutris*, harbor porpoise, *Phocoena phocoena*, harbor seals, *Phoca vitulina*, and California sea lions, *Zalophus californianus*, in the setnet fishery (Salzman, 1989; Jefferson et al., 1994; Diamond and Hanan[1]; Hanan et al.[2,3]; Hanan and Diamond[4]). In recent years the driftnet fishery has received more attention because it interacts with more cetaceans (Barlow et al., 1994; Lennert et al., 1994). Estimation for the driftnet fishery has been possible because, in July 1990, the National Marine Fisheries Service (NMFS) implemented an observer program to monitor the marine mammal bycatch. Complementing the observer program was a project by the California Department of Fish and Game (CDFG) to develop estimates of total effort in the drift and set gillnet fisheries. Results from these programs were used to estimate incidental kill with stratified ratio and mean-per-unit estimation

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[2] Hanan, D. A., S. L. Diamond, and J. P. Scholl. 1986. An estimate of harbor porpoise mortality in California set net fisheries, April 1, 1984 through March 31, 1985. NOAA/NMFS SWR Admin. Rep. SWR-86-16, 38p. [Available from Southwest Fisheries Science Center, National Marine Fisheries Service, P.O. Box 271, La Jolla, CA 92038.]

[3] Hanan, D. A., S. L. Diamond, and J. P. Scholl. 1988. Estimates of sea lion and harbor seal mortalities in California set net fisheries for 1983, 1984, and 1985. Final Rep. NA-86-ABH00018 submitted to NOAA Fisheries, SWR, 10 p. [Available from Southwest Fisheries Science Center, National Marine Fisheries Service, P.O. Box 271, La Jolla, CA 92038.]

[4] Hanan, D. A., and S. L. Diamond. 1989. Estimates of sea lion, harbor seal, and harbor porpoise mortalities in California set net fisheries for the 1986–87 fishing year. Final Rep. NA-86-ABH00018 submitted to NOAA Fisheries, SWR, 10 p. [Available from Southwest Fisheries Science Center, National Marine Fisheries Service, P.O. Box 271, La Jolla, CA 92038.]

methods (Lennert et al., 1994; Perkins et al.[5]; Julian[6, 7, 8]). Separate estimates of entanglement are provided for species that had individuals released alive. This paper documents incidental marine mammal, turtle, and seabird kill estimates in these two California gillnet fisheries, based on data from the NMFS observer program and CDFG effort estimates for the period July 1990 through December 1994, and documents the process and methods leading to these estimates.

## Methods

### Data collection

National Marine Fisheries Service observer data, daily logbooks of commercial gillnet fishermen, and receipts of landed fish sales were used in marine mammal mortality estimation. NMFS observer data were collected by trained technicians aboard commercial gillnet fishing boats that had a Marine Mammal Protection Act (MMPA) Exemption Permit and that met minimum U.S. Coast Guard safety standards. There were two general observation categories: observation of randomly selected trips and observation of approximately every fifth vessel trip. In the setnet fishery, systematically selected trips were further divided. Notification prior to the setting of nets resulted in a preset, systematic observation rather than a postset, systematic observation where notification to the vessel was given after the nets were set (see "Discussion" section). NMFS observers recorded data on location, date, marine mammal entanglements, including location of mammals in the net (by thirds of the net—vertically and horizontally), gear, bycatch, and target species catch for each net pull observed during a trip (Lennert et al., 1994).

Observers recorded twelve net-related parameters for drift and set nets. They were net type (set, drift, float, or trammel), net material (monofilament, multifilament, or a combination), net strength (pounds test or twine size depending on strength code), strength code, net length (fathoms), net depth (number of meshes), stretched mesh size (inches), extender length (feet, float, and drift nets only), hanging line material (synthetic or natural fiber), percent slack in net, number of meshes hanging (between knots to the cork line), and hanging length (distance between knots on the cork line in inches). Not infrequently, a drift or set net will consist of panels of varying characteristics. In this case, observers would record characteristics on up to 5 different panels. Net characteristics for both fisheries are summarized in Table 1. Although the variability in these characteristics contributes somewhat to the variability in mortality estimates, the significant factors for mortality estimation are the amount of effort and the general location of the effort. For some species, e.g. pinnipeds, quarter of the year is also significant (Perkins et al.[5]).

Collected data were entered into a database file, checked for accuracy, and tabulated for mortality estimation (Tables 2–5). After an initial six month period, this observation method continued unchanged in both fisheries. Realized observation rates varied between 4.4% and 17.9% yearly, but observation rates were more variable if stratified by area and quarter. Observation in the driftnet fishery continued through December 1995, whereas observation in the setnet fishery terminated by July 1994 because of a significant decrease in fishing effort in that fishery (due to regulations that restricted areas open to gillnet fishing). Observer data were complemented by information from vessel logbooks and landing receipts (i.e. receipts from sales of landed fish).

Vessel logbooks were submitted monthly to CDFG and constituted the major source of information for estimation of total effort. Data for each logbook entry included date, vessel and permit identification, area fished by CDFG block number (Lennert et al. 1994), gear, number of sets made, and number and species of fish caught (CDFG blocks are typically 10' square; larger blocks are defined for areas further from shore). Logbook information was entered into a database by technicians and checked for accuracy by biologists. Fish species targeted for catch by the fishermen were determined and assigned to each data entry by CDFG personnel according to fish caught, gear used, and other pertinent factors. Purchases of landed fish by commercial fish buyers were recorded

[5] Perkins, P., J. Barlow, and M. Beeson. 1992. Pinniped and cetacean mortality in California gillnet fisheries: 1991. International Whaling Commission Scientific Committee working paper SC/44/SM14. [Available from Southwest Fisheries Science Center, National Marine Fisheries Service, P.O. Box 271, La Jolla, CA 92038.]

[6] Julian, F. 1993. Pinniped and cetacean mortality in California gillnet fisheries: preliminary estimates for 1992, rev. 2/94. International Whaling Commission Scientific Committee working paper SC/45/O22. [Available from Southwest Fisheries Science Center, National Marine Fisheries Service, P.O. Box 271, La Jolla, CA 92038.]

[7] Julian, F. 1994. Pinniped and cetacean mortality in California gillnet fisheries: preliminary estimates for 1993. International Whaling Commission Scientific Committee working paper SC/46/O11. [Available from Southwest Fisheries Science Center, National Marine Fisheries Service, P.O. Box 271, La Jolla, CA 92038.]

[8] Julian, F. 1995. Cetacean and pinniped mortality in California gillnet fisheries: preliminary estimates for 1994. International Whaling Commission Scientific Committee working paper SC/47/O5. [Available from Southwest Fisheries Science Center, National Marine Fisheries Service, P.O. Box 271, La Jolla, CA 92038.]

**Table 1**

Observed net characteristics for the driftnet and setnet fisheries taken from nets characterized by one set of characteristics only (some nets may consist of two or more panels with differing characteristics). *n* = number of sets observed.

| Characteristic | Driftnet fishery (*n*=2,932) | Setnet fishery (*n*=7,994) |
|---|---|---|
| Net type | All 2,932 were drift nets. | 1,592 set nets and 6,278 1-panel trammel nets. |
| Net material | 2,838 (97%) were multifilament nets. | 7,520 (94%) were monofilament and 439 were multifilament. |
| Net strength and strength code | Twine size of 24 was used for 25% of the nets; size 27 was used for 36%, and size 30 was used for 22% of the nets. | 3,203 (40%) nets with twine size 66, 10% with twine size 55, and 19.4% nets with unrecorded data. |
| Net length (m) | mean=1,784.9; SD=55.4; mode=1,828.8 | mean=468.9, SD=164.7; mode=457.2 |
| Net depth (meshes) | mean=128; SD=24; mode=130 | mean=23.7; SD=8.9; mode=20 (*n*=7,880) |
| Mesh size (cm) | mean=52.1; SD=3.9; mode=53.34 | mean=21.2 ; SD=2.2; mode=21.6 (*n*=7,968) |
| Extender length (m) | mean=11.48; SD=4.37; mode=11.30 | Extenders not typically used; 98.4% of the nets did not use them. |
| Hanging line material | 2,809 (95.8%) nets were of synthetic fiber. | 7,628 (95.4%) nets were of synthetic fiber. |
| Percent slack | mean=45%; SD=5.4%; mode=50% (*n*=2,609). | No slack indicated for 38% of the nets. For nets with slack, mean=57%; SD=11%; mode=50% (*n*=4,986). |
| Meshes hanging | 60% had 2 and 35% had 1 mesh hanging between knots tied to the cork line. | 42% had 6, 26% had 4, and 17% had 6 meshes hanging between knots tied to the cork line. |
| Hanging length (cm) | mean=50.7; SD=14.6; mode=60.0 for distance between knots on the cork line. | mean = 38.4; SD=6.5; mode=38.1 for distance between knots on the cork line. |

and those records were submitted to CDFG twice monthly. Landing receipts included information on species landed, weight by species, price, gear, area fished, and vessel and permit identification. Landing information was entered into a database and checked for accuracy. A target fish species was assigned to each entry. Logbook data, landing information, and NMFS observer data (date, set position, gear, and catch) were subsequently used in estimating effort.

## Estimation of total effort

Fishing effort in both fisheries is an unknown quantity and absolute determination is impractical. Consequently, estimates of total fishing effort in each fishery were used to estimate incidental kill. These estimates were based on the combination of observer records, logbook data, and landing receipts. Effort was measured in "effort-days" which was defined as one day of fishing for one vessel. In the driftnet fishery, one effort-day was considered equivalent to setting and retrieving one net, generally 1828.8 m (1,000 fm) in length. (One vessel, targeting thresher shark, made two sets per day.) In the setnet fishery, typically two to four net settings, each of about 457.2 m (250 fm) in length, made up one effort-day. Days actually fished was used as the measure of total effort in each fishery because previous exploratory analysis determined that number of days of effort and general location of effort were significant factors in estimation of mortality (Perkins, et al.[5]). For some species, quarter of the year was also determined to be significant. These factors were available for all effort through the California Fish and Game Department and although other approaches to estimation (e.g. a modeling approach) can be developed, the current analysis is based on these factors. Data on other variables, such as total number of nets fished, total length of nets fished, or tons of target fish caught, were not readily available or contained additional variability due to nonsampling errors. Nonsampling

**Table 2**

Observed (obs) and (est) estimated cetacean, pinniped, turtle, and seabird mortality, stratified by year, in the California swordfish and shark drift gillnet fishery during the NMFS Observer Program, July 1990–December 1995. Estimates of total mortality are reported to the nearest individual. Estimated coefficients of variation (CV) are included in parentheses; (—) indicates CV was undefined. Effort and estimates for 1990 pertain to the third and fourth quarters only.

| Year | 1990 | | | 1991 | | | 1992 | | | 1993 | | | 1994 | | | 1995 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Estimated days effort | 4,078 | | | 4,778 | | | 4,379 | | | 5,442 | | | 4,248 | | | 3,673 | | |
| Observed days effort | 178 | | | 470 | | | 596 | | | 728 | | | 759 | | | 572 | | |
| Percent observer coverage | 4.4% | | | 9.8% | | | 13.6% | | | 13.4% | | | 17.9% | | | 15.6% | | |
| Observed trips effort | 54 | | | 88 | | | 97 | | | 107 | | | 134 | | | 97 | | |
| | obs | est | CV | obs | est | CV | obs | est | CV | obs | est | CV | obs | est | CV | obs | est | CV |
| Dall's porpoise | 1 | 23 | (0.95) | 2 | 20 | (0.67) | 1 | 7 | (0.92) | 9 | 67 | (0.44) | 2 | 11 | (0.64) | 1 | 6 | (0.92) |
| Pacific white-sided dolphin | 3 | 69 | (0.56) | 5 | 51 | (0.63) | 3 | 22 | (0.70) | 2 | 15 | (0.66) | 3 | 17 | (0.67) | 1 | 6 | (0.92) |
| Risso's dolphin | 0 | 0 | (—) | 5 | 51 | (0.50) | 5 | 37 | (0.48) | 7 | 52 | (0.51) | 1 | 6 | (0.91) | 6 | 39 | (0.57) |
| Bottlenose dolphin | 0 | 0 | (—) | 0 | 0 | (—) | 3 | 22 | (0.93) | 0 | 0 | (—) | 0 | 0 | (—) | 0 | 0 | (—) |
| Striped dolphin | 0 | 0 | (—) | 0 | 0 | (—) | 0 | 0 | (—) | 0 | 0 | (—) | 1 | 6 | (0.90) | 0 | 0 | (—) |
| Common dolphin (unknown stock) | 4 | 92 | (0.79) | 7 | 71 | (0.70) | 5 | 37 | (0.40) | 4 | 30 | (0.57) | 1 | 6 | (0.91) | 0 | 0 | (—) |
| Common dolphin (long beak) | 0 | 0 | (—) | 0 | 0 | (—) | 2 | 15 | (0.92) | 0 | 0 | (—) | 1 | 6 | (0.91) | 6 | 39 | (0.65) |
| Common dolphin (short beak) | 4 | 92 | (0.47) | 37 | 376 | (0.21) | 39 | 287 | (0.21) | 24 | 179 | (0.26) | 25 | 140 | (0.18) | 36 | 231 | (0.29) |
| Northern right whale dolphin | 0 | 0 | (—) | 7 | 71 | (0.41) | 2 | 15 | (0.65) | 7 | 52 | (0.39) | 7 | 39 | (0.42) | 9 | 58 | (0.59) |
| Killer whale | 0 | 0 | (—) | 0 | 0 | (—) | 0 | 0 | (—) | 0 | 0 | (—) | 0 | 0 | (—) | 1 | 6 | (0.92) |
| Short-finned pilot whale | 1 | 23 | (0.95) | 0 | 0 | (—) | 1 | 7 | (0.92) | 8 | 60 | (0.54) | 0 | 0 | (—) | 0 | 0 | (—) |
| Baird's beaked whale | 0 | 0 | (—) | 0 | 0 | (—) | 0 | 0 | (—) | 0 | 0 | (—) | 1 | 6 | (0.90) | 0 | 0 | (—) |
| Stejneger's beaked whale | 0 | 0 | (—) | 0 | 0 | (—) | 0 | 0 | (—) | 0 | 0 | (—) | 1 | 6 | (0.91) | 0 | 0 | (—) |
| Hubbs' beaked whale | 0 | 0 | (—) | 0 | 0 | (—) | 3 | 22 | (0.53) | 0 | 0 | (—) | 2 | 11 | (0.64) | 0 | 0 | (—) |
| Mesoplodont beaked whale | 1 | 23 | (0.97) | 0 | 0 | (—) | 1 | 7 | (0.93) | 0 | 0 | (—) | 0 | 0 | (—) | 0 | 0 | (—) |
| Cuvier's beaked whale | 0 | 0 | (—) | 0 | 0 | (—) | 6 | 44 | (0.36) | 3 | 22 | (0.53) | 6 | 34 | (0.36) | 5 | 32 | (0.40) |
| Unidentified beaked whale | 0 | 0 | (—) | 0 | 0 | (—) | 2 | 15 | (0.65) | 0 | 0 | (—) | 1 | 6 | (0.90) | 0 | 0 | (—) |
| Sperm whale | 0 | 0 | (—) | 0 | 0 | (—) | 1 | 7 | (0.94) | 2 | 15 | (0.66) | 0 | 0 | (—) | 0 | 0 | (—) |
| Pygmy sperm whale | 0 | 0 | (—) | 0 | 0 | (—) | 0 | 0 | (—) | 1 | 7 | (0.93) | 0 | 0 | (—) | 0 | 0 | (—) |
| Unidentified *Kogia* | 0 | 0 | (—) | 0 | 0 | (—) | 1 | 7 | (0.92) | 0 | 0 | (—) | 0 | 0 | (—) | 0 | 0 | (—) |
| Minke whale | 0 | 0 | (—) | 0 | 0 | (—) | 0 | 0 | (—) | 0 | 0 | (—) | 1 | 6 | (0.91) | 0 | 0 | (—) |
| Unidentified cetacean | 0 | 0 | (—) | 1 | 10 | (0.95) | 1 | 7 | (0.93) | 0 | 0 | (—) | 0 | 0 | (—) | 0 | 0 | (—) |
| Unidentified dolphin | 0 | 0 | (—) | 0 | 0 | (—) | 1 | 7 | (0.93) | 0 | 0 | (—) | 0 | 0 | (—) | 0 | 0 | (—) |
| Unidentified whale | 0 | 0 | (—) | 0 | 0 | (—) | 0 | 0 | (—) | 1 | 7 | (0.93) | 0 | 0 | (—) | 0 | 0 | (—) |
| Steller sea lion | 0 | 0 | (—) | 0 | 0 | (—) | 1 | 7 | (0.92) | 0 | 0 | (—) | 1 | 6 | (0.91) | 0 | 0 | (—) |
| California sea lion | 2 | 46 | (0.99) | 4 | 41 | (0.58) | 9 | 66 | (0.34) | 11 | 82 | (0.42) | 5 | 28 | (0.40) | 4 | 26 | (0.45) |
| Unidentified sea lion | 2 | 46 | (0.97) | 0 | 0 | (—) | 0 | 0 | (—) | 0 | 0 | (—) | 0 | 0 | (—) | 0 | 0 | (—) |
| Harbor seal | 1 | 23 | (0.95) | 0 | 0 | (—) | 0 | 0 | (—) | 0 | 0 | (—) | 0 | 0 | (—) | 0 | 0 | (—) |
| Northern elephant seal | 5 | 115 | (0.44) | 13 | 132 | (0.25) | 15 | 110 | (0.24) | 14 | 105 | (0.26) | 22 | 123 | (0.23) | 14 | 90 | (0.25) |
| Loggerhead turtle | 0 | 0 | (—) | 0 | 0 | (—) | 1 | 7 | (0.93) | 0 | 0 | (—) | 0 | 0 | (—) | 0 | 0 | (—) |
| Leatherback turtle | 1 | 23 | (0.97) | 0 | 0 | (—) | 2 | 15 | (0.65) | 2 | 15 | (0.66) | 0 | 0 | (—) | 4 | 26 | (0.55) |
| Unidentified turtle | 0 | 0 | (—) | 0 | 0 | (—) | 0 | 0 | (—) | 1 | 7 | (0.93) | 0 | 0 | (—) | 0 | 0 | (—) |
| Seabirds (all unidentified) | 1 | 23 | (0.98) | 0 | 0 | (—) | 0 | 0 | (—) | 0 | 0 | (—) | 1 | 6 | (0.90) | 0 | 0 | (—) |

errors, those not due to the sampling design, include, but are not limited to

1 Effort that is not recorded. This type of error may occur for several reasons, namely the times when no marketable target fish are caught during the entire day of effort and when a log entry is not made. The occurrence of this type of error implies that estimates of mortality are biased lower than actual mortality levels.

2 Incorrect reporting of effort location by fishermen. This type of error may bias estimated mortality either higher or lower.

**Table 3**

Observed (obs) and estimated (est) cetacean, pinniped, turtle, and seabird entanglement, stratified by year, in the California swordfish and shark drift gillnet fishery during the NMFS Observer Program, July 1990–December 1995. Estimates of entanglement are reported to the nearest individual. Estimated coefficients of variation (CV) are included in parentheses; (—) indicates CV was undefined. Effort and estimates for 1990 pertain to the third and fourth quarters only.

| Year | 1990 | | | 1991 | | | 1992 | | | 1993 | | | 1994 | | | 1995 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | obs | est | CV | obs | est | CV | obs | est | CV | obs | est | CV | obs | est | CV | obs | est | CV |
| Common dolphin (unknown stock) | 4 | 92 | (0.79) | 7 | 71 | (0.70) | 6 | 44 | (0.36) | 4 | 30 | (0.57) | 1 | 6 | (0.91) | 0 | 0 | (—) |
| Cuvier's beaked whale | 0 | 0 | (—) | 0 | 0 | (—) | 6 | 44 | (0.36) | 3 | 22 | (0.53) | 6 | 34 | (0.36) | 6 | 39 | (0.36) |
| Sperm whale | 0 | 0 | (—) | 0 | 0 | (—) | 3 | 22 | (0.94) | 3 | 22 | (0.69) | 0 | 0 | (—) | 0 | 0 | (—) |
| Humpback whale | 0 | 0 | (—) | 0 | 0 | (—) | 0 | 0 | (—) | 0 | 0 | (—) | 1 | 6 | (0.91) | 0 | 0 | (—) |
| California sea lion | 2 | 46 | (0.99) | 4 | 41 | (0.58) | 9 | 66 | (0.34) | 12 | 90 | (0.39) | 5 | 28 | (0.40) | 5 | 32 | (0.40) |
| Unidentified sea lion | 2 | 46 | (0.97) | 1 | 10 | (0.95) | 0 | 0 | (—) | 0 | 0 | (—) | 0 | 0 | (—) | 0 | 0 | (—) |
| Loggerhead turtle | 0 | 0 | (—) | 0 | 0 | (—) | 2 | 15 | (0.66) | 5 | 37 | (0.49) | 0 | 0 | (—) | 0 | 0 | (—) |
| Leatherback turtle | 1 | 23 | (0.97) | 1 | 10 | (0.94) | 4 | 29 | (0.46) | 3 | 22 | (0.53) | 1 | 6 | (0.91) | 5 | 32 | (0.47) |
| Unidentified turtle | 0 | 0 | (—) | 0 | 0 | (—) | 0 | 0 | (—) | 3 | 22 | (0.93) | 0 | 0 | (—) | 0 | 0 | (—) |
| Seabirds (all unidentified) | 1 | 23 | (0.98) | 0 | 0 | (—) | 1 | 7 | (0.93) | 0 | 0 | (—) | 1 | 6 | (0.90) | 0 | 0 | (—) |

3 Underestimation of effort from landing receipts. This type of error may occur when a landing receipt, in absence of additional information, is assumed to represent one effort-day (default-value).

A reliable determination of the magnitude of bias these errors cause in estimates of mortality rates has not been made; however, their characteristics indicate that estimates of mortality may be lower than actual values.

Once quarterly effort data were collected, computer programs developed by CDFG were used to assign target species to landing receipts on the basis of information provided by logbooks and observations (Beeson and Hanan[9]). Landing data were then confirmed or modified on the basis of logbook and observer data for the same target species, date, and vessel number. After all three data sources were compared, a day of effort was tallied for each record with a logbook entry or observer record. Landing receipts without corresponding logbook or observer entries three days before and after the receipt date were assumed to represent one day of effort. The numbers of days fished in each CDFG block were then tallied and the resultant data represented estimated total effort. Total effort was estimated quarterly and yearly. Delayed submission of data to CDFG was the primary reason that estimates of yearly effort differed from the sum of the quarterly estimates of effort.

[9] Beeson, M., and D. Hanan. 1996. Manuscript submitted to California Fish and Game. [Available from the authors at California Department of Fish and Game, 330 Golden Shore, Suite 50, Long Beach, CA 90802.]

## Mortality estimation

**Sampling design** The NMFS observer program began in July 1990. Initially, the plan was to sample every fifth trip made by a drift gillnet vessel according to an assignment schedule. The order in which vessels with MMPA exemption certificates were scheduled to be observed was randomly selected. It became evident during the 1990 season that this scheme would not work because of logistical difficulties in adhering to the sampling plan.

Beginning in January 1991, gillnet vessel trips were selected according to the targeted coverage rate (20%), the availability of observer personnel, call-ins (fishermen called in prior to departure), and the ability to notify fishermen of their obligation to carry an observer. (Occasionally fishermen did not call the Observer Program administrator for possible observer assignment.) In addition, the NMFS Fisheries Observer Branch began monitoring vessel activity (arrivals and departures) to estimate observer coverage for placement purposes. If estimated observer coverage dropped below 20% for a vessel, the owner was notified of the obligation to carry an observer. In the setnet fishery, most fishermen were notified after their nets were set whether they would be required to carry an observer. As the program evolved, setnet fishermen began to expect an observer about every fifth trip.

**Mortality estimation in the drift gillnet fishery** In the swordfish and shark drift gillnet fishery, vessels made trips lasting from one to about 15 days so that

**Table 4**

Observed (obs) and estimated (est) cetacean, pinniped, turtle, and seabird mortality, stratified by year, in the California halibut and angel shark set gillnet fishery during the NMFS Observer Program, July 1990–December 1995. Estimates of total mortality are reported to the nearest individual. Estimated coefficients of variation (CV) are included in parentheses; (—) indicates CV was undefined. Effort and estimates for 1990 pertain to the third and fourth quarters only.

| Year | 1990 | | | 1991 | | | 1992 | | | 1993 | | | 1994 | | | 1995[1] | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Estimated days effort | 3,041 | | | 7,171 | | | 5,577 | | | 5,680 | | | 1,943 | | | 2,257 | | |
| Observed days effort | 158 | | | 706 | | | 698 | | | 875 | | | 150 | | | 0 | | |
| Percent observer coverage | 5.2% | | | 9.8% | | | 12.5% | | | 15.4% | | | 7.7% | | | 0% | | |
| Observed trips effort | 406 | | | 2,233 | | | 2,123 | | | 2,642 | | | 547 | | | 0 | | |
| | obs | est | CV | obs | est | CV | obs | est | CV | obs | est | CV | obs | est | CV | obs | est | CV |
| Harbor porpoise | 4 | 37 | (0.56) | 5 | 38 | (0.47) | 6 | 48 | (0.46) | 2 | 13 | (0.64) | 1 | 14 | (0.96) | — | 14 | (0.64) |
| Common dolphin (unknown stock) | 0 | 0 | (—) | 0 | 0 | (—) | 2 | 15 | (0.65) | 0 | 0 | (—) | 0 | 0 | (—) | — | — | (—) |
| Unidentified cetacean | 0 | 0 | (—) | 0 | 0 | (—) | 1 | 8 | (0.92) | 0 | 0 | (—) | 0 | 0 | (—) | — | — | (—) |
| California sea lion | 67 | 867 | (0.22) | 142 | 1,842 | (0.16) | 338 | 3,418 | (0.28) | 237 | 1,942 | (0.13) | 109 | 905 | (0.15) | — | 724 | (0.08) |
| Unidentified sea lion | 1 | 23 | (0.96) | 6 | 109 | (0.53) | 7 | 54 | (0.34) | 0 | 0 | (—) | 0 | 0 | (—) | — | — | (—) |
| Harbor seal | 30 | 411 | (0.23) | 42 | 601 | (0.23) | 90 | 1,204 | (0.47) | 71 | 475 | (0.13) | 23 | 227 | (0.33) | — | 228 | (0.13) |
| Northern elephant seal | 13 | 119 | (0.40) | 3 | 30 | (0.55) | 7 | 51 | (0.35) | 11 | 70 | (0.27) | 2 | 16 | (0.66) | — | 47 | (0.29) |
| Unidentified pinniped | 2 | 42 | (0.79) | 3 | 30 | (0.55) | 7 | 50 | (0.39) | 7 | 32 | (0.90) | 1 | 8 | (0.94) | — | 17 | (0.83) |
| Sea otter | 3 | 27 | (0.53) | 0 | 0 | (—) | 0 | 0 | (—) | 0 | 0 | (—) | 0 | 0 | (—) | — | — | (—) |
| Green/black turtle | 0 | 0 | (—) | 0 | 0 | (—) | 1 | 8 | (0.92) | 1 | 6 | (0.90) | 0 | 0 | (—) | — | 2 | (0.61) |
| Loggerhead turtle | 0 | 0 | (—) | 0 | 0 | (—) | 1 | 8 | (0.92) | 0 | 0 | (—) | 0 | 0 | (—) | — | — | (—) |
| Leatherback turtle | 0 | 0 | (—) | 0 | 0 | (—) | 0 | 0 | (—) | 0 | 0 | (—) | 1 | 8 | (0.94) | — | — | (—) |
| Unidentified turtle | 0 | 0 | (—) | 0 | 0 | (—) | 0 | 0 | (—) | 1 | 6 | (0.90) | 0 | 0 | (—) | — | 2 | (0.61) |
| Pacific loon | 0 | 0 | (—) | 1 | 13 | (0.94) | 0 | 0 | (—) | 0 | 0 | (—) | 0 | 0 | (—) | — | — | (—) |
| Common loon | 0 | 0 | (—) | 2 | 22 | (0.68) | 1 | 7 | (0.92) | 0 | 0 | (—) | 0 | 0 | (—) | — | — | (—) |
| Unidentified loon | 1 | 23 | (0.96) | 4 | 48 | (0.48) | 0 | 0 | (—) | 0 | 0 | (—) | 0 | 0 | (—) | — | — | (—) |
| Western grebe | 0 | 0 | (—) | 1 | 8 | (0.92) | 3 | 23 | (0.70) | 1 | 6 | (0.90) | 0 | 0 | (—) | — | 2 | (0.61) |
| Unidentified grebe | 0 | 0 | (—) | 0 | 0 | (—) | 4 | 31 | (0.92) | 1 | 6 | (0.90) | 0 | 0 | (—) | — | 3 | (0.83) |
| Double-crested cormorant | 2 | 18 | (0.93) | 0 | 0 | (—) | 1 | 7 | (0.92) | 0 | 0 | (—) | 1 | 8 | (0.94) | — | — | (—) |
| Brandt's cormorant | 2 | 41 | (0.78) | 36 | 409 | (0.44) | 14 | 279 | (0.67) | 3 | 13 | (0.64) | 2 | 16 | (0.66) | — | 3 | (0.43) |
| Pelagic cormorant | 1 | 33 | (0.98) | 1 | 8 | (0.92) | 0 | 0 | (—) | 0 | 0 | (—) | 0 | 0 | (—) | — | — | (—) |
| Unidentified cormorant | 9 | 132 | (0.45) | 15 | 450 | (0.92) | 9 | 68 | (0.30) | 5 | 32 | (0.40) | 0 | 0 | (—) | — | 10 | (0.35) |
| Common murre | 142 | 1,300 | (0.21) | 289 | 2,201 | (0.27) | 292 | 2,333 | (0.28) | 137 | 879 | (0.32) | 20 | 284 | (0.29) | — | 967 | (0.32) |
| Unidentified alcid | 1 | 9 | (0.93) | 0 | 0 | (—) | 0 | 0 | (—) | 0 | 0 | (—) | 0 | 0 | (—) | — | — | (—) |
| Unid. seabird | 0 | 0 | (—) | 2 | 22 | (0.68) | 3 | 23 | (0.53) | 1 | 6 | (0.90) | 0 | 0 | (—) | — | 3 | (0.83) |

[1] Estimates for 1995 were based on stratified rates from 1993 results.

when a trip was chosen to be observed, the NMFS technician observed all net pulls during the trip. A single net per day was set at dusk and retrieved before dawn. Net pulls and effort-days were equivalent units for this fishery. For estimation of incidental kill, the collection of observed trips during a year was treated as a random sample (an approximation) and a ratio estimator was used. Trips were treated as sampling units and the number of days per trip was treated as an auxiliary variable. Stratification by quarter of year or set location was not used for yearly estimates because previous exploratory analysis had not found this type of stratification to be significantly related to incidental kill. Yearly estimates, 1991–95, were calculated for each species observed entangled ("Results" section). Estimates for 1990 correspond only to the last two quarters of that year. Formulae from Cochran (1977) were used for estimating kill rate, $\hat{r}$, total incidental kill, $\hat{m}$, and variances:

$$\hat{r} = \frac{\Sigma_i k_i}{\Sigma_i d_i}, \quad (1)$$

$$\hat{\sigma}_r^2 = \left(1 - \frac{d}{D}\right)\left(\frac{1}{n}\right)\left(\frac{1}{d_{avg}^2}\right)\left(\hat{r}^2\sigma_d^2 + \hat{\sigma}_k^2 - 2\hat{r}\hat{\sigma}_{d,k}\right), \quad (2)$$

**Table 5**

Observed and estimated cetacean, pinniped, turtle, and seabird entanglement, stratified by year, in the California halibut and angel shark set gillnet fishery during the NMFS Observer Program, July 1990–December 1995. Estimates of entanglement are reported to the nearest individual. Estimated coefficients of variation (CV) are included in parentheses; (—) indicates CV was undefined. Effort and estimates for 1990 pertain to the third and fourth quarters only.

| Year | 1990 | | | 1991 | | | 1992 | | | 1993 | | | 1994 | | | 1995[1] | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Unidentified sea lion | 67 | 867 | (0.22) | 143 | 1,850 | (0.16) | 341 | 3,438 | (0.28) | 239 | 1,977 | (0.13) | 109 | 905 | (0.15) | — | 729 | (0.08) |
| Harbor seal | 30 | 411 | (0.23) | 43 | 615 | (0.23) | 90 | 1,204 | (0.47) | 71 | 475 | (0.13) | 23 | 227 | (0.33) | — | 228 | (0.13) |
| Unidentified turtle | 0 | 0 | (—) | 0 | 0 | (—) | 0 | 0 | (—) | 2 | 13 | (0.64) | 0 | 0 | (—) | — | 5 | (0.59) |
| Common loon | 0 | 0 | (—) | 4 | 48 | (0.60) | 1 | 7 | (0.92) | 0 | 0 | (—) | 0 | 0 | (—) | — | — | (—) |
| Western grebe | 0 | 0 | (—) | 2 | 22 | (0.68) | 3 | 23 | (0.70) | 1 | 6 | (0.90) | 0 | 0 | (—) | — | 2 | (0.61) |
| Brandt's cormorant | 2 | 41 | (0.78) | 41 | 494 | (0.37) | 20 | 321 | (0.58) | 5 | 25 | (0.45) | 2 | 16 | (0.66) | — | 9 | (0.40) |
| Unidentified seabird | 0 | 0 | (—) | 2 | 22 | (0.68) | 5 | 37 | (0.41) | 1 | 6 | (0.90) | 0 | 0 | (—) | — | 3 | (0.83) |

[1] Estimates for 1995 were based on stratified rates from 1993 results.

$$\hat{m} = D\hat{r}\,, \tag{3}$$

$$\hat{\sigma}_m^2 = D^2\hat{\sigma}_r^2\,. \tag{4}$$

Variables $k_i$ and $d_i$ represent the observed kill and number of days for the $i^{th}$ trip; $d_{avg}$ is the sampled mean number of days per trip; $\hat{\sigma}_d^2$, $\hat{\sigma}_k^2$, and $\hat{\sigma}_{d,k}$ are the sample variances and covariance of $d_i$ and $k_i$; $d$ and $n$ are the observed number of days and trips, and $D$ represents the total number of days of effort. The finite population correction factor, $(1 - n/N)$, where $N$ is the total number of trips, was approximated by using $(1 - d/D)$ because the total number of driftnet trips was not determined during the estimation of effort.

**Mortality estimation in the set gillnet fishery** In the setnet fishery, a trip was selected and all net pulls during the trip were observed. Because greater than 99% of all observed set gillnet trips were one day in length, a trip was considered equivalent to an effort-day. Net pulls were not randomly sampled and total number of net pulls per trip was not recorded for unobserved trips, therefore a trip was considered the sampling unit. For observed trips, the overall average number of net pulls per trip (or effort-day) was 3.08 (CV=0.43), and the overall average number of marine mammal entanglements per trip was 0.48 (CV=3.10) during the NMFS Observer Program.

Researchers had previously shown (Perkins et al.[5]) that quarter of year and set location were significant predictors of sea lion and harbor seal entanglement. Consequently, estimation of incidental kill in the setnet fishery was stratified by area for all mammal species. The geographic area fished was divided into four strata: southern California, Channel Islands, Ventura, and central California. Central California included all effort south of Bodega Bay and north of Point Conception, 34°30'N (CDFG blocks 437–650). There was no legal coastal setnet fishing north of Bodega Bay. The Channel Islands stratum included all effort within CDFG blocks containing part of any Channel Islands (CDFG blocks 684–690, 707–713, 760–762, 765, 806–807, 813–814, 829, 849–850, and 867). The southern California stratum included all effort south of 33°50' N (blocks 718–918), excluding CDFG block 776 and the Channel Islands stratum. The Ventura stratum contained the remaining area. Incidental kill estimation for sea lions and harbor seals included additional stratification by quarter of the year for the southern California and Ventura areas because for these species, overstratification was not a problem.

Yearly estimates of incidental kill in the setnet fisheries were calculated for all species of marine mammals observed entangled (Tables 4 and 5). Estimates for turtles and seabirds were calculated by the same method. For each species, kill rate, $r_s$, and total incidental kill, $m_s$, were estimated for each area by using a mean-per-unit (MPU) estimator with effort-days as the sampling unit (Diamond and Hanan[1]). Formulae for MPU estimators and their estimated variances for each area are (Cochran, 1977)

$$\hat{r}_s = \frac{\Sigma_i k_{i,s}}{d_s}\,, \tag{5}$$

$$\hat{\sigma}_{r,s}^2 = \left(1 - \frac{d_s}{D_s}\right)\left(\frac{1}{d_s}\right)\hat{\sigma}_{k,s}^2\,, \tag{6}$$

$$\hat{m}_s = D_s\hat{r}_s\,, \tag{7}$$

$$\hat{\sigma}^2_{m,s} = D_s^2 \hat{\sigma}^2_{r,s}. \quad (8)$$

The variable $k_{i,s}$ represents observed kill for the $i^{th}$ observed day in stratum $s$, and $\hat{\sigma}^2_{k,s}$ is the sample variance of the observed kill. Variables $d_s$ and $D_s$ are observed and total number of days of effort in the stratum, respectively. Estimates of overall kill rate, $\hat{r}$, and total incidental kill, $\hat{m}$, across all strata, and variances, are then weighted averages:

$$\hat{r} = \frac{\Sigma_s D_s \hat{r}_s}{D}, \quad (9)$$

$$\hat{\sigma}^2_r = \frac{\Sigma_s D_s^2 \hat{\sigma}^2_{r,s}}{D^2}, \quad (10)$$

$$\hat{m} = \hat{D}r, \quad (11)$$

$$\hat{\sigma}^2_m = D^2 \hat{\sigma}^2_r, \quad (12)$$

where $D$ is total number of days of effort during the year.

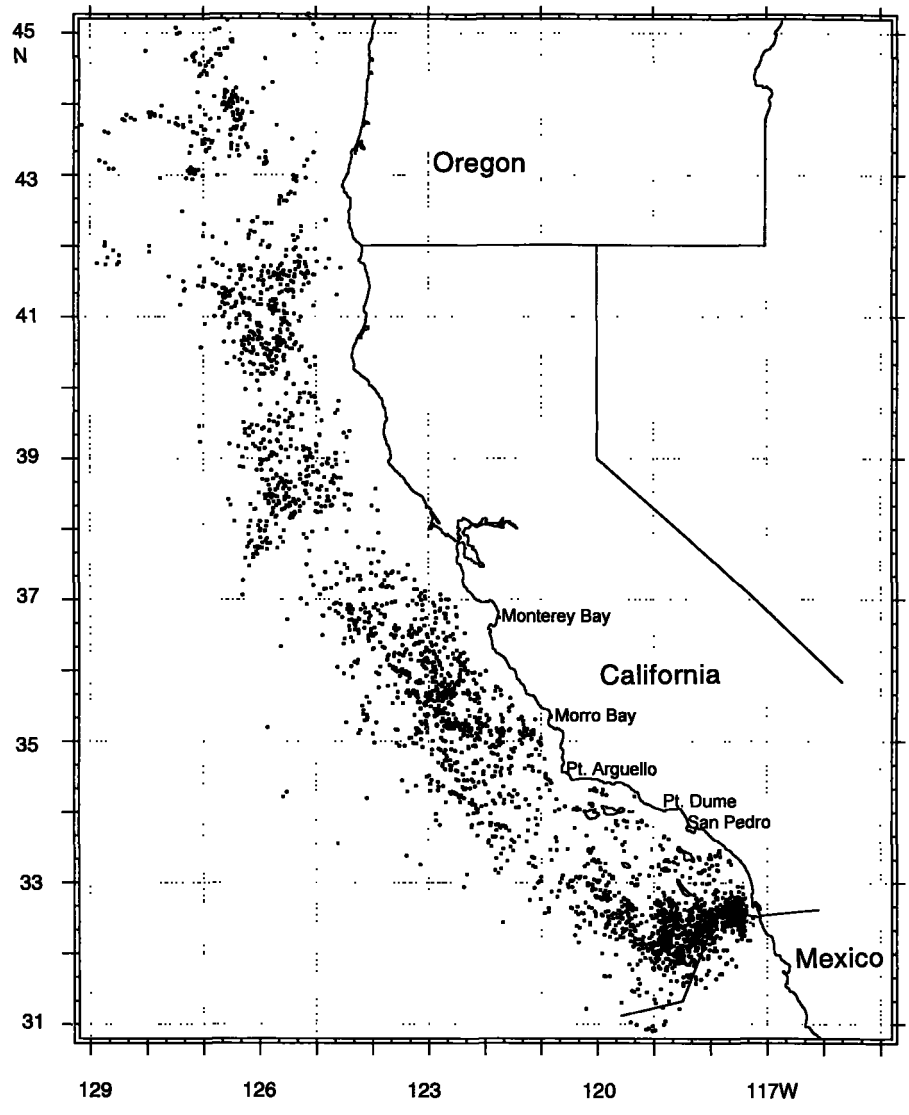


**Figure 1**

Approximate location of observed sets in the driftnet fishery during the period July 1990–December 1995.

## Results

### Driftnet fishery

During the observed period, the driftnet fishery was subject to area and time restrictions inside 370.4 km (200 nautical miles [n mi]) for effort that took place largely (80% of seasonal effort) from 15 August to 31 January. Between 1 February and 30 April, fishing effort was restricted to locations farther than 370.4 km offshore. From 1 May through 14 August (15 July for 1990–92) effort was required to be located farther than 138.9 km (75 n mi) offshore. For the remainder of the year, fishing was allowed within 138.9 km of shore. Since the beginning of the NMFS observer program in 1990, estimated total effort-days for the fourth quarter increased each year except for 1994. Combined effort for third and fourth quarters was consistently over 3,500 sets each year (Table 2). Even though there was effort along the entire California coast, the highest concentration of observed sets was south of 33°N (Fig. 1). Observer coverage in this fishery typically ranged between 10% and 15% of estimated total yearly effort for most areas and quarters. (Exceptions as low as 2% and as high as 25% were noted for some quarters and areas.) Bias of a ratio estimate is typically a problem in the case of small sample sizes such as may occur in a per-fishing block situation. Because sample size was generally quite large and stratification was not used, estimates were not corrected for bias. During the study period, July 1990–December 1995, nine (2%) of the 472 marine mammals observed entangled were released alive (one unidentified sea lion, one common dolphin, *Delphinus* spp., two California sea lions, one humpback whale, *Megaptera novaeangliae*, one Cuvier's beaked whale, *Ziphius cavirostris*, and

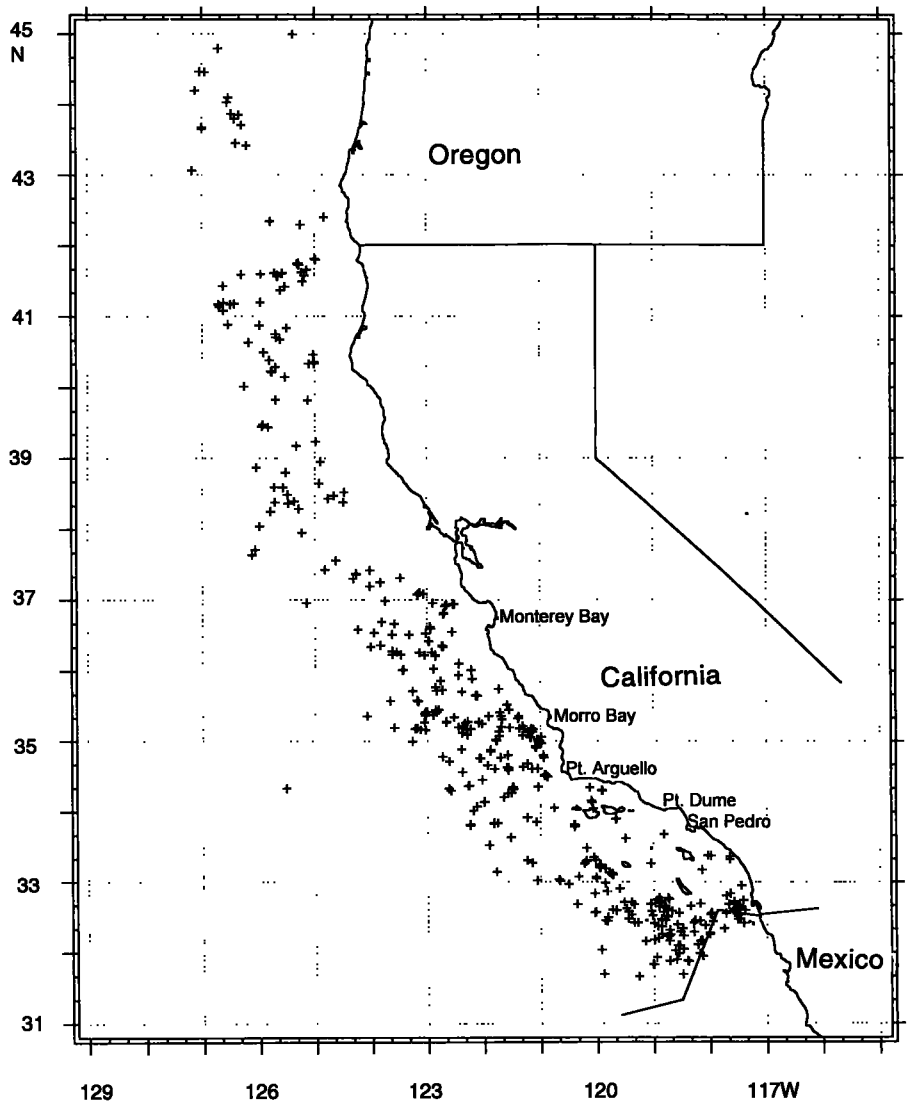


**Figure 2**

Approximate location of observed incidental marine mammal kills in the driftnet fishery during the period July 1990–December 1995, all species.

three sperm whales, *Physeter macrocephalus*). Observed mammal bycatch in this fishery consisted predominantly of common dolphins (196). Northern elephant seals, *Mirounga angustirostris*, were the second most commonly entangled mammal (83). The wide variety of mammal species incidentally entangled, over 25, is notable.

There was no statistically discernible trend in the estimates of total effort during the study period. Coefficients of variation for estimates of marine mammal incidental kill ranged from 0.18 to 0.95. The highest observed incidental kill in a single CDFG fishing block was in block 918, the southernmost block, which had 10% of the total observed mammal bycatch. Waters off central California west of 122°W longitude also had 10% of the observed mammal bycatch. Locations of marine mammal mortality from observer records indicate that mortality was concentrated in areas of heavy effort but geographically unrestricted (Figs. 1–2). On a quarterly basis, observed mammal bycatch and swordfish catch were correlated ($r$=0.8), but on a per set basis this correlation was not evident ($r$=0.0). This change in correlation is perhaps due to the inclusion of substantial effort (quarterly) versus per set consideration, i.e. both catch and bycatch are related to effort.

Observed seabird mortality was very low in the driftnet fishery (three kills observed during the period). Marine turtle entanglement was more common, with 25 observed (13 released alive). All but one of the 15 leatherback entanglements occurred north of 35°N latitude. Estimated turtle entanglement increased from 23 for 1990 to 81 for 1993 and then fell to 32 for 1995.

## Setnet fishery

Mortality estimates in the setnet fishery pertain to fishing effort targeting halibut or angel shark. By law, effort targeting these species required gillnets with stretched mesh sizes of 21.6 cm (8.5 inches) or greater. This resulted in the elimination of 665 out of 8,614 observer records (net pulls) with mesh size less than 21.6 cm from the original data because they pertained to effort in another fishery. There were an additional 179 observed net pulls with no position data. This effort was assigned to geographic strata based on the specific vessel's known fishing grounds or was apportioned out to strata according to fishing effort from NMFS observer records with known positions.

From 1990 through 1993, estimated effort in the halibut and angel shark fishery was fairly stable with heavy setnet fishing effort along the southern California coast up to Pt. Conception (excluding the region from Rocky Pt. to Pt. Dume, where there was no commercial fishing, and an area around Newport

Beach; Fig. 3). There was also effort in the Morro Bay and Monterey Bay areas, as well as in some areas around the Channel Islands. Estimated effort for 1994 decreased sharply because gillnet fishing was banned inside the area within 5.6 km (3 n mi) of shore from Pt. Arguello south to the U.S.-Mexico border. During each year, observed mammal bycatch peaked during the second quarter, as did estimated total effort (Tables 4 and 5). California sea lions were the most frequently killed mammal (899), followed by harbor seals (257), northern elephant seals (36), and then harbor porpoises (18). Fourteen of the eighteen observed harbor porpoise mortalities occurred in the northern portion of Monterey Bay; three others were observed in the Monterey Bay area, and the remaining mortality was in the Morro Bay area (none was released alive). There were 1,025 seabird mortalities: 1 Pacific loon, *Gavia pacifica*, 5 common loon, *Gavia immer*, 5 unidentified loon, *Gavia* spp., 6 western grebe, *Aechmophorus occidentalis*, 5 unidentified grebe, *Podiceps* spp., 4 double-crested cormorant, *Phalacrocorax auritus*, 70 Brandt's cormorant, *Phalacrocorax penicillatu*, 2 pelagic cormorant, *Phalacrocorax pelagicus*, 38 unidentified cormorant, *Phalacrocorax* spp., 880 were common murre, *Uria aalge*, 1 unidentified alcid, *Alcidae*, and 8 unidentified seabirds, *Aves*. Of the common murre mortalities, 99% occurred north of Pt. Conception—predominantly in the Morro Bay area (Fig. 4). All other bird species were entangled south of Pt. Conception with few (12) exceptions (Tables 4 and 5). The six observed marine turtle kills were separated either in time or location, but four occurred offshore of Ventura. Locations of observer-recorded effort and bycatch indicated that no fished area was entirely free of mammal mortality due to gillnets (Figs. 3 and 5). Estimated total marine mammal mortalities for the setnet fishery rose from approximately 1,500 in 1990, to 4,800 in 1992, and fell to 1,300 in 1994.

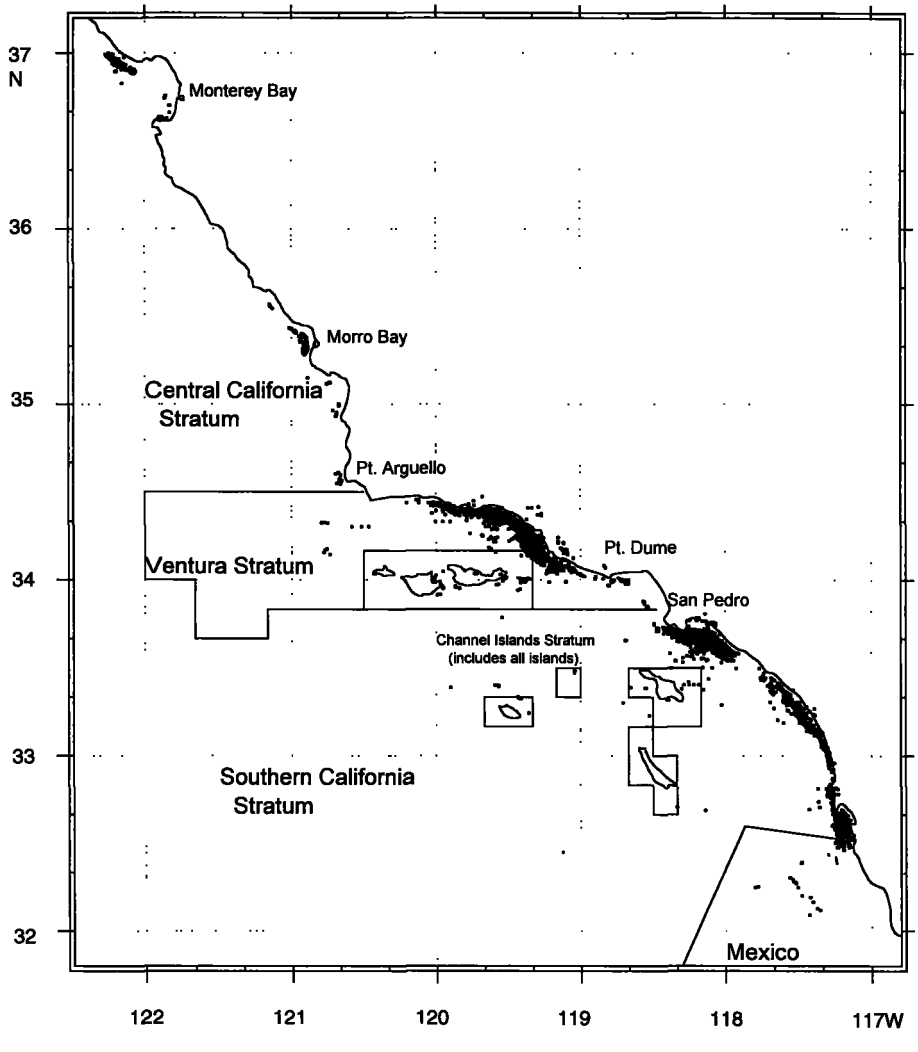


**Figure 3**

Approximate location of observed sets in the setnet fishery during the period July 1990–December 1995.

## Discussion

### Data collection and effort estimation

Although many resources were used to obtain accurate estimates of mortality and fishing effort, several significant difficulties were encountered in data collection and estimation of total effort. Difficulties in implementing the sampling plan included availability of observers and type of notification given to fishermen. Generally, observers were hired by the Program according to how much fishing effort was expected. Because this aspect of the program was well monitored, little seasonal bias was expected. Previous exploratory analysis has indicated that pre- and post-notification is a significant factor for the setnet fishery (Perkins et al.[5]). In this fishery, out of 2,588 days of observations,

only 74 (3%) were classified as preset notification. In the driftnet fishery, out of 3,338 observations, only 29 were categorized as postset notification. Because these data are so unbalanced in terms of type of notification, further analysis involving type of notification was not pursued. Apart from the overall difficulty of implementing an appropriate sampling plan, perhaps the most common difficulty was with accurate determination of location. Frequently, navigational equipment would not be "working" or was not available to the observer. In some cases, location was incorrectly relayed to the observer and under other circumstances observers were not able to determine location from major landmarks on shore owing to inclement weather. A second difficulty was that observers may not have been able to determine accurately the total number of animals or the species of the animals entangled in gillnets owing to obstruction of view by gear or crew. Also, mammals may have dropped out of a gill net prior to observation. Events of this type were considered nonsampling errors and may have biased estimates of incidental kill.

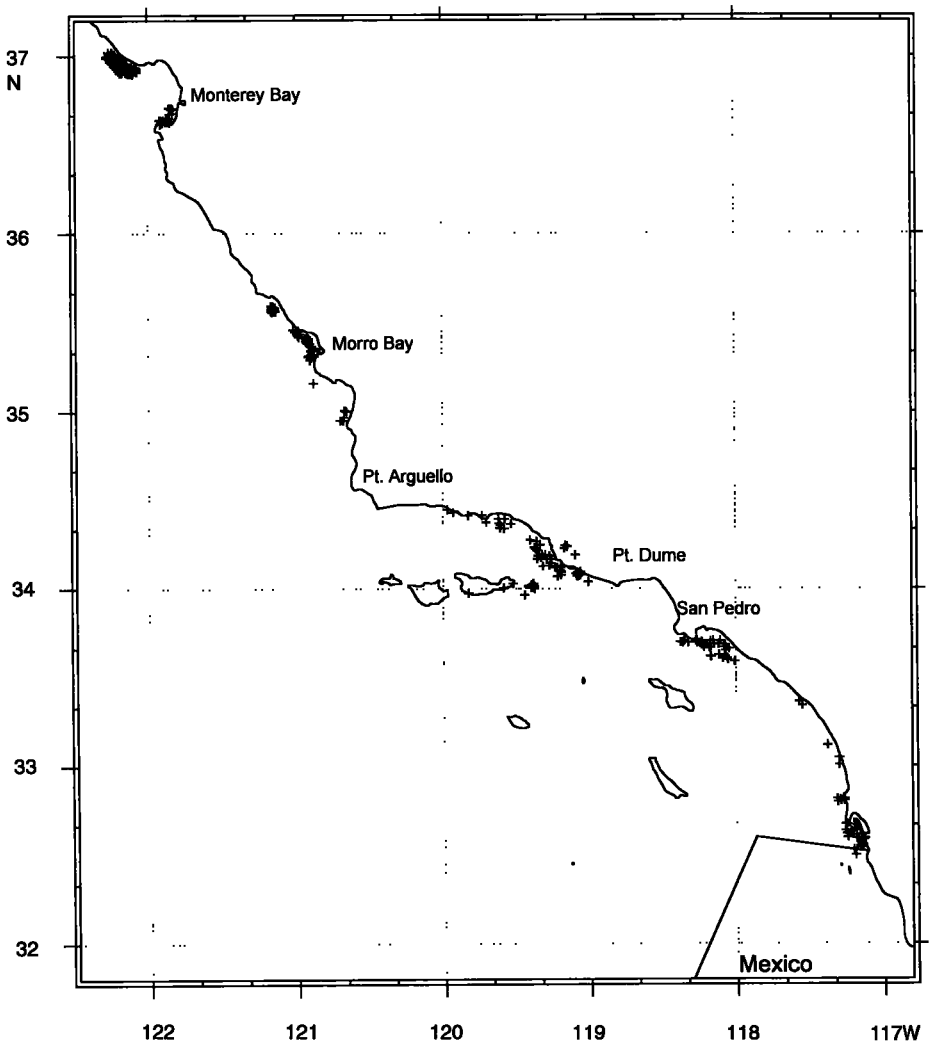


**Figure 4**

Approximate location of observed incidental seabird kills in the setnet fishery during the period July 1990–December 1995, all species.

Estimates of total effort were also subject to error, although they were treated as accurate for the purpose of bycatch estimation. They contained inaccuracies due to at least three nonsampling errors:

1 Completely unrecorded effort —A typical example of this was when no marketable target fish were caught during a trip and a logbook entry was not made. It was not possible to determine the size of this error; however, given that there were three chances for effort to be monitored (logbooks, observer records, and landing receipts), this error was probably small.

2 Absent or imprecise reporting of location—Even though location data were inaccurate, a record of effort was tallied. Thus, because estimates were not stratified by area in the driftnet fishery, this type of error had no impact on the determination of estimates of total effort or mortality for this fishery. (This type of error may be important in more detailed studies.) In the setnet fishery this type of error would not have produced an error in an estimate of total effort but may have produced errors in effort estimates for individual geographic strata. For purposes of mortality estimation, the setnet fishery was divided into four geographic strata, and effort without a recorded location was assigned, with good accuracy, to a stratum based on the vessel's known activity. If no information on a vessel's behavior was known, effort was divided among strata according to the proportion of effort in known locations. No additional error

was included in variance estimates because strata were large enough and vessels predictable enough that "assignment error" was most likely negligible compared with other assumptions. There was no way to determine accurately the direction of bias in effort estimates for each area.

3 Underestimation of effort from landing receipts—Underestimation of effort from landing receipts occurred when no effort was logged by fishermen or recorded by a NMFS observer for three days prior and subsequent to the date of the landing receipt. In these cases, a landing receipt was assumed to represent one day of fishing effort. Of the three types of nonsampling errors examined, this was potentially significant for the driftnet fishery because trips in this fishery may last over two weeks. For example, in 1993, the median length of a driftnet trip was 7 days; the mean was 6.8 (SE=3.3). Consequently, the number of times this approximation occurred was important. In the setnet fishery, with shorter trips, this assumption had less impact. It applied to multiple-day trips around the Channel Islands area, off the coast north of Santa Barbara, or when a fisherman held catch for more than one effort-day. Setnet trips were seldom more than a day in length because of catch storage and preservation limitations. In both the drift and setnet situations, the minimum effort representing a landing receipt was used, namely one effort-day, because a more appropriate approximation would have required a case-by-case investigation. The assumption contributed toward a possible negative bias of estimates of total effort and incidental kill.

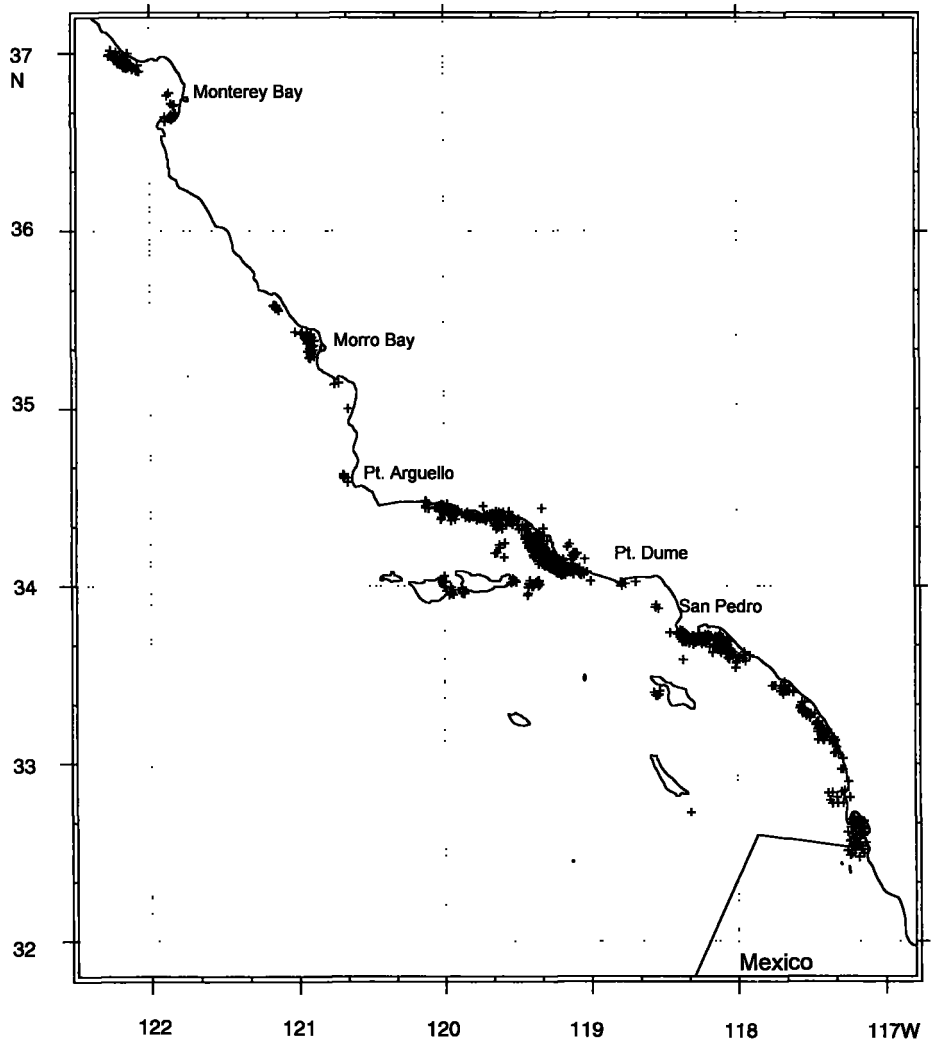


**Figure 5**

Approximate location of observed incidental marine mammal kills in the setnet fishery during the period July 1990–December 1995, all species.

Combined, these three difficulties in estimation of total effort may have produced a negative bias in estimates of total effort and, consequently, in estimates of incidental kill (i.e. current estimates of total effort may reasonably be considered a minimum). An accurate estimate of bias would be difficult and costly to obtain.

## Mortality

Infrequent entanglement of marine mammals, turtles, and seabirds makes accurate estimation of species-specific incidental kill difficult. In spite of our good intentions, estimates may have been confounded by distribution of fishing effort or movement of species. In the future, the variability of estimates can be decreased by more strictly implementing a sampling plan. For some species, a posthoc analysis may be productive as information on movement and abundance of stocks becomes available. For infrequently entangled species, only increased observer coverage will improve estimation of incidental entanglement and kill rates.

In the driftnet fishery, the wide variety of cetacean species killed is attributable to the large geographic range of the mammals, nonselectivity of gear, and the amount and location of fishing effort. Cetacean bycatch in the driftnet fishery is greater and more diverse than for the setnet fishery because area of driftnet effort contains more diverse habitat than the area of setnet fishery. Data from recent years show that effort is increasing off the coasts of northern California and Oregon, and beginning in 1995, the state of Oregon allowed 10 driftnet fishing vessels to land fish in a limited number of Oregon ports (landings were not permitted prior to 1995). Yearly effort is expected to continue at 3,500–4,500 sets per year. The mortality rate averaged 0.11 (SD=0.25) mammals/set (or day) during the observer program, from January 1991 through December 1995; initial effort in 1990 was omitted because of low coverage rate. Incidental seabird catch has been almost nonexistent and there is currently no reason to expect an increase. The amount of seabird bycatch contrasts with the Japanese driftnet fishery in which many seabirds are incidentally caught (Ito et al., 1993), in part, because swordfish drift nets are extended below the surface, typically 11 m. The Japanese salmon drift nets, set at the surface, would naturally entangle more seabirds. Migration of seabirds in relation with the fishing season and effort location may play a role in seabird bycatch. No trend is evident in the estimated yearly turtle entanglements. Regarding cetaceans, at this time there are 10 species that are being entangled at a rate greater than potential biological removal (PBR) according to the U.S. Pacific Marine Mammal Stock Assessment Report (Barlow et al., 1995). The impact of driftnet mortality on individual cetacean stocks is examined in this report. In order to reduce entanglement of cetaceans, NMFS, in conjunction with driftnet fishermen and the California Department of Fish and Game, have implemented a Pacific Cetacean Take Reduction Team whose goal is to decrease cetacean bycatch.

Over the past five years, estimated effort in the halibut and angel shark setnet fishery was fairly stable until 1994, when a restrictive California voter proposition banned gillnet fishing within three miles of the coast from Pt. Arguello south to the US-Mexico border. Before 1994, effort in this fishery varied substantially during the year. Since early 1994, gillnet fishing has occurred mainly off Ventura, Morro Bay, and Bodega Bay (Fig. 3). There has also been some effort off Imperial Beach, near the US-Mexico border. Effort north of Pt. Arguello has not been affected by the 1994 resolution and is not expected to change.

Pinniped mortality in the setnet fishery was substantial during 1990–95. More pinnipeds were observed entangled in the setnet fishery than the driftnet fishery because effort coincided substantially with pinniped habitat. In particular, setnet effort around the Channel Islands and near the ports San Pedro, Ventura, and Santa Barbara frequently entangled pinnipeds. Effort in the driftnet fishery results in less overall pinniped entanglement by virtue of this effort being placed farther from shore. It is interesting to note, however, that entanglement of northern elephant seals in the driftnet fishery is substantially greater than for the setnet fishery because these mammals typically range greater distances from shore than do sea lions and harbor seals. Estimates of California sea lion and harbor seal mortality are expected to decline and then stabilize because of reduced effort south of Pt. Arguello.

Similarly, we expect the number of seabirds killed south of Pt. Conception to decline, because setnet effort was been pushed offshore 5.6 km (3 n mi) by regulation. There has been more bycatch of birds in the set fishery because the entangled species are typically resident and their habitat overlaps substantially with setnet effort. Driftnet effort results in few seabird entanglements because drift nets are retrieved after an overnight soak (set nets typically soak 24 hours) and drift nets are typically extended over 11 m below the surface. In addition, mesh size for drift nets is almost three times greater than mesh size for set nets, resulting in fewer entanglements. The mortality of common murres entangled in set nets is expected to continue at the same level. Murre were primarily observed entangled in the Monterey Bay area. The nets in this area are set on the bottom in typically 55.8 m (30.5 fm, SE=0.2 fm) of water. Using a chi-square ($\chi^2$) test, we determined that there is some dependency between entanglement and soak time of the net ($P<0.05$). Odds of entanglement more than doubled for an increase from 1 to 2 days of soak time (reasonable checking for confounding factors was done). Turtles will continue to be entangled in the setnet fishery, but the number and rate of entanglement will be unknown because observer coverage in this fishery has been eliminated.

## Acknowledgments

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# Feeding habits of juvenile Pacific salmon in marine waters of southeastern Alaska and northern British Columbia

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**Abstract.**—First ocean-year feeding habits were determined for juvenile salmon (*Oncorhynchus* spp.) collected with purse seines in marine waters of southeastern Alaska in 1983 and 1984 and northern British Columbia in 1984. Associated prey assemblages were sampled with neuston and plankton nets in 1984. Salmon diets included at least 30 taxa of prey. Crustaceans (principally hyperiid amphipods), fish, and tunicates were the most important prey of pink (*O. gorbuscha*), chum (*O. keta*), and sockeye (*O. nerka*) salmon. Fish were the most important prey of coho (*O. kisutch*) and chinook (*O. tshawytscha*) salmon and made up the highest percentage of stomach content weight for all salmon species. Diet shifted from crustaceans in 1983 to fish in 1984 for juvenile pink, sockeye, and chum salmon. Diet overlapped significantly ($\hat{C}_\lambda$>0.60) between pink and sockeye salmon, pink and chum salmon, and chum and sockeye salmon. Coho salmon diet overlap was <0.60 in all paired comparisons. Nearly all (98.6%) of the 2,210 stomachs examined were at least half full. Although, in general, prey consumed were not very similar to prey observed in the environment, the composition of salmon diets was more similar to neuston collections than to zooplankton collections.

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All Pacific salmon (*Oncorhynchus* spp.) migrate as juveniles from shallow waters near shore to coastal and oceanic feeding areas of the North Pacific Ocean, where species, stocks, and age classes mix (Hartt and Dell, 1986; Ware and McFarlane, 1989; Pearcy, 1992). Substantial evidence suggests that salmon production around the Gulf of Alaska increased dramatically in the late 1970's, possibly owing to enhanced early ocean survival (Pearcy, 1992; Beamish and Bouillon, 1993; Brodeur and Ware, 1995). Increased densities are evident in the commercial harvest of salmon in Alaska; for example, salmon catch reached record numbers in 1993, nearly doubling over 25 years to approach 200 million fish (Wertheimer, 1997). This increase is attributed to several factors, including growing enhancement efforts and environmental conditions that favor survival of both wild and hatchery salmon stocks.

The increase in numbers of subadult and adult salmon feeding in marine waters has prompted interest in possible density-dependent effects on survival, growth, and production of salmon stocks around the Pacific rim (e.g. Helle, 1989; Kaeriyama, 1989; Ishida et al., 1993; Helle and Hoffman, 1995). Fishery managers are concerned about the effects of increasing interactions between salmon populations—both wild and enhanced—in the various marine habitats where they mature (McNeil and Himsworth, 1980; Peterson et al., 1982; Brodeur, 1989; Brodeur and Pearcy, 1990; Pearcy, 1992). The feeding ecology of juvenile salmon is a pertinent, but not well known, topic.

The objective of this study was to describe the feeding habits of juvenile salmon during their first summer in coastal waters of the eastern Gulf of Alaska. Although Hartt and Dell (1986) summarized the distribution, migration, and growth of juvenile salmon in the North Pacific Ocean and the Bering Sea, diet and feeding were addressed superficially. Other references concerning juvenile salmon feeding habits during early marine residence, especially along the open coast, are limited (Pearcy, 1992; Brodeur[1]), and juvenile salmon diets are often

[1] See next page for footnote.

treated as a subset of adult diets (e.g. Groot and Margolis, 1991). Therefore, as a first step to understanding trophic interactions during their first marine summer, our research focused on the feeding habits and diet overlap of juvenile chinook (*O. tshawytscha*), coho (*O. kisutch*), sockeye (*O. nerka*), chum (*O. keta*), and pink (*O. gorbuscha*) salmon. We compared diet overlap between species, habitats, months, and years and also examined the similarity of salmon diets with samples of prey collected concurrently.

## Methods

### Fish collection

Juvenile salmon were collected in 120 purse-seine sets made along transects with two vessels and two seines (Table 1; see also Jaenicke and Celewycz, 1994). The 28-m NOAA RV *John N. Cobb* fished a table seine in the marine waters of southeastern Alaska during August 1983 and July and August 1984 (Fig. 1). The 24-m FV *Bering Sea* fished a drum seine in the open coastal waters of northern British Columbia during July 1984. Purse-seine sets at all locations were standardized to compensate for different sizes, meshes, and areas enclosed; both nets had 25-mm mesh in the bunt (Jaenicke and Celewycz, 1994). Each station was fished only once during a period, except on a few occasions when a set was repeated following an empty haul. Fishing was conducted almost exclusively between 0600 and 1800 hours. All sets were round hauls (i.e. the seine was not towed or held open to increase catches). The distribution, size, and abundance of juvenile salmon examined for our study have been summarized in a companion paper by Jaenicke and Celewycz (1994).

The waters sampled were partitioned into discrete habitats: 1) outside waters: the open waters adjacent to the Gulf of Alaska; 2) inside waters: the enclosed marine waters of the Alexander Archipelago; and 3) protected outer-coast inlets (Fig. 1). Outside waters were further partitioned into nearshore (0–37 km offshore) and offshore (46–74 km offshore) during August 1984; seining was restricted to within 37 km of shore during other sampling periods. Inside waters were partitioned into bays and passages (connecting to the Gulf of Alaska). Sampling in outside waters was along transects about 72 km apart in southeastern Alaska and 108 km apart in British Columbia. Transects began as close to shore as submarine topography and seine depth permitted and continued up to 74 km offshore, depending on fish abundance and weather.

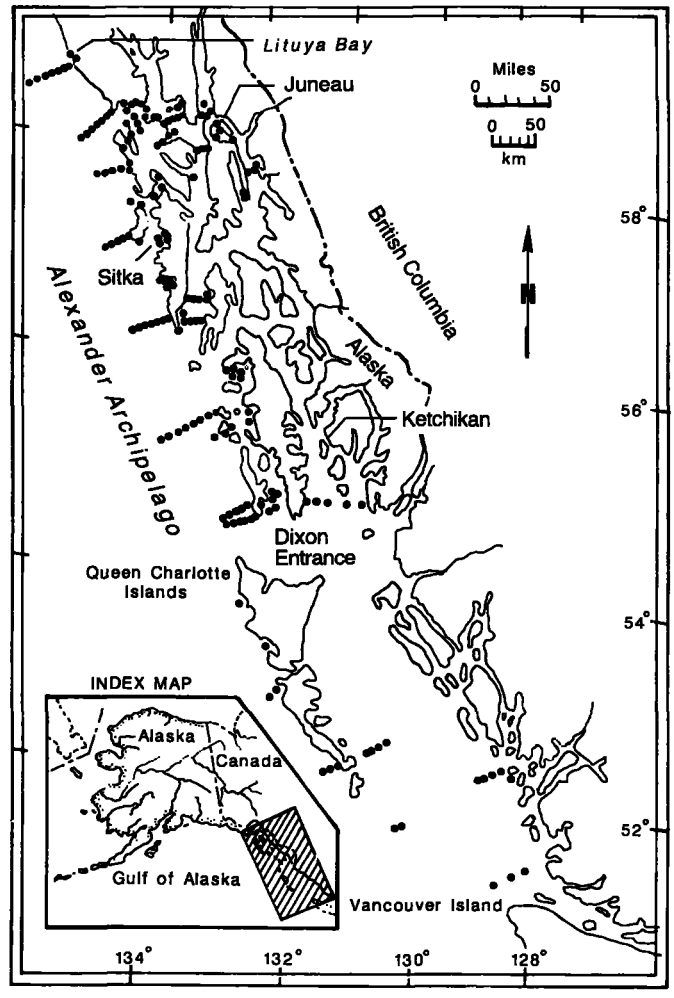


**Figure 1**
Location of purse-seine sets in southeastern Alaska in 1983 and 1984 and in British Columbia in 1984.

Fish from each purse-seine haul were anesthetized with MS 222 (tricaine methanesulfonate), sorted, identified, and measured on board the vessel. A subsample of each salmon species ($n \leq 25$) was preserved in 10% formalin-seawater solution for later stomach analysis (Table 1). Nonsalmonids caught incidentally were identified and enumerated, catch per unit of effort (CPUE) was estimated, and a subsample was measured for length as part of prey assemblage assessments (see below). Sea surface temperature (SST) to the nearest 0.2°C was recorded at every purse-seine site.

[1] Brodeur, R. D. 1990. A synthesis of the food habits and feeding ecology of salmonids in marine waters of the North Pacific (INPFC Doc.) FRI-UW-9016. Fish. Res. Inst., Univ. Washington, Seattle, 38 p.

**Table 1**

Number of purse-seine sets by time period and habitat and subsample size by species of juvenile salmon used in diet analyses. BC = British Columbia; AK = Alaska.

| Habitat | Number of sets | Number of sets catching juvenile salmon | Number of fish | | | | |
|---|---|---|---|---|---|---|---|
| | | | Pink | Chum | Sockeye | Coho | Chinook |
| August 1983 | | | | | | | |
| Inside inlet | 15 | 3 | 21 | 23 | 2 | 14 | 1 |
| Inside passage | 39 | 23 | 142 | 112 | 44 | 88 | 2 |
| Outer coast inlet | 27 | 8 | 60 | 47 | 0 | 21 | 0 |
| Outside waters | 8 | 4 | 15 | 2 | 9 | 26 | 0 |
| Total | 89 | 38 | 238 | 184 | 55 | 149 | 3 |
| July 1984 | | | | | | | |
| Inside inlet | 13 | 5 | 14 | 17 | 12 | 63 | 10 |
| Inside passage | 5 | 2 | 20 | 3 | 9 | 44 | 0 |
| Outer coast inlet | 14 | 5 | 8 | 3 | 0 | 28 | 0 |
| Outside waters (BC) | 21 | 11 | 69 | 30 | 55 | 7 | 3 |
| Outside waters (AK) | 33 | 15 | 94 | 40 | 83 | 27 | 1 |
| Total | 86 | 38 | 205 | 93 | 159 | 169 | 14 |
| August 1984 | | | | | | | |
| Inside inlet | 18 | 6 | 35 | 16 | 10 | 82 | 6 |
| Inside passage | 19 | 7 | 61 | 10 | 5 | 73 | 10 |
| Outer coast inlet | 4 | 1 | 0 | 12 | 0 | 3 | 0 |
| Outside nearshore | 26 | 20 | 183 | 97 | 80 | 55 | 5 |
| Outside offshore | 11 | 10 | 93 | 41 | 52 | 12 | 0 |
| Total | 78 | 44 | 372 | 176 | 147 | 225 | 21 |
| All periods combined | | | | | | | |
| Inside inlet | 46 | 14 | 70 | 56 | 24 | 159 | 17 |
| Inside passage | 63 | 32 | 223 | 125 | 58 | 205 | 12 |
| Outer coast inlet | 45 | 14 | 68 | 62 | 0 | 52 | 0 |
| Outside waters | 99 | 60 | 454 | 210 | 279 | 127 | 9 |
| Total | 253 | 120 | 815 | 453 | 361 | 543 | 38 |

## Stomach analysis

Each fish was weighed to the nearest milligram and measured to the nearest millimeter fork length (FL) in the laboratory. Stomachs were excised and placed in 70% isopropyl alcohol. During analysis, stomach fullness on a scale of 0–6 (0=empty, 6=distended) and digestion on a scale of 1–4 (1=fresh prey items, 4=completely digested) were visually estimated. Stomach contents were weighed, and prey items were separated, identified to the lowest convenient taxon, and counted. Up to 100 individuals of each prey category that had been removed in good condition from the stomach were used to measure initial wet weights. Prey fish in an advanced state of digestion were assigned to discrete weight categories based on the most complete specimens encountered: small (estimated 6.0 mg), medium (184.4 mg), and large (580.5 mg). Dry weights were obtained by drying the samples in an oven at 60°C until constant weights were obtained.

## Sampling and analysis of prey assemblages

Prey assemblages were sampled with neuston and plankton nets in the areas fished in 1984. Neuston collections were made with a rectangular 100 × 35-cm-opening neuston-net frame containing a conical 505-µm-mesh net; tows were made at 45 of 54 outside-water locations, 7 of 14 outer-coast-inlet locations, and 5 of 18 inside-water locations. The neuston net was towed horizontally, half-submerged, so that it sampled the water column from the surface to approximately 17 cm depth (Brodeur, 1989; Brodeur[2]). The plankton collections were made with a 70-cm diameter conical plankton net of 303-µm mesh; tows were made along purse-seine transects at four 4-km locations and six 16-km locations in

[2] Brodeur, R. D., W. G. Pearcy, B. C. Mundy, and R. W. Wisseman. 1987. The neustonic fauna in coastal waters of the northeast Pacific: abundance, distribution, and utilization by juvenile salmonids. Oregon State Univ. Publ. ORESU-T-87-001, 61 p.

outside waters, and at six locations in inside waters. All plankton tows were oblique from the surface to a depth of 50 m. Samples were preserved in a 10%-formalin-seawater solution after debris was removed.

Plankton and neuston samples were sorted to remove large organisms, such as gelatinous zooplankton. We then split the sample with a Folsom splitter until a subsample of about 500 organisms remained. Plankton organisms were identified to the lowest convenient taxon and counted. Detailed composition of many of the neuston samples has been presented elsewhere (Brodeur[2]).

### Data analysis

Stomach data were partitioned into subsets according to salmon species, geographic area, habitat, distance offshore, month, and year. The index of relative importance (IRI; Pinkas etal., 1971) was calculated for each data subset. The modified IRI (dry weight rather than volume) was used to characterize the diet of each species and to rank prey taxa:

$$IRI = (N + W)F,$$

where $N$ is numerical percentage, $W$ is weight percentage, and $F$ is frequency of occurrence (FO) percentage. In all comparisons, the IRI is expressed as a percentage of total IRI for each data subset.

Morisita's index of overlap as modified by Horn (1966) was used to calculate overlap between species pairs; values range from 0 (no overlap) to 1 (complete overlap):

$$\hat{C}_\lambda = \frac{2\sum_{i=1}^{S} x_i y_i}{\sum_{i=1}^{S} x_i^2 + \sum_{i=1}^{S} y_i^2},$$

where $x_i$ and $y_i$ are proportions of the numbers of individuals of prey species $i$ found in the predator species $x$ and $y$, respectively.

The percent similarity index (PSI; Whittaker, 1975) was used to compare stomach samples to plankton samples:

$$PSI = \sum \min(p_a \text{ or } p_b),$$

where $p_a$ is percentage number for a given species in sample A, and $p_b$ is percentage number for the same species in sample B. A PSI value of 1.00 shows complete similarity; a value of 0 indicates no similarity. We considered values ≥0.60 to be significant for both overlap indices. Chinook salmon were not included in the analysis of overlap because of small sample sizes (Table 1). Following Brodeur and Pearcy (1990), we tested for differences in the occurrence of principal prey between years, months, areas, and distance offshore using $\chi^2$.

We examined data for neuston and plankton prey samples collected at locations where stomachs of at least five specimens of one salmon species were available and included a taxon in the prey collections. To measure prey selection, we used Strauss's linear food selection index (Strauss, 1979):

$$L = r_i - p_i,$$

where $r_i$ and $p_i$ are the proportional abundances of prey item $i$ in the gut and habitat, respectively. Selection values range from −1, indicating avoidance or negative accessibility, to +1, indicating preference or positive selection; 0 indicates random feeding. Values are extreme only when the prey item is proportionately abundant but rarely consumed (−1), or is proportionately rare but consumed almost exclusively (+1). We tabulated selection values >0.10 or <−0.10 for an indication of the positive or negative selection of a particular taxon.

To compare the number of stomachs required to characterize the breadth of diet for each species of salmon, we pooled the stomachs over all periods and habitats. Stomachs were selected randomly, and the cumulative number of taxa were plotted versus the number of stomachs until the asymptote was reached (Hurtubia, 1973).

## Results

### Description of diet

**All salmon species** The prey spectrum for juveniles of five Pacific salmon species comprised at least 30 taxa (Table 2). The six taxonomic groups of greatest importance (IRI) were calanoid copepods, hyperiid amphipods, euphausiids, decapods, tunicates, and fishes (Table 3). In pooled samples, fish were the most important prey for coho and chinook salmon (IRI=63.8% and 76.4%) but were only moderately important for the other species (IRI 28.3–40.3%). Hyperiid amphipods, most commonly *Themisto* spp., were also important prey for pink, chum, and sockeye salmon (IRI 28.0–39.6%). However, the biomass of teleost prey made up more than 75% of the total biomass consumed by each of the juvenile salmon species in pooled samples.

The full breadth of the prey spectrum for juvenile salmon species was obtained by randomly selecting

16–95% of the actual number of stomachs analyzed (Fig. 2). The highest cumulative numbers of prey taxa ($n$=25 and 26, respectively) were observed after we had randomly subsampled 86 coho and 396 pink salmon stomachs (Fig. 3). Virtually all chinook salmon analyzed (39) were needed to reach the 14 cumulative prey taxa observed. The curves of cumulative number of taxa for pink and chum salmon were more similar than for any other pair of species (Fig. 3).

**Pink salmon** The prey of juvenile pink salmon (85–222 mm FL; $\bar{x}$=142 mm; SD=22.9) encompassed 26 taxa and several life-history stages. Hyperiid amphipods, especially the genus *Themisto*, had the highest total IRI (Fig. 4) and highest FO and mean abundance over all periods and habitats (Table 3). Juvenile fish had the second-highest IRI and the greatest biomass—76% of pooled weight of stomach contents. In 1984, the IRI for fish prey did not rank first, but it was more than twice the 1983 value; fish prey ranked higher in Alaska than in British Columbia. Tunicates, primarily the larvacean *Oikopleura dioica*, were the third most important prey in pooled samples.

**Chum salmon** The prey spectrum for juvenile chum salmon (80–276 mm FL; $\bar{x}$=151 mm; SD=28.4) included 22 taxonomic groups and several life-history stages. Juvenile fish, tunicates (salps and the larvacean *O. dioica*), and hyperiid amphipods (*Themisto* spp.) had the highest IRI's overall (Fig. 5).

**Sockeye salmon** The prey spectrum for juvenile sockeye salmon (91–202 mm FL; $\bar{x}$=151 mm; SD=18.9) encompassed 18 taxonomic groups and several life-history stages. Fish prey had the highest IRI (40.3%) and the greatest average weight (87.2%) pooled over all habitats and periods (Table 3; Fig. 6), although no fish were sampled from outer-coast inlets (Table 1). Fish prey were more important in 1984 than in 1983, especially in the outside waters of southeastern Alaska in July 1984 and inside inlets and outside waters (>37 km) in August 1984 (Fig. 6). Hyperiid amphipods (*Themisto* spp.) were the second

**Table 2**

Prey from juvenile salmon stomachs as index of relative importance (IRI). $IRI = (N + W)FO$, where $N$= numerical percentage, $W$ = weight percentage, and $FO$ = frequency of occurrence percentage. Numbers in parentheses are totals of taxonomic groups for which more than one taxon is listed.

| | IRI (%) | | | | |
|---|---|---|---|---|---|
| Prey | Pink | Chum | Sockeye | Coho | Chinook |
| Polychaeta | | | | | |
| Unidentified | <0.01 | <0.01 | — | <0.01 | <0.01 |
| Mollusca | (0.90) | (0.16) | (0.17) | (0.02) | (—) |
| Gastropoda | | | | | |
| *Limacina helicina* | 0.82 | 0.16 | 0.15 | 0.02 | — |
| Bivalvia | | | | | |
| Unidentified | <0.01 | <0.01 | — | — | — |
| Cephalopoda | | | | | |
| Unidentified | 0.08 | <0.01 | 0.02 | <0.01 | 0.18 |
| Copepoda | (3.71) | (2.93) | (4.15) | (0.02) | (<0.01) |
| *Neocalanus cristatus* | <0.01 | — | — | — | — |
| *Epilabidocera longipedata* | <0.01 | — | <0.01 | — | — |
| Unidentified | 3.70 | 2.93 | 4.14 | 0.02 | <0.01 |
| Cumacea | | | | | |
| Unidentified | <0.01 | <0.01 | — | — | — |
| Amphipoda | | | | | |
| Hyperiidea | (39.61) | (28.03) | (36.48) | (6.84) | (0.10) |
| *Hyperia* sp. | 0.01 | 0.01 | 0.01 | 0.02 | 0.01 |
| *Themisto* spp. | 38.75 | 27.44 | 36.11 | 6.73 | 0.08 |
| *Primno macropa* | 0.83 | 0.58 | 0.36 | 0.09 | 0.01 |
| *Vibilia* sp. | 0.02 | <0.01 | 0.01 | <0.01 | — |
| Euphausiacea | (5.95) | (6.18) | (12.62) | (3.88) | (18.34) |
| *Euphausia pacifica* | <0.01 | — | — | <0.01 | — |
| *Thysanoessa spinifera* | <0.01 | 0.01 | — | 0.01 | 0.08 |
| Unidentified | 5.94 | 6.17 | 12.62 | 3.86 | 18.26 |
| Decapoda | | | | | |
| Unidentified | 4.67 | 3.16 | 3.64 | 25.26 | 4.81 |
| Insecta | | | | | |
| Unidentified | 0.01 | <0.01 | <0.01 | 0.01 | — |
| Chaetognatha | | | | | |
| Unidentified | 0.01 | 0.01 | <0.01 | <0.01 | — |
| Urochordata | | | | | |
| (tunicates) | (13.56) | (30.32) | (2.26) | (0.03) | — |
| Salpidae | | | | | |
| Unidentified | <0.01 | 0.21 | — | <0.01 | — |
| Larvacea | | | | | |
| *Oikopleura dioica* | 13.56 | 30.11 | 2.26 | 0.03 | — |
| Osteichthyes | (31.11) | (29.88) | (40.27) | (63.78) | (76.42) |
| *Clupea pallasi* | — | — | — | 0.01 | 0.26 |
| Osmeridae | <0.01 | 0.02 | — | <0.01 | 0.61 |
| Myctophidae | 0.02 | 0.02 | <0.01 | — | — |
| *Theragra chalcogramma* | — | — | — | 0.01 | — |
| *Sebastes* spp. | 0.04 | — | 0.03 | 0.04 | — |
| Cottidae | — | — | — | <0.01 | — |
| Stichaeidae | <0.01 | — | <0.01 | <0.01 | 0.02 |
| *Ammodytes hexapterus* | <0.01 | 0.03 | — | 0.30 | 0.47 |
| Pleuronectidae | — | <0.01 | <0.01 | 0.02 | — |
| Unidentified | 31.04 | 29.80 | 40.22 | 63.39 | 75.06 |

**Table 3**

Stomach contents of juvenile salmon in marine waters of southeastern Alaska and northern British Columbia in 1983 and 1984. *N* is numerical percentage, *W* is dry weight percentage, *FO* is frequency of occurrence percentage of fish with prey item *i*, and *IRI* is percent of total IRI for all prey taxa. $IRI = (N + W)FO$. Taxa are omitted if IRI is ≤1% for all salmon.

| | Pink salmon | | | | Chum salmon | | | | Sockeye salmon | | | | Coho salmon | | | | Chinook salmon | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | N (%) | W (%) | FO (%) | IRI (%) | N (%) | W (%) | FO (%) | IRI (%) | N (%) | W (%) | FO (%) | IRI (%) | N (%) | W (%) | FO (%) | IRI (%) | N (%) | W (%) | FO (%) | IRI (%) |
| All periods combined | | | | | | | | | | | | | | | | | | | | |
| Calanoids | 5.6 | 0.9 | 47.9 | 3.7 | 5.4 | 0.8 | 32.9 | 3.0 | 9.0 | 0.5 | 41.5 | 4.2 | — | — | — | — | — | — | — | — |
| Decapods | 3.8 | 4.0 | 48.6 | 4.7 | 2.4 | 3.6 | 36.6 | 3.1 | 5.4 | 2.6 | 43.2 | 3.6 | 52.0 | 0.1 | 56.3 | 25.3 | 11.2 | 0.2 | 38.5 | 4.8 |
| Euphausiids | 5.2 | 5.5 | 46.2 | 6.0 | 6.0 | 5.9 | 39.8 | 6.1 | 16.5 | 4.3 | 57.4 | 12.6 | 12.8 | 0.1 | 35.8 | 3.9 | 52.6 | 0.2 | 33.3 | 18.3 |
| Hyperiids | 45.2 | 5.8 | 90.3 | 39.6 | 29.5 | 5.7 | 73.6 | 28.0 | 46.2 | 3.7 | 90.1 | 36.5 | 22.9 | 0.1 | 46.4 | 6.8 | 1.5 | 0.2 | 7.7 | 0.1 |
| Tunicates | 32.2 | 0.1 | 35.2 | 13.6 | 52.5 | 0.1 | 46.7 | 30.1 | 16.4 | <0.1 | 13.1 | 2.3 | — | — | — | — | — | — | — | — |
| Teleosts | 1.3 | 76.0 | 39.1 | 31.2 | 0.9 | 82.7 | 28.6 | 28.3 | 2.9 | 87.2 | 47.0 | 40.3 | 8.4 | 99.5 | 73.2 | 63.8 | 30.2 | 99.0 | 71.8 | 76.4 |
| Total | 93.3 | 92.3 | | 98.8 | 96.7 | 98.7 | | 98.6 | 96.4 | 98.3 | | 99.5 | 96.1 | | 99.8 | 99.8 | 95.5 | | 99.5 | 99.6 |
| August 1983 | | | | | | | | | | | | | | | | | | | | |
| Calanoids | 6.4 | 2.9 | 62.6 | 6.6 | 2.0 | 4.7 | 39.7 | 3.1 | 10.9 | 4.6 | 52.7 | 6.0 | 0.4 | <0.1 | 10.1 | <0.1 | | | | |
| Decapods | 4.3 | 8.6 | 60.9 | 8.9 | 0.9 | 12.1 | 32.6 | 4.8 | 1.1 | 8.3 | 30.9 | 2.2 | 46.4 | 0.5 | 63.1 | 26.4 | | | | |
| Euphausiids | 4.9 | 14.1 | 52.9 | 11.4 | 5.3 | 32.7 | 46.2 | 18.4 | 17.0 | 39.0 | 76.4 | 31.5 | 5.8 | 0.6 | 36.9 | 2.0 | | | | |
| Hyperiids | 37.0 | 12.4 | 71.0 | 33.6 | 31.5 | 28.0 | 64.7 | 38.5 | 58.5 | 30.7 | 94.5 | 55.1 | 41.5 | 0.6 | 59.7 | 21.7 | | | | |
| Tunicates | 38.7 | 0.2 | 48.7 | 20.3 | 56.8 | 0.5 | 60.9 | 28.8 | 8.7 | 0.1 | 14.5 | 0.9 | 0.1 | <0.1 | 6.0 | <0.1 | | | | |
| Teleosts | 0.4 | 56.7 | 29.9 | 16.6 | 0.2 | 20.2 | 19.6 | 4.6 | 0.3 | 16.7 | 21.8 | 2.7 | 2.7 | 96.4 | 61.1 | 49.1 | | | | |
| Total | 91.7 | 94.9 | | 97.4 | 96.7 | 98.2 | | 98.2 | 96.5 | 99.4 | | 98.4 | 96.9 | | 98.1 | 99.2 | | | | |
| July 1984 | | | | | | | | | | | | | | | | | | | | |
| Calanoids | 15.0 | 0.8 | 39.0 | 7.3 | 23.4 | 1.4 | 28.0 | 11.0 | 12.1 | 0.4 | 4.3 | 5.6 | 0.7 | <0.1 | 7.1 | <0.1 | | | | |
| Decapods | 4.7 | 1.9 | 42.0 | 3.3 | 1.1 | 2.1 | 26.9 | 1.4 | 8.8 | 0.8 | 32.1 | 3.2 | 54.3 | 0.1 | 65.7 | 27.6 | | | | |
| Euphausiids | 7.0 | 5.0 | 46.3 | 6.6 | 4.8 | 8.1 | 37.6 | 7.7 | 23.0 | 3.4 | 62.3 | 17.0 | 16.6 | 0.1 | 33.7 | 3.8 | | | | |
| Hyperiids | 45.2 | 4.3 | 68.3 | 39.4 | 26.0 | 6.3 | 53.8 | 27.1 | 37.8 | 2.0 | 70.4 | 28.9 | 6.1 | 0.1 | 25.4 | 0.8 | | | | |
| Tunicates | 11.9 | <0.1 | 17.6 | 2.5 | 34.3 | 0.1 | 29.0 | 15.8 | 9.1 | <0.1 | 7.5 | 0.7 | 4.1 | <0.1 | 5.3 | <0.1 | | | | |
| Teleosts | 3.6 | 84.2 | 39.0 | 38.4 | 3.9 | 77.4 | 32.3 | 35.0 | 4.2 | 92.0 | 45.9 | 43.9 | 15.5 | 99.7 | 84.0 | 67.6 | | | | |
| Total | 87.4 | 96.2 | | 97.5 | 93.5 | 95.4 | | 98.0 | 95.0 | 98.6 | | 99.3 | 97.3 | | 100 | 99.8 | | | | |
| August 1984 | | | | | | | | | | | | | | | | | | | | |
| Calanoids | 2.3 | 0.7 | 37.9 | 1.3 | 3.8 | 0.3 | 25.1 | 1.5 | 4.7 | 0.5 | 32.7 | 1.8 | 0.2 | <0.1 | 2.7 | <0.1 | | | | |
| Decapods | 3.2 | 3.9 | 43.4 | 3.7 | 5.0 | 2.9 | 42.9 | 5.0 | 4.5 | 5.3 | 61.2 | 6.4 | 58.3 | 0.1 | 42.7 | 24.7 | | | | |
| Euphausiids | 4.8 | 3.7 | 39.3 | 3.9 | 7.3 | 2.4 | 29.7 | 4.2 | 9.6 | 3.8 | 41.5 | 5.9 | 19.7 | 0.1 | 32.4 | 6.3 | | | | |
| Hyperiids | 50.1 | 5.0 | 65.3 | 40.8 | 27.9 | 3.0 | 53.1 | 22.6 | 47.5 | 5.1 | 68.7 | 36.5 | 10.3 | 0.1 | 24.0 | 2.1 | | | | |
| Tunicates | 34.4 | <0.1 | 34.7 | 14.4 | 52.8 | <0.1 | 37.1 | 28.9 | 28.3 | <0.1 | 19.7 | 5.9 | <0.1 | <0.1 | 0.1 | <0.1 | | | | |
| Teleosts | 1.1 | 85.1 | 38.5 | 35.5 | 0.8 | 90.8 | 28.0 | 37.3 | 3.1 | 83.1 | 47.6 | 43.4 | 10.7 | 99.6 | 72.9 | 66.8 | | | | |
| Total | 95.9 | 98.4 | | 99.6 | 97.6 | 99.4 | | 99.5 | 97.7 | 97.8 | | 99.9 | 99.2 | | 99.9 | 99.9 | | | | |

most important prey group (IRI=36.5%) and had the highest FO and average count (Table 3).

**Coho salmon** The prey spectrum of juvenile coho salmon (112–309 mm FL; $\bar{x}$=222 mm; SD=35.1) encompassed 25 taxonomic groups, including eight identifiable fish families (Table 2). Teleosts made up 99.5% of the total prey weight, with a mean number of 8.4 fish consumed by 73.2% of the coho predators (Table 3). Juvenile fishes were the principal component of coho salmon diet in all habitats except in the outside waters during August 1983 (Fig. 7), when decapod larvae were more important (IRI=66%). The IRI for prey fish ranged from 51% to 81% in the other habitats, with Pacific sand lance (*Ammodytes hexapterus*) the most prevalent species. Other identifiable prey fish (in order of importance) included walleye pollock (*Theragra chalcogramma*), rockfish (*Sebastes* spp.), flatfish (Pleuronectidae), Pacific herring (*Clupea pallasi*), smelt (Osmeridae), pricklebacks (Stichaeidae), and sculpins (Cottidae). Fish were more important in 1984 than in 1983 and higher in Alaska than in British Columbia.

**Chinook salmon** The prey spectrum of juvenile chinook salmon (139–324 mm FL; $\bar{x}$=224 mm; SD=58.4) encompassed 14 taxonomic categories and four identifiable fish families (Table 2). Fish were the most important prey: IRI's ranged from 28% to 100% among habitats (data not shown). Fish made up 99% (biomass) of chinook salmon stomach contents in pooled samples, with a mean of 30.2 individuals con-

sumed by approximately 72% of the predators (Table 3). Identifiable fish (in order of importance) included smelt, Pacific sand lance, Pacific herring, and pricklebacks. Euphausiids were an important prey principally in inside inlets during July 1984. Incidental prey included decapod larvae, squid, and hyperiid amphipods.

## Variation in principal prey

Diets of all four species varied greatly (Table 4). Variation in the FO of the six principal prey (calanoids, decapod larvae, euphausiids, fish, hyperiid amphipods, and tunicates) was greatest when compared between years: the FO of most invertebrate taxa decreased significantly ($P \leq 0.05$) in the diets from August 1983 to August 1984, whereas the FO of teleost prey increased (Tables 3 and 4). Except for coho salmon, variation in the FO of fish was greatest for inshore-offshore comparisons; significantly more fish were consumed by the other species offshore (>37 km from the coast) than inshore (0–37 km from the coast) (Table 4; $12.69 < \chi^2 < 47.72$; $P \leq 0.001$). In 1984, the FO of two principal prey taxa differed consistently in opposite directions between areas: pink, chum, and sockeye salmon ate teleost prey significantly less often ($6.94 < \chi^2 < 13.42$; $P \leq 0.01$), whereas all four species consumed euphausiids significantly more often ($5.66 < \chi^2 < 17.13$; $P \leq 0.05$) in British Columbia waters than in Alaska. The diet of sockeye salmon varied more than that of the other species between years (August 1983 and August 1984), months (July and August), and areas (British Columbia and southeastern Alaska; Table 4).

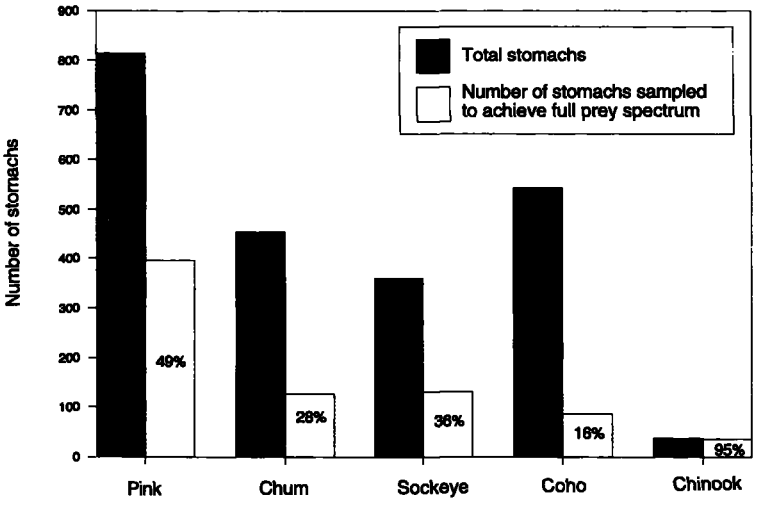


**Figure 2**

Total number of stomachs sampled for five species of juvenile Pacific salmon and number and percentage of randomly selected stomachs, from samples pooled over habitats and time periods, which were required to achieve the full prey spectrum for each species as defined in this study.

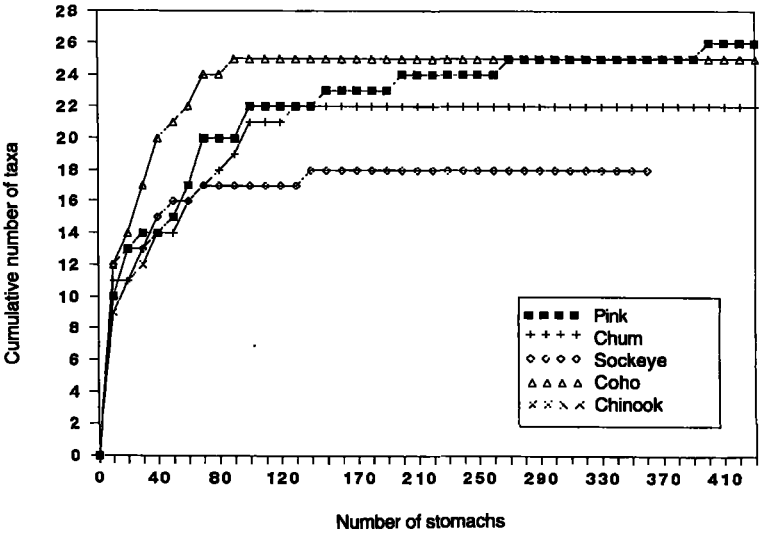


**Figure 3**

Curves of cumulative number of prey taxa versus pooled number of fish examined from five Pacific salmon species in marine waters of southeastern Alaska and northern British Columbia.

## Diet overlap

**Samples pooled over time and habitat** Significant diet overlap ($\hat{C}_\lambda > 0.60$) was found between pink and sockeye salmon, pink and chum salmon, and chum and sockeye salmon when all samples were pooled. Coho salmon diet overlap was less than 0.60 in all comparisons. Diet overlap was not calculated for chinook salmon because of small sample sizes (Table 1). The greatest diet overlap was between pink and sockeye salmon juveniles ($\hat{C}_\lambda = 0.93$; Table 5); both species ate fish and hyperiid amphipods. The second-greatest diet overlap ($\hat{C}_\lambda = 0.91$) was between pink

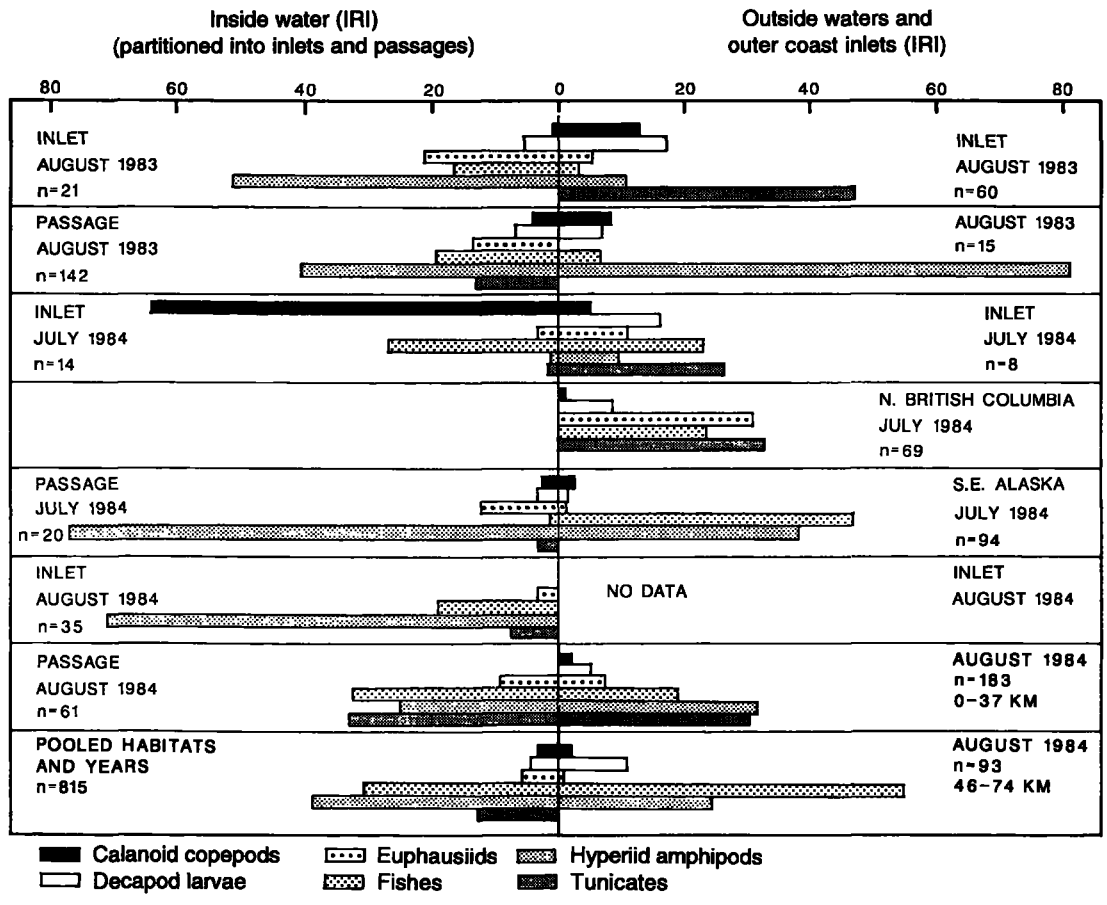


**Figure 4**

Index of relative importance (IRI) of principal prey of juvenile pink salmon in inside and outside waters and outer coast inlets of southeastern Alaska in 1983 and 1984 and outside waters and outer coast inlets of northern British Columbia in 1984.

and chum salmon; both ate hyperiid amphipods, fish, and *Oikopleura dioica*. The third-highest diet overlap in all pooled samples was between chum and sockeye salmon ($\hat{C}_\lambda$=0.73); both species consumed fish, hyperiid amphipods, and euphausiids.

**Temporal diet overlap** The degree of diet overlap among salmon species pairs varied by time period when habitat was not considered. In August 1983, diet overlap, based on the consumption of hyperiid amphipods, was greatest for pink and chum salmon juveniles ($\hat{C}_\lambda$=0.95; Table 5), *O. dioica*, and euphausiids. Diets of juvenile pink and sockeye salmon overlapped significantly ($\hat{C}_\lambda$=0.72) on the basis of hyperiid amphipods and euphausiids. A lesser, but still significant, diet overlap ($\hat{C}_\lambda$=0.62) occurred between sockeye and coho salmon on the basis of hyperiid amphipods, decapod larvae, and fish.

Diet overlap was lower in July 1984, when samples included waters outside of British Columbia, than in August 1984. Diet overlap was significant for combinations of pink, chum, and sockeye salmon, but not for combinations including coho salmon (Table 5). The greatest overlap occurred between pink and chum salmon ($\hat{C}_\lambda$=0.80), pink and sockeye salmon ($\hat{C}_\lambda$=0.79), and chum and sockeye salmon ($\hat{C}_\lambda$=0.73), which was principally due to similar proportions of hyperiid amphipods and juvenile fish. The relative importance of larvaceans accounted for the greatest difference in the diets of these three species: *O. dioica* made up nearly 20% of the IRI for chum salmon, compared with less than 3% for pink and sockeye salmon.

In August 1984, the diets of pink, sockeye, and chum salmon overlapped greatly, whereas coho salmon diet did not overlap with that of any other species (Table 5). Diets of pink and sockeye salmon overlapped almost

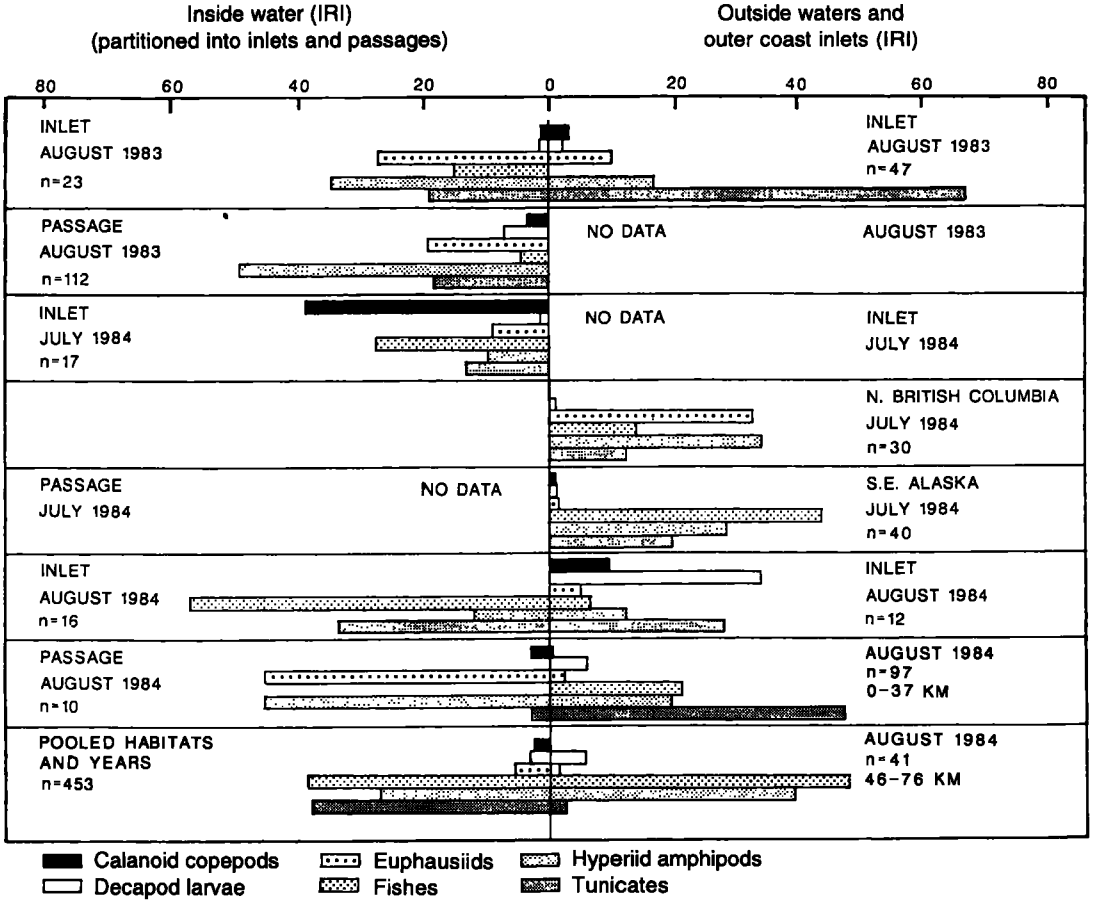


**Figure 5**

Index of relative importance (IRI) of principal prey of juvenile chum salmon in inside and outside waters and outer coast inlets of southeastern Alaska in 1983 and 1984 and outside waters and outer coast inlets of northern British Columbia in 1984.

completely ( $\hat{C}_\lambda$=0.99); prey composition and IRI for each prey category were highly similar (Table 2). Pink and chum salmon diets ( $\hat{C}_\lambda$=0.88) and sockeye and chum salmon diets ( $\hat{C}_\lambda$=0.85) had almost identical prey species compositions, although proportions of prey categories differed (Table 2).

**Spatial diet overlap** Diet overlap was more common for species comparisons in outside waters than in inside waters. Of all possible habitat comparisons, diet overlap was significant ( $\hat{C}_\lambda \geq 0.60$) in 42% of the outside-waters comparisons, 39% of inside-passage comparisons, and 29% of inside-inlet comparisons (Table 5). Within each habitat, mean overlap (all periods) was significant in inside inlets for pink and chum salmon ( $\hat{C}_\lambda$=0.66), inside passages for pink and chum salmon ( $\hat{C}_\lambda$=0.91), and chum and sockeye salmon ( $\hat{C}_\lambda$=0.73), and outside waters for pink and sockeye salmon ( $\hat{C}_\lambda$=0.83), chum and sockeye salmon ( $\hat{C}_\lambda$=0.68), and pink and chum salmon ( $\hat{C}_\lambda$=0.67).

## Fullness and digestion

Most salmon stomachs were evaluated to be at least half full (fullness index of 3); coho salmon stomachs were more full than those of other species (Table 6). Stomach fullness was always greater for fish from the inside waters than from outside waters; stomachs of fish caught 0–37 km offshore were less full than those of fish caught >37 km offshore. Only 32 of 2,210 (1.4%) stomachs sampled were empty: 72% in outside waters, 3% in coastal inlets, and 25% in inside waters. The contents of most stomachs were "partly digested" (digestion index of 2). Pink, chum, and coho salmon from inside waters had stomach contents in an earlier stage of digestion than fish

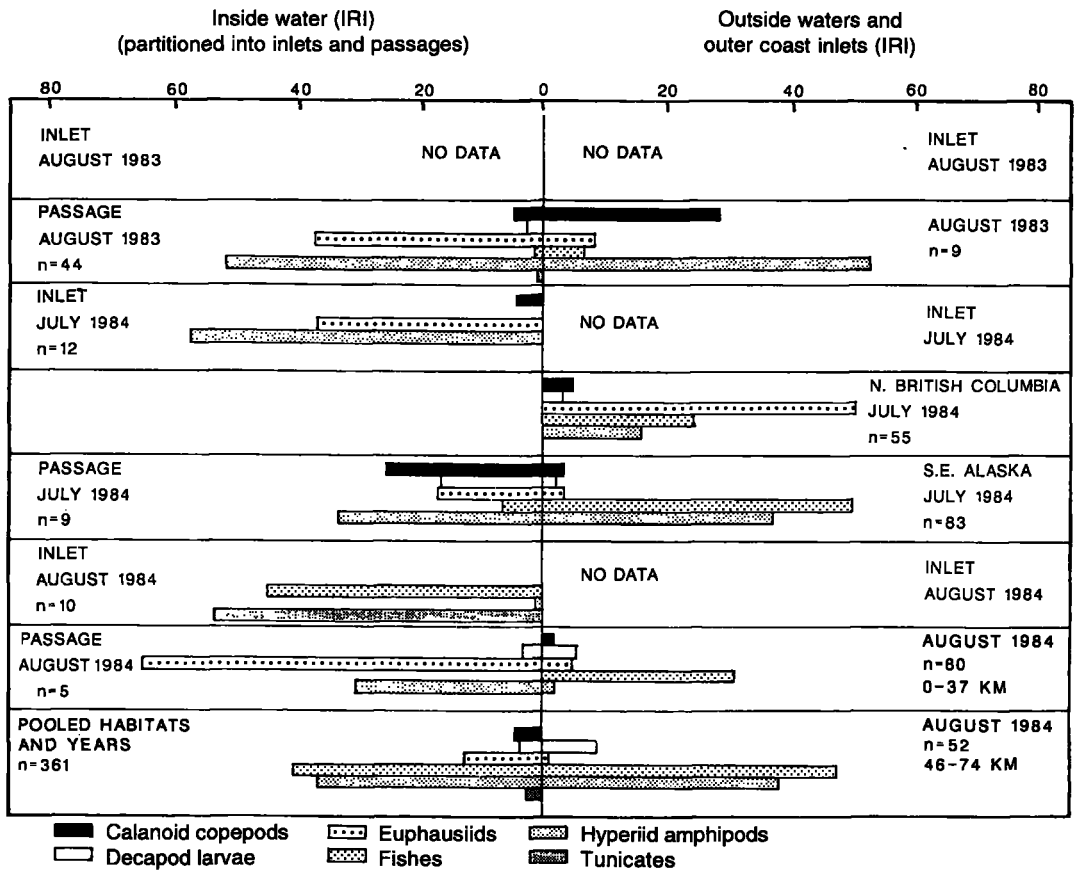


**Figure 6**

Index of relative importance (IRI) of principal prey of juvenile sockeye salmon in inside and outside waters and outer coast inlets of southeastern Alaska in 1983 and 1984 and outside waters and outer coast inlets of northern British Columbia in 1984.

from outside waters; the reverse was observed for sockeye salmon.

## Salmon diet and the prey assemblages

Neuston samples from the outside waters of British Columbia and southeastern Alaska included 13 and 14 major taxa, respectively (Table 7). In British Columbia, decapod larvae made up 83% of the number of prey, hyperiid amphipods 12%, calanoid copepods 4%, and all other taxa <1%. Prey diversity of neuston samples was more even for southeastern Alaska than for British Columbia; half of the 14 taxa represented ≥2% of the total abundance. In Alaska, calanoid copepods were the most abundant organism (59% of the total), decapod larvae were second (21%), and gammarid amphipods were third (9%). The density of neustonic organisms was about five times greater in samples from British Columbia than in those from southeastern Alaska.

In zooplankton samples, the number of individuals and dominant taxa differed with time and habitat (Table 7). Zooplankton abundance in outside waters was about twice that of inside waters of southeastern Alaska in July 1984. Calanoid copepods were the dominant organisms in the samples (90% of total abundance).

The PSI indicated little relationship between prey consumed by salmon and prey available in the environment (Table 8). Neuston samples were generally more similar to salmon diet than were zooplankton samples. Similarity for the neuston samples ranged from 0% to 37.8% and averaged from 9.1% for sockeye salmon to 16.7% for coho salmon (Table 8). The PSI values for the plankton samples ranged from 0.2% to 24.9% and averaged from 2.2% for chum salmon to 9.3% for sockeye salmon.

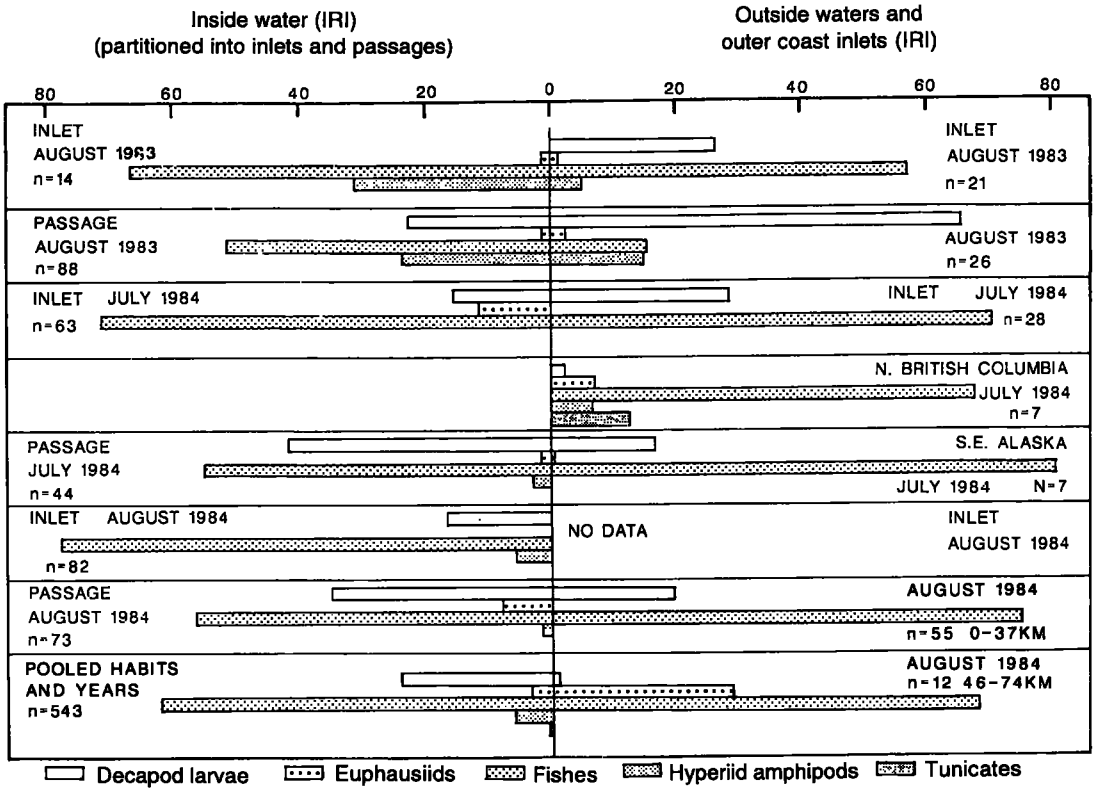


**Figure 7**

Index of relative importance (IRI) of principal prey of juvenile coho salmon in inside and outside waters and outer coast inlets of southeastern Alaska in 1983 and 1984 and outside waters and outer coast inlets of northern British Columbia in 1984.

We examined patterns of prey selectivity by applying Strauss's linear index of food selection to the same sets of predator-prey samples that had been analyzed for similarity. Pink and sockeye salmon selected ($L>0.10$) neustonic prey more often than planktonic prey, and neustonic hyperiid amphipods were the most frequently selected organism. Chum and coho salmon selected neustonic and planktonic prey in nearly equal frequencies (Table 9). All salmon species avoided ($L<-0.10$) neustonic decapod larvae. Selection patterns for planktonic prey varied more than for neustonic prey; however, salmon generally selected planktonic decapod larvae, hyperiid amphipods, euphausiids, and fishes and avoided the proportionately more abundant calanoid copepods.

## Discussion

This study of the food habits of five sympatric species of Pacific salmon during their first summer in the marine waters of southeastern Alaska and northern British Columbia is the first detailed study for this geographic area. Feeding patterns were dynamic, with shifts in the important prey categories between salmon species, years, and areas.

We analyzed the importance of two major prey categories, zooplankton and teleosts, and examined data for temporal and spatial shifts in feeding patterns among salmon species. First, in pooled samples (all periods and habitats), zooplankton were much more important in pink, chum, and sockeye salmon diets (60–70% IRI) than in coho and chinook salmon diets (36% and 24% IRI; Table 3). When the two years of data were analyzed separately, however, contrasting patterns emerged. In 1983 (August), pink, chum, and sockeye salmon were mostly planktivorous (83–97% IRI), and zooplankton IRI was over 50% even for coho salmon. In 1984 (July and August), the proportional number, weight, and FO of teleost prey increased in diets of all salmon species; however, whereas zooplankton remained most important in the diets of pink,

chum, and sockeye salmon (56–65% IRI), teleosts were most important in coho salmon diets (68%IRI).

Spatial factors that influence both predator and prey, especially latitude and proximity to shore, may account for similarities or differences in principal prey (Andrievskaya, 1970; Brodeur and Pearcy, 1990). Most species of salmon are opportunistic and feed on a wide variety of prey (Beacham, 1986; Brodeur[1]), but their diets are commonly composed of a few taxa readily available at a given time and location. The importance of zooplankton in the diets of juvenile pink, sockeye, and chum salmon in our study is similar to results reported in other studies from the eastern Gulf of Alaska (Manzer, 1969; Jaenicke et al., 1984; Hartt and Dell, 1986), the Sea of Okhotsk (Andrievskaya, 1968, 1970), and other regions of the northeastern Pacific Ocean (Peterson et al., 1982; Brodeur, 1989; Brodeur and Pearcy, 1990). We found that hyperiid amphipods were especially important in pink and sockeye salmon diets, and less so in chum salmon diets. The principal hyperiid amphipod found in diets of these species in the northeastern Pacific Ocean, Iincluding our study, was *Themisto pacifica*. In the more southern latitudes of coastal Washington and Oregon, another hyperiid amphipod (*Hyperoche medusarum*) is an important component in chum, coho, chinook, and sockeye salmon diets (Brodeur and Pearcy, 1990). In that area, however, euphausiids are more important in juvenile chum diets and, to a lesser extent in juvenile coho and chinook salmon diets, than are hyperiid amphipods (Peterson et al., 1982; Brodeur and Pearcy, 1990). Similarly, we found that euphausiids occurred less frequently and were less important in diets of all juvenile salmon located off southeastern Alaska, a downwelling region, compared to diets of salmon from southern British Columbia to Oregon, where upwelling is more prevalent (Ware and McFarlane, 1989).

**Table 4**

Chi-square ($\chi^2$) values for variation in frequency of occurrence of principal prey in four species of juvenile salmon. Comparisons were made between years (August 1983 and August 1984), months (July 1984 and August 1984), area (northern British Columbia and southeastern Alaska), and distance offshore (0–37km vs. 46–76km). No asterisk indicates $P > 0.05$. * = $P \leq 0.05$; ** = $P \leq 0.01$; and *** = $P \leq 0.001$.

| | $\chi^2$ | | | |
|---|---|---|---|---|
| Taxon | Between years | Between months | Between areas | Between inshore and offshore |
| Pink salmon | | | | |
| Calanoids | 35.29*** | 0.07 | 2.47 | 0.35 |
| Decapods | 18.41*** | 0.07 | 1.82 | 13.04*** |
| Euphausiids | 11.35*** | 2.90 | 17.13*** | 3.86* |
| Hyperiids | 2.34 | 0.62 | 1.18 | 8.60*** |
| Tunicates | 7.13** | 19.48*** | 6.08* | 13.83*** |
| Teleosts | 6.39* | 0.00 | 7.33** | 47.72*** |
| Chum salmon | | | | |
| Calanoids | 8.62*** | 0.25 | 6.08* | 0.37 |
| Decapods | 4.02* | 6.63* | 2.04 | 5.94* |
| Euphausiids | 9.06*** | 1.74 | 5.66* | 5.15* |
| Hyperiids | 4.93* | 0.01 | 0.12 | 15.30*** |
| Tunicates | 3.78 | 1.77 | 3.43 | 1.36 |
| Teleosts | 3.53 | 0.53 | 6.94** | 26.46*** |
| Sockeye salmon | | | | |
| Calanoids | 6.84** | 3.73 | 3.72 | 0.08 |
| Decapods | 14.77*** | 26.12*** | 1.74 | 1.36 |
| Euphausiids | 19.47*** | 13.21*** | 14.81*** | 0.68 |
| Hyperiids | 73.17*** | 57.10*** | 0.34 | 0.04 |
| Tunicates | 0.72 | 9.77*** | 5.45* | 4.51* |
| Teleosts | 11.05*** | 0.09 | 13.42*** | 12.69*** |
| Coho salmon | | | | |
| Calanoids | 9.26*** | 4.35* | — | — |
| Decapods | 14.96*** | 20.50*** | 0.00 | 1.46 |
| Euphausiids | 0.80 | 0.07 | 7.20** | 3.98* |
| Hyperiids | 48.46*** | 0.11 | 3.86* | — |
| Tunicates | 0.86 | 7.00** | 0.33 | — |
| Teleosts | 5.77* | 6.90** | 1.84 | 0.59 |

Although our study showed that chum salmon are primarily planktivorous, like pink and sockeye salmon, we observed another difference in their most important prey. Tunicates (larvacea and salps) were important only in the diets of chum salmon. The IRI for tunicates, especially the larvacean *Oikopleura dioica*, was greater than for any other taxon in chum salmon diets (30.1%). Tunicates were most prevalent in samples from outer coast inlets and outside waters (0–37 km). This finding is not unusual. *Oikopleura* was the dominant prey item in two other studies of the diet of juvenile chum salmon from northern British Columbia: 62% FO in fish 32–106 mm FL from Chatham Sound (Manzer, 1969) and 70–76% FO in fish 105–158 mm FL from Hecate Strait (Healey, 1991).

In addition to interspecific differences in the most important prey, shifts in diet differed among the four salmon species both spatially and temporally. We observed spatial differences in July 1984, when sampling included waters of northern British Columbia, and in August 1984, when sampling was extended to 76 km offshore. Pink, chum, and sockeye salmon consumed fish prey about twice as often offshore as they did inshore, and more often in British Colombia than in Alaska. The more piscivorous coho salmon, however, consumed fish just as frequently inshore as offshore and just as frequently in marine waters of Alaska and British Columbia. Diet varied by season and distance offshore for the highly similar pink,

**Table 5**

Diet overlap values ($\hat{C}_\lambda$, Morisita's index for prey numbers; Horn, 1966) for inside and outside waters of British Columbia (BC) and Alaska by sampling period and pooled over time. Nearshore = 0–37 km; offshore = >37 km. An asterisk indicates a significant value.

| | Diet overlap ($\hat{C}_\lambda$) | | | | | |
|---|---|---|---|---|---|---|
| | | July 1984 | | August 1984 | | |
| Comparison | Aug 1983 | BC | Alaska | Nearshore | Offshore | Pooled over time |
| Inside inlets | | | | | | |
| Pink-chum | 0.55 | | 0.87* | 0.56 | | 0.66* |
| Pink-coho | 0.89* | | 0.04 | 0.29 | | 0.41 |
| Pink-sockeye | — | | 0.21 | 0.15 | | 0.37 |
| Chum-coho | 0.47 | | 0.11 | 0.14 | | 0.24 |
| Chum-sockeye | — | | 0.25 | 0.85* | | 0.51 |
| Coho-sockeye | — | | 0.64* | 0.01 | | 0.55 |
| Inside passages | | | | | | |
| Pink-chum | 0.94* | | — | 0.91* | | 0.91* |
| Pink-coho | 0.54 | | 0.11 | 0.09 | | 0.25 |
| Pink-sockeye | 0.85* | | 0.49 | — | | 0.58 |
| Chum-coho | 0.45 | | — | 0.20 | | 0.25 |
| Chum-sockeye | 0.74* | | — | — | | 0.73* |
| Coho-sockeye | 0.65* | | 0.46 | — | | 0.49 |
| Outside waters | | | | | | |
| Pink-chum | — | 0.44 | 0.82* | 1.00* | 0.85* | 0.67* |
| Pink-coho | 0.26 | 0.24 | 0.10 | 0.12 | 0.11 | 0.20 |
| Pink-sockeye | 0.77* | 0.85* | 0.97* | 0.67* | 0.79* | 0.83* |
| Chum-coho | — | 0.96* | 0.10 | 0.10 | 0.09 | 0.32 |
| Chum-sockeye | — | 0.39 | 0.82* | 0.53 | 0.97* | 0.68* |
| Coho-sockeye | 0.16 | 0.20 | 0.17 | 0.13 | 0.09 | 0.17 |
| All habitats | | | | | | |
| Pink-chum | 0.95* | | 0.80* | 0.88* | | 0.91* |
| Pink-coho | 0.43 | | 0.21 | 0.18 | | 0.38 |
| Pink-sockeye | 0.72* | | 0.79* | 0.99* | | 0.93* |
| Chum-coho | 0.31 | | 0.15 | 0.25 | | 0.24 |
| Chum-sockeye | 0.58 | | 0.73* | 0.85* | | 0.73* |
| Coho-sockeye | 0.62* | | 0.37 | 0.18 | | 0.49 |

chum, and sockeye salmon in the Sea of Okhotsk and the Bering Sea (Andrievskaya, 1968). In our study, temporal patterns based on seasonal (monthly) differences in the FO of fish prey were rare; the diets of pink, chum, or sockeye salmon included fish as frequently in July 1984 (when transects extended only to 37 km) as in August 1984. However, interannual differences were observed: all species, except chum salmon, ate fish more frequently in August 1984 than in August 1983. These observations suggest that increased frequency of fish prey in salmon diets is related more to annual variations in teleost prey abundance than to distance offshore.

Juvenile fishes are often identified as important prey for juvenile salmon, although seldom to the extent that we observed in 1984 in northern southeastern Alaska. Comparison of our results with other studies of juvenile salmon diet in Alaska suggests that, although pink, chum, and sockeye salmon feed principally on planktonic taxa, they readily switch to teleost prey when available. For example, crustaceans were the principal prey of pink, chum, and sockeye salmon in the outside waters of southeastern Alaska in 1982, whereas fish were the principal prey of coho salmon (Jaenicke etal., 1984). In our study in southeastern Alaska in 1983, prey fish made up only half as much biomass as that observed in juvenile sockeye salmon stomachs collected from the Gulf of Alaska and Bering Sea in 1967 and 1968 (Hartt and Dell, 1986); in 1984, however, we recorded substantially higher teleost prey biomass than that observed by Hartt and Dell (Table10). Although we found that sockeye salmon diet varied more than that of the other species, increases in the FO of predation on teleosts were consistent among pink, chum, and sockeye salmon.

Some of the interspecific differences in the utilization of fish prey may also be attributed to differences in predator size. The mean size of juvenile coho and chinook salmon was greater than that of pink, chum, and sockeye salmon. Although the importance of size-related variability in prey consumption of juvenile salmon is recognized (e.g. Brodeur, 1991), we considered that a detailed analysis by predator size was beyond the scope of this study.

Increased fish prey in the diets of juvenile salmon in 1984 may reflect higher abundances of larval and juvenile stages of certain prey species compared with the previous year. Unfortunately, most fish prey species found in the salmon stomachs in our study could not be identified. However, we noted opposite trends in the CPUE for two potential teleost prey species from 1983 to 1984: the CPUE of juvenile walleye pollock in our seine catches increased 25-fold whereas that of juvenile herring declined 40-fold. In 1984, juvenile walleye pollock were important in the diet of adult coho salmon (Fisk[3]); the conditions that prolonged offshore feeding by adult coho salmon on these fish in 1984 may also have favored increased piscivory by juveniles.

An increase in available fish prey between years may also correlate with an increase in environmental temperature. The average SST in 1984 ($\bar{x}$=14.5°C) was higher than in 1983 ($\bar{x}$=13.7°C). Increased SST in northern waters may have beneficial effects on the early life history of fish preyed upon by juvenile salmon (Bailey and Incze, 1985). Temperatures in outside waters in 1984 followed a long-term warming trend related to the 1982–83 El Niño event. Temperature increased at depth as well as at the surface, and positive temperature anomalies persisted in northern waters beyond 1983 (Cannon et al., 1985; Royer, 1985). In coastal waters off Oregon and Washington, oceanographic conditions varied greatly owing to the 1982–83 El Niño event and affected prey species composition, but the proportion of fish biomass in juvenile salmon diets generally did not vary for the same months between years (Brodeur and Pearcy, 1990).

Changes in salmonid diet patterns may reflect density-dependent species interactions. Other workers have noted such changes with respect to an increase in the density of pink salmon, typically the most abundant species: 1) the diet of other salmonids became more diverse, particularly in chum salmon; and 2) diet overlap among pink, chum, and sockeye salmon decreased (Birman, 1969; Andrievskaya, 1970; Tadokoro et al., 1996). In the Sea of Okhotsk, diet overlap was lower in the coastal zone, where salmon density was greatest (Andrievskaya, 1970). We did not observe such density effects. We found significant diet overlap even in the four cases out of five where density effects could have been demonstrated among these species (see Jaenicke and Celewycz, 1994). The exception, when chum salmon diet did not overlap significantly with either pink or sockeye salmon diets, occurred during July 1984 in the outside waters of British Columbia.

Density-dependent effects on diet may be reflected in a third dietary attribute, the amount of food consumed. In the eastern coastal zone of the Sea of Okhotsk, for example, 30% of juvenile pink salmon and 66% of juvenile chum salmon sampled with gill nets (time of day not presented) had empty stomachs, a condition not found offshore, where juvenile salmon density was lower (Andrievskaya, 1970). Feeding conditions appeared to be much better for

**Table 6**

Estimated mean fullness (0=empty, 6=distended), degree of digestion (1=fresh, 4=completely digested), and percentage of empty stomachs for pooled habitats and time periods for juvenile salmon collected in marine waters of southeastern Alaska and northern British Columbia in 1983 and 1984; $n$ = sample size.

| Habitat | $n$ | Stomach fullness (0–6) | Degree of digestion (1–4) | Empty stomachs (%) |
|---|---|---|---|---|
| Pink salmon | | | | |
| Inside inlet | 70 | 4.0 | 1.9 | 0 |
| Inside passage | 223 | 3.9 | 2.3 | 0.4 |
| Outer coast inlet | 68 | 3.5 | 2.7 | 1.5 |
| Outside (0–37 km) | 361 | 3.0 | 2.2 | 3.3 |
| Outside (>37 km) | 93 | 4.0 | 2.3 | 0 |
| Chum salmon | | | | |
| Inside inlet | 56 | 4.2 | 2.3 | 0 |
| Inside passage | 125 | 4.7 | 2.4 | 0 |
| Outer coast inlet | 62 | 4.6 | 2.2 | 0 |
| Outside (0–37 km) | 169 | 2.6 | 2.7 | 5.3 |
| Outside (>37 km) | 41 | 3.3 | 2.4 | 0 |
| Sockeye salmon | | | | |
| Inside inlet | 24 | 4.3 | 2.5 | 0 |
| Inside passage | 58 | 4.5 | 3.0 | 1.7 |
| Outer coast inlet | 0 | — | — | — |
| Outside (0–37 km) | 227 | 3.4 | 2.3 | 0.9 |
| Outside (>37 km) | 52 | 3.6 | 2.5 | 0 |
| Coho salmon | | | | |
| Inside inlet | 159 | 4.2 | 2.3 | 1.3 |
| Inside passage | 205 | 4.4 | 2.3 | 0.5 |
| Outer coast inlet | 52 | 4.2 | 2.5 | 0 |
| Outside (0–37 km) | 115 | 4.0 | 2.4 | 0 |
| Outside (>37 km) | 12 | 4.3 | 3.0 | 0 |

[3] Fisk, G. 1985. Final report 1984 troll logbook program. Alaska Trollers Assoc., 130 Seward St., No. 213, Juneau, AK 99801, 41 p.

**Table 7**

Neuston and zooplankton organisms (number per 100 $m^3$) from outside- and inside-water habitats in British Columbia (BC) and Alaska, collected in July 1984.

| | Neuston | | Zooplankton | | |
|---|---|---|---|---|---|
| | | | Outside | | |
| | Outside BC | Combined Alaska | BC | Alaska | Inside Alaska |
| Number of samples | 20 | 16 | 3 | 9 | 5 |
| Invertebrate eggs | — | — | 343.00 | 1,449,78 | 304.20 |
| Polychaeta | 0.13 | 0.13 | — | — | — |
| Gastropoda | | | | | |
| *Limacina helicina* | — | — | 124.67 | 243.67 | 62.80 |
| Bivalvia | — | — | — | — | 26.60 |
| Cephalopoda | 0.05 | 0.13 | 31.00 | — | — |
| Cladocera | — | — | 145.33 | 524.00 | 234.20 |
| Calanoida | 39.77 | 114.56 | 48,672.34 | 60,074.67 | 25,956.00 |
| Harpacticoida | 0.50 | 4.31 | 0 | 34.33 | 5.20 |
| Cirripedia | 1.90 | 0.75 | 187.00 | 3,203.44 | 543.40 |
| Mysidacea | — | 0.13 | 0 | 579.89 | — |
| Gammariidea | 0.92 | 18.17 | 0 | 2.22 | — |
| Hyperiidea | 126.12 | 5.21 | 436.33 | 566.33 | 1,142.00 |
| Euphausiacea | 8.86 | 0.17 | 4,072.70 | 126.78 | 164.80 |
| Decapoda | 873.11 | 40.18 | 363.67 | 510.33 | 230.00 |
| Insecta | 0.21 | 0.21 | — | — | 3.00 |
| Chaetognatha | 0.34 | 5.63 | 249.33 | 171.67 | 42.20 |
| Larvacea | 0.15 | 5.00 | 62.33 | 262.78 | 204.00 |
| Teleosts[1] | 1.46 | 0.79 | 31.00 | 6.11 | — |

[1] Eggs, larvae, and juveniles combined.

salmon in our study (seined during the day); of 2,216 stomachs examined, only 32 (1.4%) were empty. Although we found few empty stomachs, we did find evidence of decreased feeding in the 0–37 km region of outside waters, which includes the region of peak catches of pink and chum salmon (Jaenicke and Celewycz, 1994); fullness was lower for all species, and empty stomachs were most common for pink and chum salmon collected in these outside waters.

Juvenile coho salmon diet rarely showed significant overlap with pink, chum, and sockeye salmon diets. Coho salmon differed in distribution and size from the other three species (Jaenicke and Celewycz, 1994) and were more piscivorous. Curves of cumulative number of taxa (Fig. 3) sloped more steeply for coho salmon than for the other species; this rapid rate of increase in prey types may reflect opportunistic feeding of juvenile coho salmon. Diets are even more diverse among coho salmon individuals than among pink salmon individuals, which consumed a similarly broad array of prey taxa. Less aggregation and lower densities (CPUE) than those for other salmon (Jaenicke and Celewycz, 1994) allow coho salmon to exploit fully all locations within a habitat type. The other three species tended to occur in fewer locations (although they were well represented within habitat types) and tended to be more highly aggregated, increasing the tendency toward more

**Table 8**

Mean percent similarity index (PSI) values indicating amount of overlap between prey fields and juvenile salmon diet. Stations where prey were collected were included in the analysis for a particular salmon species if at least five stomachs were collected at the station.

| | Number of stations | Similarity values | |
|---|---|---|---|
| | | Mean | Range |
| Neuston collection | | | |
| Pink | 8 | 10.8 | 0–24.6 |
| Chum | 2 | 9.3 | 0–18.5 |
| Sockeye | 8 | 9.1 | 0–37.8 |
| Coho | 2 | 16.7 | 0–33.3 |
| Zooplankton collection | | | |
| Pink | 8 | 8.0 | 1.0–22.7 |
| Chum | 5 | 2.2 | 0.2–6.8 |
| Sockeye | 4 | 9.3 | 1.0–24.9 |
| Coho | 6 | 6.2 | 0.7–11.7 |

## Table 9

Prey selection frequencies (Strauss's linear index of food selection (L); Strauss 1979) in juvenile salmon diet for neuston and zooplankton collections, July and August 1984. A positive (pos.) value indicates that a prey was more abundant in the diet than in the environment at a level of ≥0.10. A negative (neg.) value indicates that a prey was less abundant in the diet than in the environment at a level of ≤0.10. A random (ran.) value indicates that a prey was about equally abundant in the diet and in the environment. Absent indicates that a prey item was absent from the diet and from the environment in a particular location. $N$ = number of groups tested, where group size was 5 or more of a species.

| | Prey selection frequency | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Pink salmon | | | | Chum salmon | | | | Sockeye salmon | | | | Coho salmon | | | |
| Taxon | Pos. | Neg. | Ran. | Absent | Pos. | Neg. | Ran. | Absent | Pos. | Neg. | Ran. | Absent | Pos. | Neg. | Ran. | Absent |
| Neuston | | | | | | | | | | | | | | | | |
| Polychaetes | 0 | 0 | 1 | 7 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 2 |
| Pteropods | 1 | 0 | 2 | 5 | 0 | 0 | 2 | 2 | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 2 |
| Squid | 0 | 1 | 0 | 7 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 2 |
| Calanoid copepods | 1 | 1 | 4 | 2 | 0 | 0 | 0 | 2 | 4 | 2 | 1 | 1 | 0 | 0 | 0 | 2 |
| Barnacle larvae | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 7 | 0 | 0 | 0 | 2 |
| Gammarid amphipods | 0 | 2 | 2 | 4 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 6 | 0 | 1 | 0 | 1 |
| Hyperiid amphipods | 5 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 6 | 2 | 0 | 0 | 0 | 1 | 0 | 1 |
| Euphausiids | 4 | 1 | 1 | 2 | 0 | 0 | 1 | 1 | 3 | 1 | 1 | 3 | 0 | 0 | 1 | 1 |
| Decapod larvae | 2 | 4 | 1 | 1 | 0 | 2 | 0 | 0 | 2 | 3 | 1 | 2 | 1 | 1 | 0 | 0 |
| Insects | 0 | 0 | 1 | 7 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 2 |
| Chaetognaths | 0 | 0 | 2 | 6 | 1 | 0 | 0 | 2 | 0 | 0 | 1 | 7 | 0 | 0 | 0 | 2 |
| Salps | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 8 | 0 | 0 | 1 | 1 |
| Larvaceans | 1 | 0 | 3 | 4 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 7 | 1 | 0 | 1 | 0 |
| Teleosts | 1 | 0 | 5 | 2 | 0 | 0 | 1 | 1 | 0 | 0 | 5 | 3 | 1 | 0 | 0 | 1 |
| Percent selection | 13.5 | 9.0 | 20.7 | 57.4 | 7.2 | 10.7 | 14.3 | 74.8 | 14.4 | 9.0 | 9.0 | 67.9 | 10.8 | 10.8 | 10.8 | 67.7 |
| Plankton | | | | | | | | | | | | | | | | |
| Cnidaria | 0 | 0 | 3 | 5 | 0 | 0 | 2 | 3 | 0 | 0 | 2 | 2 | 0 | 0 | 1 | 5 |
| Polychaetes | 0 | 0 | 0 | 8 | 0 | 0 | 1 | 4 | 0 | 0 | 0 | 4 | 0 | 0 | 1 | 5 |
| Pteropods | 1 | 0 | 1 | 6 | 0 | 0 | 0 | 5 | 0 | 0 | 1 | 3 | 0 | 0 | 1 | 5 |
| Bivalve larvae | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 4 | 0 | 1 | 1 | 4 |
| Squid | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 5 | 0 | 0 | 1 | 3 | 0 | 0 | 0 | 6 |
| Invertebrate eggs | 0 | 2 | 1 | 5 | 0 | 1 | 0 | 4 | 0 | 1 | 0 | 3 | 0 | 0 | 1 | 5 |
| Calanoid copepods | 0 | 7 | 0 | 1 | 0 | 4 | 0 | 1 | 0 | 4 | 0 | 0 | 0 | 6 | 0 | 0 |
| Barnacle larvae | 0 | 0 | 2 | 6 | 0 | 0 | 1 | 4 | 0 | 1 | 1 | 2 | 0 | 1 | 1 | 4 |
| Mysids | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 6 |
| Hyperiid amphipods | 2 | 0 | 2 | 4 | 2 | 0 | 1 | 2 | 2 | 0 | 1 | 1 | 1 | 0 | 4 | 1 |
| Euphausiids | 2 | 0 | 2 | 4 | 1 | 0 | 1 | 3 | 1 | 0 | 1 | 2 | 2 | 0 | 3 | 1 |
| Decapod larvae | 4 | 0 | 1 | 3 | 1 | 0 | 2 | 2 | 2 | 0 | 1 | 1 | 5 | 0 | 1 | 0 |
| Insects | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 5 | 0 | 0 | 0 | 4 | 0 | 0 | 2 | 4 |
| Cladocera | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 5 | 0 | 0 | 1 | 3 | 0 | 0 | 2 | 4 |
| Chaetognaths | 0 | 0 | 2 | 6 | 0 | 0 | 0 | 5 | 0 | 0 | 2 | 2 | 0 | 0 | 1 | 5 |
| Salps | 0 | 0 | 1 | 7 | 0 | 0 | 1 | 4 | 0 | 0 | 0 | 4 | 0 | 0 | 1 | 5 |
| Larvaceans | 2 | 0 | 1 | 5 | 2 | 0 | 1 | 2 | 0 | 0 | 2 | 2 | 1 | 0 | 3 | 2 |
| Teleosts | 1 | 0 | 2 | 5 | 1 | 0 | 1 | 3 | 1 | 0 | 3 | 0 | 3 | 0 | 2 | 1 |
| Percent selection | 8.4 | 6.3 | 12.6 | 73.5 | 7.7 | 5.5 | 12.1 | 73.7 | 8.4 | 8.4 | 21.0 | 61.6 | 11.1 | 7.4 | 23.1 | 58.2 |

similar diets. Many seine sets caught only coho salmon, whereas catches of the more highly aggregated species often also contained coho salmon. In laboratory experiments, coho salmon smolts in seawater demonstrated agonistic behavior which, if occurring in the wild, would maintain discrete feeding territories and a dispersed population (Paszkowski and Olla, 1985).

Differences in diet, distribution, and size indicate that juvenile coho salmon have a distinct feeding ecology in comparison with these other, more planktivorous, juvenile salmon co-occurring in the southern Gulf of Alaska. In both our study and that of Brodeur and Pearcy (1990), fish were more important in the diets of juvenile coho salmon than in other species. During the second year of our study—when

**Table 10**

Principal prey of juvenile sockeye salmon in southeastern Alaska and northern British Columbia in 1983 and 1984 and in the Gulf of Alaska and Bering Sea in 1967 and 1968 (Hartt and Dell, 1986). Values are percent biomass of total diet. The number of fish sampled is shown in parantheses, followed by fork length ranges (mm).

| Prey | Pooled 1967–68 (996) 130–180 | Pooled 1983–84 (361) 100–300 | August 1983 (55) 130–249 | July 1984 (159) 100–209 | August 1984 (147) 110–300 |
|---|---|---|---|---|---|
| Copepods | 5.1 | 0.5 | 4.6 | 0.4 | 0.5 |
| Decapod larvae | — | 2.6 | 8.3 | 0.8 | 5.3 |
| Euphausiids | 42.0 | 4.3 | 39.0 | 3.4 | 3.8 |
| Amphipods | 1.6 | 3.7 | 30.7 | 2.0 | 5.1 |
| Pteropods | 6.2 | — | — | — | — |
| Larval fish | 30.8 | 87.2 | 16.7 | 92.0 | 83.1 |

teleost prey increased in all diets—pink, chum, and sockeye salmon readily switched from small zooplankton to larger teleost prey in response to an apparent increase of available larval fish prey. The ability of salmon species to maintain plasticity in their diets may be an adaptation to changing ocean conditions—one that may improve marine survival.

On the basis of our comparisons between the prey composition of juvenile salmonids and the taxa found in neuston and plankton tows, we conclude that these juveniles are selecting a limited subset of available prey. Although other factors besides feeding preferences (e.g. prey patchiness, gear selectivity, differential digestion rates of prey) could lead to low selectivity values, certain taxa do appear to be consumed in high proportions in relation to their abundance. Our results suggest that juvenile salmon are visual predators and select prey on the basis of prey size and visibility and not on local abundance. For example, relatively rare hyperiid amphipods were selected by most salmon, whereas slightly smaller but much more numerous copepods were ignored. As observed by Peterson et al. (1982), this prey selection may be due to the heavy pigmentation and unusual swimming motion of hyperiids in contrast to the light pigmentation and fast swimming motion of copepods.

Although the diets of both chum and coho salmon appear to be more similar to the neuston than the zooplankton catches, a reliance on neustonic fauna, as suggested by Brodeur (1989) for coho salmon off Washington and Oregon, is not conclusively demonstrated because of the small number of comparisons that we were able to make. More detailed field and laboratory studies are required to determine whether juvenile salmon show a reliance on certain prey or an inability to switch to alternate prey when preferred prey resources are depleted. Under these conditions, the availability of the right kinds of prey may have more important implications for the survival of juvenile salmon in coastal waters than the overall production of prey.

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# Interspecific comparisons of searobin (*Prionotus* spp.) movements, size structure, and abundance in the temperate western North Atlantic

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**Abstract.**—Northern searobins, *Prionotus carolinus*, and striped searobins, *P. evolans*, are commonly taken in bottom trawl, pound-net, and hook-and-line fisheries of the temperate, western North Atlantic. Seasonal movements, size structure, and interannual variations in population size of both species were examined with data from three fishery-independent trawl surveys. Geographic distributions of both species overlapped year-round, but on average, northern searobins were found in colder, deeper water than were striped searobins. Northern searobins were found north and east of Cape Cod during the warmest months and northeast of Hudson Canyon during the coldest months, whereas striped searobins were rarely found in these regions during these seasons. Furthermore, northern searobins moved north and nearshore earlier in spring and left these habitats earlier in autumn. Modal size of adult northern searobins was generally between 17 and 21 cm total length, about 5 cm shorter than that of adult striped searobins. Overall, northern searobins were collected more frequently and were more numerous than striped searobins. Because they were smaller and occurred in cooler waters, however, they were not dominant by weight in coastal habitats during autumn. During the past 25–30 years, the annual population size of both species has varied by an order of magnitude, fluctuating without any clear trend. Although seasonally abundant in coastal and continental shelf waters, searobins, because of their small size in relation to other species, are usually discarded and contribute little to landings from the mid-Atlantic states.

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Searobins (family Triglidae) are commonly taken in pound-net and bottom trawl fisheries along the United States east coast but are only occasionally sold as foodfish, lobster bait, or livestock feed (e.g. Goode, 1888; Smith, 1894a). Commercial landings of 100–200 metric tons annually were reported from the mid-Atlantic states during the 1880's (Collins, 1892), 1930's (Marshall, 1946), and 1950's (McHugh, 1977). Millions of searobins are also taken incidentally by hook-and-line recreational anglers (Table 1). Researchers have long recognized the potential for increasing U.S. landings by developing a searobin fishery (Smith, 1894b; Marshall, 1946; Merriman and Warfel, 1948; Perlmutter, 1959–60), but the market potential for searobins is limited by their relatively small size and a false perception that they are poisonous or difficult to handle (Johnson et al., 1987; Murray et al., 1987).

Two searobin species are common in the temperate, western North Atlantic: northern searobin, *Prionotus carolinus* (Linnaeus, 1771), and striped searobin, *P. evolans* (Linnaeus, 1766). They range from Canada to northern Florida (Bigelow and Schroeder, 1953; Gilmore, 1977; Scott and Scott, 1988; Russell et al., 1992) but are most common year-round on the continental shelf from Cape Cod to Cape Hatteras (Nichols and Breder, 1926; Hildebrand and Schroeder, 1928; Edwards et al., 1962). Life history information is provided in Marshall (1946), Wong (1968), McEachran and Davis (1970), Richards et al.

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(1979), Yuschak and Lund (1984), Yuschak (1985), Keirans et al. (1986), and McBride and Able (1994).

This study describes and compares the seasonal movements, size structure, and interannual variations in population size of northern and striped searobins in the Mid-Atlantic Bight. No previous study has synthesized searobin data over such a large geographic scale. The present and potential roles of searobins in fisheries of the temperate western North Atlantic are also discussed.

**Table 1**

Estimated numbers of searobins (all triglid species combined) caught by marine recreational anglers from 1979 to 1991 in the Mid-Atlantic, as well as in all subregions of the U.S. east coast combined: Gulf of Maine, Mid-Atlantic, South Atlantic, and Gulf of Mexico. Data prior to 1979 are not available.

| | Numbers (in millions) | | |
|---|---|---|---|
| Year | Mid-Atlantic | U.S. east coast | Source |
| 1979 | 3.548 | 5.145 | Holliday, 1984 |
| 1980 | 7.102 | 7.957 | Holliday, 1984 |
| 1981 | 1.624 | 2.613 | NMFS, 1985a |
| 1982 | 2.795 | 5.074 | NMFS, 1985a |
| 1983 | 8.750 | 10.058 | NMFS, 1985b |
| 1984 | 6.189 | 6.752 | NMFS, 1985b |
| 1985 | 3.562 | 4.361 | NMFS, 1986 |
| 1986 | 10.908 | 11.858 | NMFS, 1987 |
| 1987 | 4.824 | 5.071 | Essig et al., 1991 |
| 1988 | 5.182 | 5,899 | Essig et al., 1991 |
| 1989 | 2.631 | 2.947 | Essig et al., 1991 |
| 1990 | 4.896 | 5.518 | Van Voorhees, et al.,1992 |
| 1991 | 7.254 | 7.799 | Van Voorhees, et al.,1992 |
| Mean (per yr) | 5.328 | 6.235 | |
| Total | 69.265 | 81.052 | |

## Materials and methods

Data were derived from three fishery-independent bottom trawl surveys (Table 2). One survey, conducted by the National Marine Fisheries Service, covered the entire Mid-Atlantic Bight (i.e. the coastal region from Cape Cod to Cape Hatteras), as well as Georges Bank and the Gulf of Maine (Fig. 1). Data from two regional surveys were also examined: one at the northern extent of the Mid-Atlantic Bight near Cape Cod, the other within a central portion of the Mid-Atlantic Bight offshore of New Jersey. In each survey a stratified, random design was used for allocating trawl tows. Strata were established by depth categories and other physiographic boundaries. Numbers of tows within each stratum were proportional to stratum area; within each stratum, tow locations were randomly assigned. Fishes were counted and weighed; measurements were reported to the nearest centimeter total length (TL). In preliminary analyses geographic and length-distribution data were plotted for all years available, but herein only data from selected cruises (1991–92) are graphed. Preliminary calculations of abundance showed that

**Table 2**

Sources and details of trawl data examined for this study. Data for the period 1982–91 were the focus of most analyses. Data regarding distribution and size structure for the years 1991–92 were plotted (Figs. 2–7) as representative years.

| Data source | Trawl headrope (m) (mesh [mm]) | Tow time (min) | Season | Month | Sampling depth (m) | Years |
|---|---|---|---|---|---|---|
| Throughout the Mid-Atlantic Bight | | | | | | |
| NEFSC, NMFS[1] | 18.3–19.8 | 30 | Spring | Mar–May | 9–366 | 1968–95 |
| | (12.7) | 30 | Summer | Jun–Aug | 9–200 | 1963–65,69,77–81 |
| | | 30 | Autumn | Sep–Nov | 9–366 | 1963–95 |
| | | 30 | Winter | Dec–Feb | 9–200 | 1964–6,78,81,91–2 |
| Offshore of Massachusetts and New Jersey | | | | | | |
| MDMF[2] | 11.9 | 20 | Spring | May | 9–55 | 1978–95 |
| | (12.7) | 20 | Autumn | Sep | 9–55 | 1978–95 |
| NJBMF[3] | 24.4 | 20[4] | 5–6/year | Jan–Dec | 6–27 | 1988–92 |
| | (6.3) | | | | | |

[1] Northeast Fisheries Science Center, National Marine Fisheries Service.
[2] Massachusetts Division of Marine Fisheries.
[3] New Jersey Bureau of Marine Fisheries.
[4] Tows in 1988 were for 30 minutes.

fish numbers and weight had similar trends (McBride, 1994); therefore only weight indices are reported here. Some descriptive statistics were also based on subsets of data (1982–91), as noted below. Statistical significance was evaluated at $P<0.05$. The above comments pertain to all data examined, and comments below outline procedures specific to each sampling program.

## NMFS sampling

Survey data from the National Marine Fisheries Service (NMFS), Northeast Fisheries Science Center (NEFSC), were examined. The survey area was divided into 76 strata from Cape Fear, North Carolina, to Cape Sable, Canada, in waters 9–366 m deep. Spring and autumn cruises sampled a total of about 350 stations during a 6–8 week period, whereas summer and winter cruises sampled about half as many stations (Table 2). The primary gear used was a no. 36 Yankee trawl. In spring, summer, and autumn cruises a roller-rigged footrope was used; however, in winter cruises a cookie sweep and ground cable designed to target flatfish were used. Latitude, longitude, and depth were recorded at the start of each tow. Bottom temperature was usually recorded by using an XBT cast or a CTD probe. See Grosslein (1969, 1976), Azarovitz (1981), and Despres-Patanjo et al. (1988) for further sampling details.

Exploratory data analyses considered all 76 strata, but interannual comparisons of abundance considered only latitudinal strata within the Mid-Atlantic Bight because both species were uncommon or absent in the Gulf of Maine and on Georges Bank and because sampling south of Cape Hatteras was not broad in coverage or consistent between years. Because the distribution of both species varied seasonally, largely as an onshore–offshore pattern, different depth strata sets were used for calculating spring and autumn abundances; the autumn strata selected were generally <27 m and the spring strata were >27 m deep. Because the purpose here was to compare interspecific abundances, the final selection of strata included the broadest possible latitudinal range within the Mid-Atlantic Bight where both species occurred.

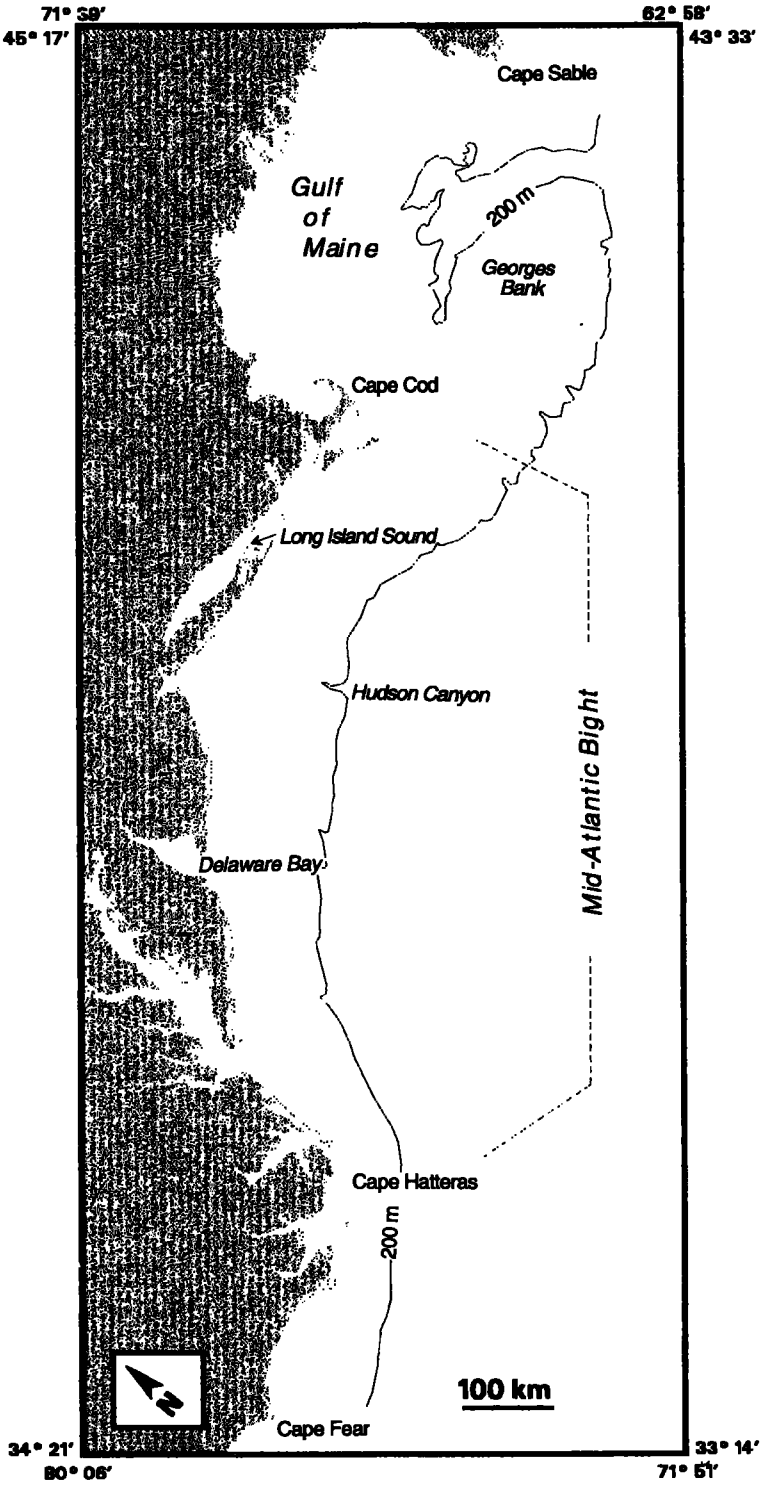


**Figure 1**

Study area of the U.S. east coast, with some landmarks identified in the text (additional landmarks are depicted in Fig. 3). The Mid-Atlantic Bight is defined as the coastal region between Cape Cod and Cape Hatteras. Sampling strata for the Mid-Atlantic Bight survey (NEFSC, NMFS, Table 2) extended in total from Cape Fear to Cape Sable. Sampling regions for the Massachusetts and New Jersey surveys (Mass. Div. Mar. Fisheries and New Jersey Bureau of Mar. Fisheries; Table 2) are depicted in Figures 3 and 4.

The autumn strata selected were NMFS inshore strata identification numbers 01–61, and the spring strata were NMFS offshore strata 01–12, 25, and 61–72. The summer and winter seasons were not sampled consistently enough to be included in these comparisons of abundance. Abundance of each species was estimated as a stratified mean weight per tow with the methods of Finney (1941) and Pennington (1983). These values are log-transformed ($\ln[x+1]$) means, weighted by stratum area.

### Regional sampling

The Massachusetts Division of Marine Fisheries (MDMF) sampled 23 strata along the Massachusetts shoreline (<55 m). Approximately 80–90 stations were sampled in May and again in September (Table 2) with a 3/4 North Atlantic type-2 seam trawl at random locations, except where precluded by untowable bottom and extensive fixed commercial gear (Howe, 1989). Abundance indices were calculated in the same manner as those calculated for the sampling by NMFS (see above). Strata were selected to encompass an area where both species occurred in each season (MDMF strata no. 10–19 for spring; 11–12 for autumn).

The New Jersey Bureau of Marine Fisheries (NJBMF) sampled 15 strata along the New Jersey coast (<27 m). Cruises occurred every 6–10 weeks during 1988–92 (Table 2). Each cruise sampled 25–39 stations during a 1–4 week period using a 3-in-1 trawl at random locations (Byrne, 1989). Mean weight per tow ($\ln[x+1]$) was calculated without weighting for strata areas, and tows from all strata were used because both species occurred throughout the NJBMF sampling area during most of the year.

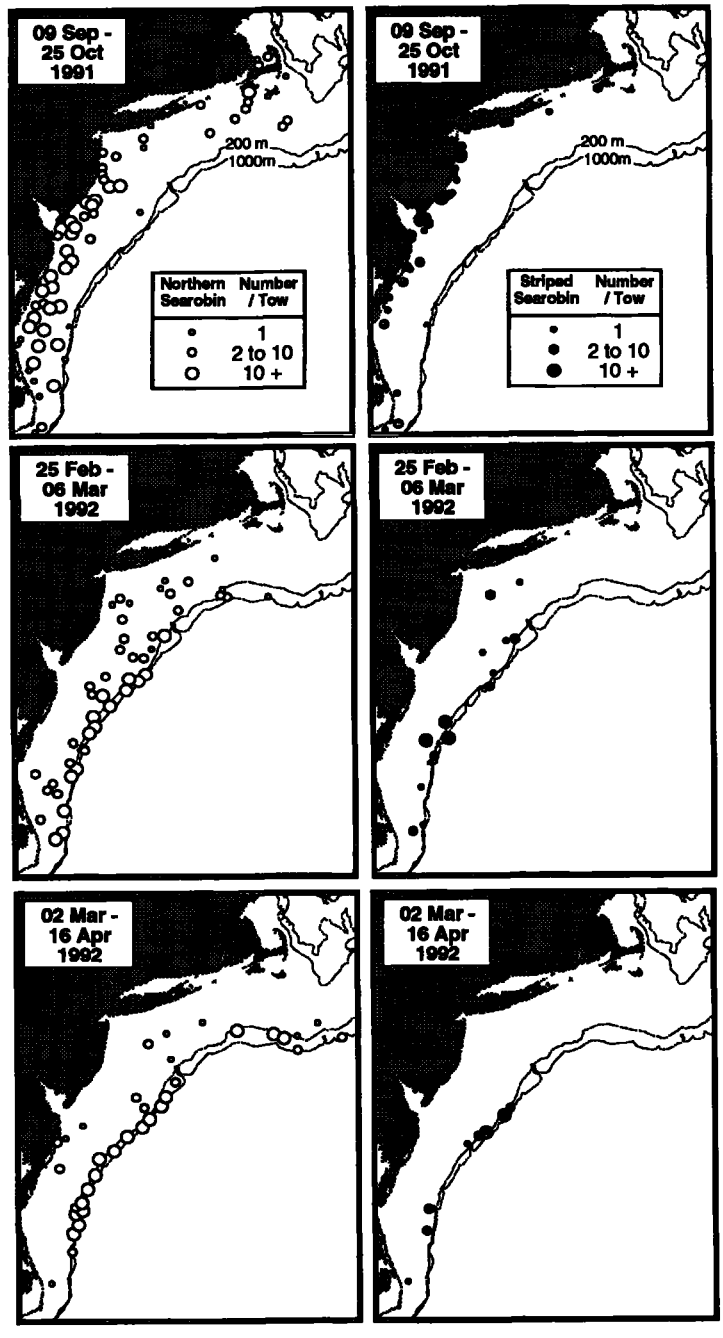


**Figure 2**

Geographic distribution of northern searobins (open symbols, left column) and striped searobins (filled symbols, right column) in the Mid-Atlantic Bight during autumn, 1991 (top), winter, 1992 (middle), and spring, 1992 (bottom) based on Northeast Fish. Sci. Center, NMFS, resource surveys (Table 2). Much of the Gulf of Maine and Georges Bank are not depicted here because sampling there collected only a single northern searobin (at a station immediately north of Cape Ann; see Fig. 3 for landmark reference).

## Results and discussion

### Movements

Northern searobins, but not striped searobins, moved seasonally between the Mid-Atlantic Bight and the Gulf of Maine, and they used habitats on Georges Bank (Figs. 2 and 3). Striped searobins occurred rarely north or east of Cape Cod in any year, but northern searobins, although not common there, oc-

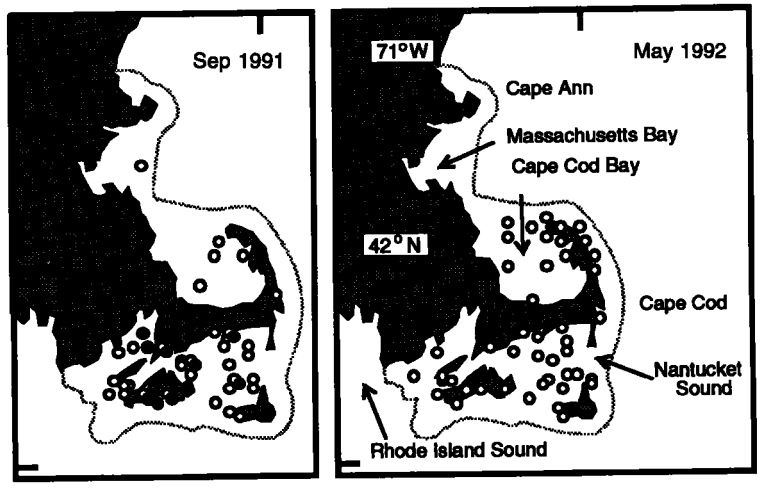


**Figure 3**

Geographic distribution of northern searobins (open symbols) and striped searobins (filled symbols) during two consecutive sampling seasons for the Massachusetts coastal survey (Table 2). The dotted line represents the offshore limit of sampling (55 m).

curred annually on parts of Georges Bank and in the southern portion of the Gulf of Maine during summer and autumn. In general, both species were broadly distributed within the central Mid-Atlantic Bight but moved southward during winter and spring (Figs. 2 and 4). Striped searobins moved well south and west of Hudson Canyon, which appears as an approximate northern limit for striped searobins during the overwintering season, whereas northern searobins had a broader latitudinal distribution in the Mid-Atlantic Bight while overwintering (see also McBride and Able, 1994). These data suggest that by spring large striped searobins moved either farther offshore into continental slope waters (>200 m) or migrated south of the zoogeographic boundary represented by Cape Hatteras (i.e. between the Mid-Atlantic and the South Atlantic Bight) because sizes > 25 cm TL are uncommon during spring cruises (Fig. 5). We cannot prove this hypothesis, however, because these southern and offshore regions were not well sampled during the overwintering season (see Table 2 for sampling area limits).

Both searobin species migrated seasonally in an onshore–offshore direction as well as in a north–south direction (Fig. 2). Northern searobins were, however, consistently found in significantly deeper waters than were striped searobins during both spring (78.3 m ± 5.27 vs. 60.4 m ± 9.30; mean depth ± 95% confidence limits [CL]) and autumn (30.7 m ± 1.73 vs. 20.0 m ± 1.44) during 1982–91. Northern searobins were also found in significantly colder bottom temperatures than were striped searobins in spring (9.2 ± 0.3°C vs. 11.8 ± 0.56°C; mean ± 95% CL) and autumn (17.6 ± 0.40°C vs. 19.6 ± 0.40°C), although both species were collected in a wide range of temperatures (4–28°C) during 1982–91. These results support McBride and Able's (1994) postulation that temperature is the principal factor producing distinctive geographic distributions for each species. Other western North Atlantic searobins (*Prionotus* and *Bellator* species) that are distributed in subtropical and tropical waters reside within species-specific depth regions but show little tendency to migrate seasonally (Lewis and Yerger, 1976; Ross, 1977; Floyd, 1980; Hoff, 1992). South of Cape Hatteras, where temperatures fluctuate less between seasons than in the Mid-Atlantic Bight, even northern searobins show little tendency to migrate seasonally (Floyd, 1980).

## Size structure

Modal size of northern searobins was consistent between seasons (17–21 cm TL), but striped searobins were both larger and more variable in size (18–28 cm TL; Fig. 5). The larger size of *P. evolans* is largely accounted for by its faster growth rate and greater maximum age (Richards et al., 1979). An earlier analysis of NMFS survey data has reported northern searobins as large as 34 cm and striped searobins as large as 41 cm (Wilk et al., 1978). The maxima observed in our study were 5–7 cm larger, but these

are most likely the result of much larger sample sizes (total for combined species was 1,314 fish measured in 1974–75 [Wilk et al., 1978] vs. 69,072 in 1982–91[our study]). Briggs (1977) reported a single record of a striped searobin measuring 485 mm TL, which equaled the size of our largest striped searobin. Floyd (1980) reported the largest northern searobin as 26 cm TL ($n$=1795) and the largest striped searobin as 35 cm TL ($n$=47) based on trawl collections south of Cape Hatteras. These findings support Ginsburg's (1950) observation that searobin size increases with higher latitudes.

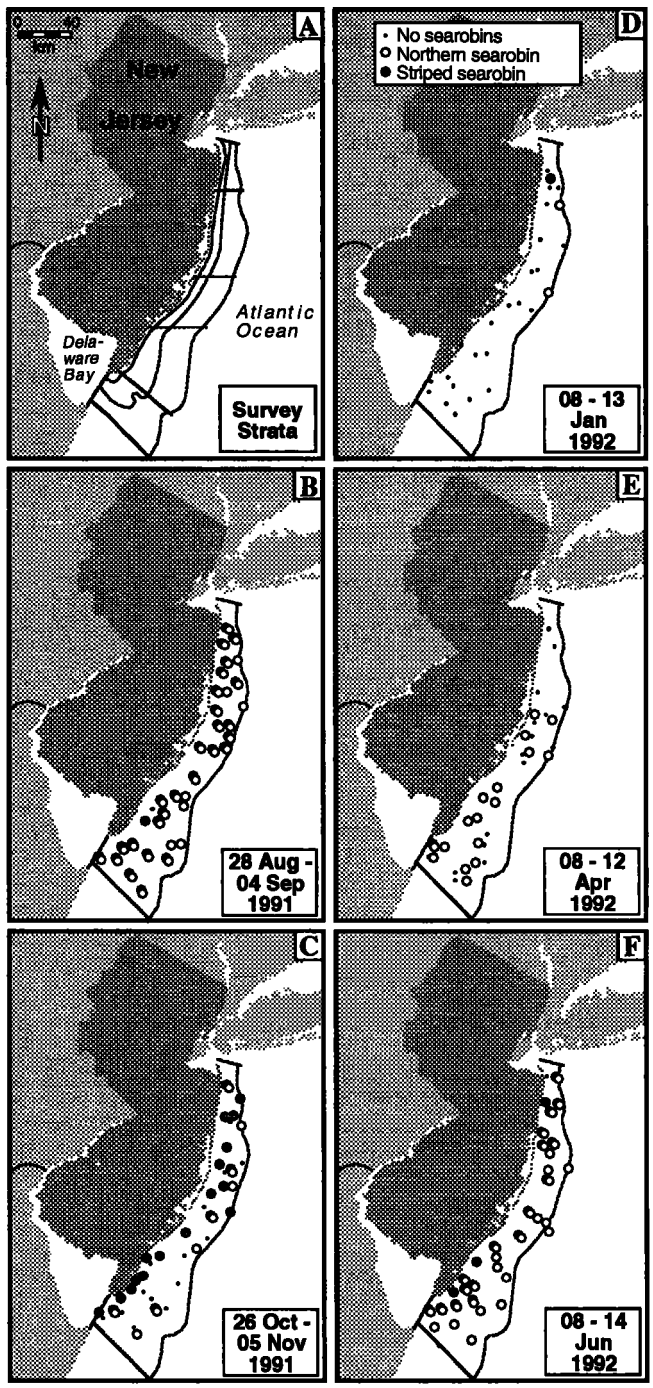


**Figure 4**

Seasonal distributions of northern searobins (open symbols) and striped searobins (filled symbols) during five consecutive cruises for the New Jersey coastal survey (Table 2).

Young-of-the-year (YOY) of both species were evident in all surveys (Figs. 5–7), particularly during autumn months, when a size of 15 cm TL was used to separate YOY from older year classes (Richards et al., 1979; McBride and Able, 1994). Collections from Massachusett waters did not indicate overwintering by YOY searobins near Cape Cod, a finding similar to that reported by Richards et al. (1979). In New Jersey nearshore waters, YOY northern searobins were evident in April, suggesting that they had migrated back inshore in this region much sooner than had been observed farther north.

## Abundance

Northern searobins were more abundant than striped searobins by numbers and frequency of occurrence. A total of 66,064 northern searobins were collected in 1,125 tows, whereas only 3,008 striped searobins were collected in 366 tows out of a total of 7,369 NMFS tows during spring and autumn, 1982–91. Both species were caught together in 202 of these 7,369 tows. In Massachusetts waters, northern searobins were also more numerous than striped searobins in spring (88,565 vs. 75 fish) and autumn (10,966 vs. 374 fish) during 1982–91. And in New Jersey waters, northern searobins were more numerous than striped searobins (35,471 vs. 5,258 fish) in 700 tows during 1989–92. Northern searobin aggregate weight was not, however, always heavier in coastal waters during autumn (Figs. 8 and 9) because striped searobins weigh more on average and because striped searobins occupy inshore habitats more frequently in the warmest season. In proximity to New Jersey, northern searobins appear to migrate inshore earlier, peak in abundance earlier, and move offshore earlier than striped searobins, a behavior consistent with their postulated temperature preference.

The Mid-Atlantic Bight (NMFS) time series of stratified mean weight per tow was

highly variable (for northern searobins, CV=48 in spring and 49 in autumn; for striped searobins, CV= 68 in spring and 101 in autumn; Fig. 8) but showed no clear trend over time. There was one notable period of decline for northern searobins during spring surveys throughout the 1970's, but there was also a modest rebound in abundance during the 1980's. The low values in the early 1990's were similar to values measured in the late 1960's. The abundance of northern searobins during autumn cruises suggested no trend but was punctuated with sporadic peaks. Striped searobins also appeared to be more abundant during the 1970's than in the 1960's or 1990's, according to spring indices. The autumn time series for striped searobins declined overall, until the last year (1995), which showed a sudden increase. Abundance was compared between species to establish if each species' population size followed similar seasonal and interannual trends. Correlation analyses detected a significant relation between northern and striped searobin annual indices measured in the spring survey (Spearman rank correlation, $r_s$=0.47, $P$=0.01, $n$=28), but the correlation between species abundance in the autumn surveys was not significant ($r_s$=0.006, $P$=0.97, $n$=24). The spring and autumn indices for a given year were not significantly correlated for northern searobins ($r_s$=0.14, $P$=0.51, $n$=24) but were significantly correlated for striped searobins ($r_s$=0.65, $P$=0.0006, $n$=24). These latter results suggested that the selected spring and autumn strata measured similar trends of abundance for striped searobins but not for northern searobins.

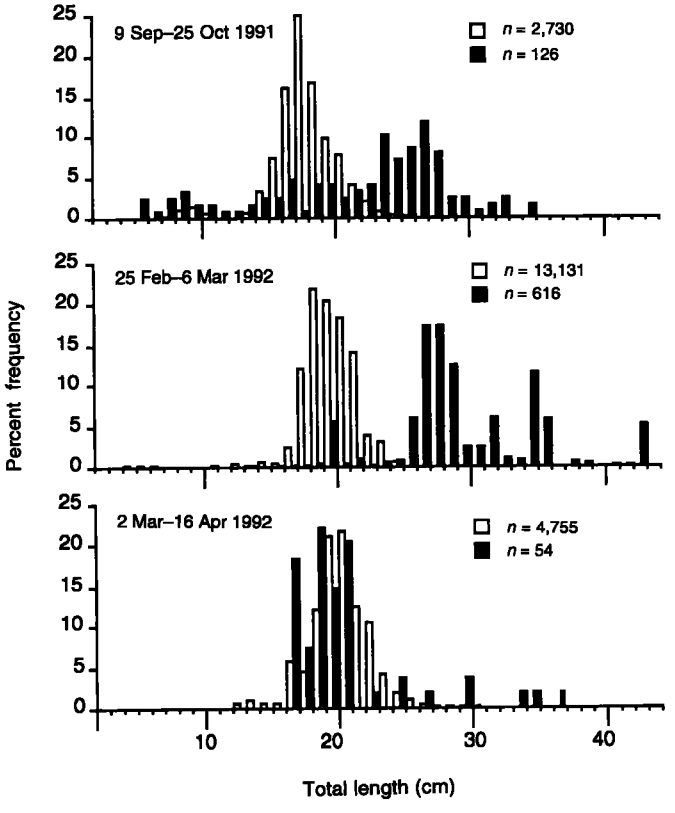


**Figure 5**

Length-frequency distributions of northern searobins (open bars) and striped searobins (filled bars) in the Mid-Atlantic Bight during autumn, winter, and spring, 1991–2, based on the Northeast Fish. Sci. Center, Natl. Mar. Fish. Serv. resource surveys (Table 2). Sampling periods are the same as those shown in Figure 2. $n$=number of fish.

Earlier estimates of searobin population size also noted considerable yearly variations in abundance. Clark and Brown (1977) reported a dramatic 97% decline in abundance (by weight) of searobins in the southern Mid-Atlantic region (also depicted in Grosslein [1976]) based on the same database during the period 1967–74. But they also reported a 143% increase in abundance of searobins in the southern New England region. It is difficult to compare their results with our Figure 8 because they grouped northern and striped searobins together. They also used autumn collections from offshore strata sets, but our autecological analyses revealed these strata as only marginally appropriate, at least for striped searobins that are still inshore during autumn. Their analysis of abundance reviewed years during which fairly rapid change was occurring for both searobins and the groundfish assemblage in general, but our analyses demonstrate that searobin abundance has fluctuated up and down since the early 1970's.

Northern searobin annual abundance in the Massachusetts coastal survey has also shown large long-term variations (Fig. 8). Modest increases for northern searobin abundance in the early 1990's barely offset dramatic declines during the 1980's. In contrast, there was no trend in abundance of striped searobins during this 20-year period. These indices could be biased with respect to interannual variations in coastal temperatures because Murawski (1993) demonstrated that the latitudinal range of northern searobins varied between years with respect to sea-temperature anomalies. Thus, one might expect that searobins are more abundant in coastal Massachusetts waters during warmer years. Such does not appear to be the case, however, because

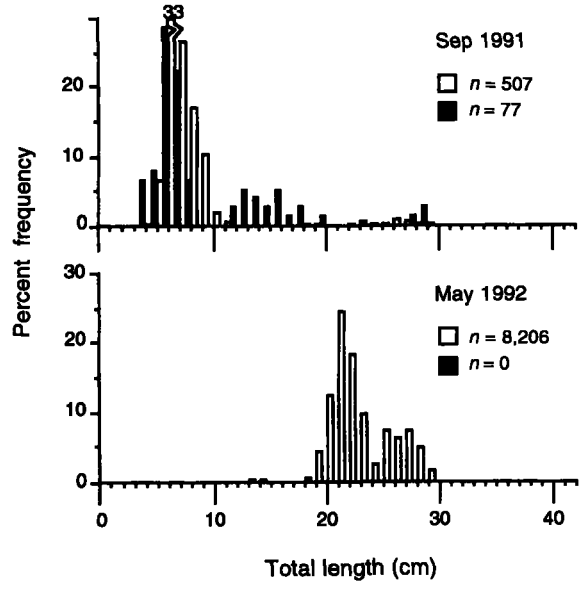


**Figure 6**

Length-frequency distributions of northern searobins (open bars) and striped searobins (filled bars) for the Massachusetts coastal survey. Sampling periods are the same as those shown in Figure 3. *n*=number of fish.

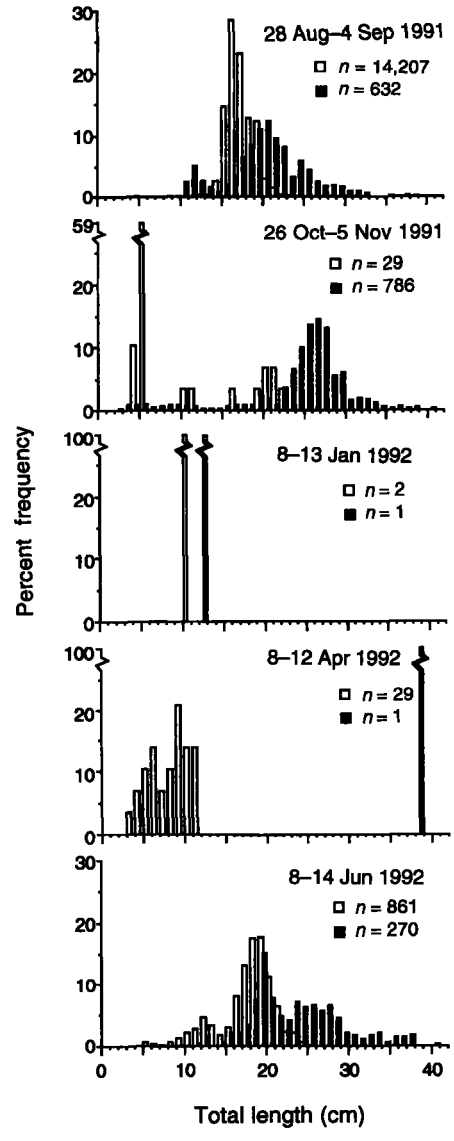


**Figure 7**

Length-frequency distributions of northern searobins (open bars) and striped searobins (filled bars) during five consecutive cruises for the New Jersey coastal survey (Table 2). Sampling periods are the same as those shown in Figure 4. *n*=number of fish.

Murawski reported that after an anomalously warm period in the 1970's (when northern searobin abundance did increase) temperatures in the 1980's fluctuated without a trend (but northern searobin abundance declined dramatically; see Fig. 8).

The indices of stratified mean weight per tow between the Mid-Atlantic Bight (NMFS) and the Massachusetts (MDMF) surveys were compared to examine how robust these measures of abundance were. Correlation analyses revealed a significant relation between northern searobin abundance in spring ($r_s$=0.51, $P$=0.032, $n$=18) between the two surveys, but autumn abundances in similar years were negatively correlated between the two surveys ($r_s$=-0.60; $P$=0.008, $n$=18). There was a significant relation between these surveys for striped searobin abundance in spring ($r_s$=0.51, $P$=0.029, $n$=18) but not for autumn ($r_s$=0.077, $P$=0.76, $n$=18). These significant, positive relations between the two surveys support our use of spring but not autumn indices for examining northern and striped searobin population trends.

## Implications for fishery ecology

Northern and striped searobins belong to a "warm-temperate" group (Musick et al., 1989), an assemblage that migrates onshore and north as temperatures increase, offshore and south as temperatures decline. Our descriptive analysis supports this characterization of both species but reveals interspecific differences in the timing and extent of seasonal movements, as well as in size and abundance. Selection of sampling strata for calculating abundance indices was constrained by our goal to compare the ecology of both species. Nevertheless, indices from spring cruises in the Mid-Atlantic Bight and along the Massachusetts coast were significantly and positively

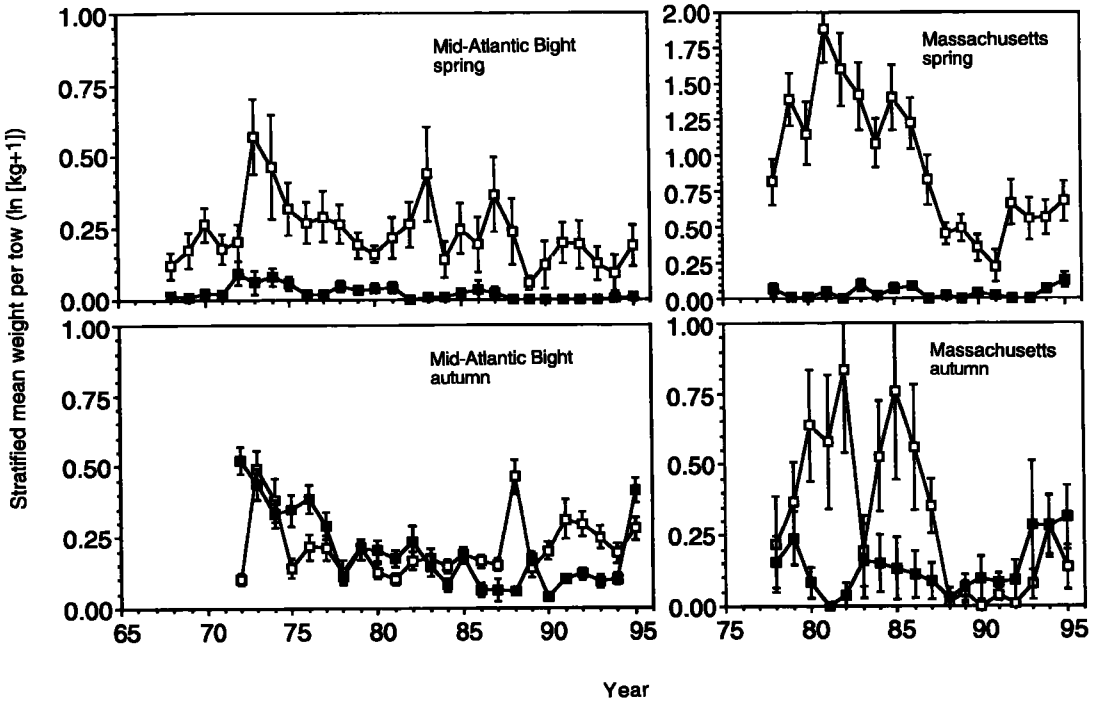


**Figure 8**

Annual biomass indices for northern searobins (open symbols) and striped searobins (filled symbols). Mid-Atlantic Bight indices (left) are based on sampling by Northeast Fish. Sci. Center, NMFS, resource surveys (Table 2). Massachusetts indices (right) are based on the Massachusetts (Mass. Div. Mar. Fisheries [MDMF]) coastal surveys (note the scale of the ordinate is doubled for MDMF Spring). All values are log-transformed and plotted with ±1 standard error bar. See text for details of strata selection and statistical calculations (e.g. spring and autumn strata are different).

correlated, so that they were especially useful in evaluating population trends. On the other hand, the inshore strata selected for autumn cruises in the Mid-Atlantic Bight were adequate for sampling striped searobins but were too shallow for northern searobins because the latter occupied a mean depth of 31 m during that season.

Searobins are not important fishery species in the United States but are components of bycatch in commercial and sport fisheries; their population sizes could be affected by fishing or other factors. However, their population size varied without a specific directional trend during three decades. The long-term trend of annual biomass indices for searobins is similar to other demersal finfish such as white hake (*Urophycis*

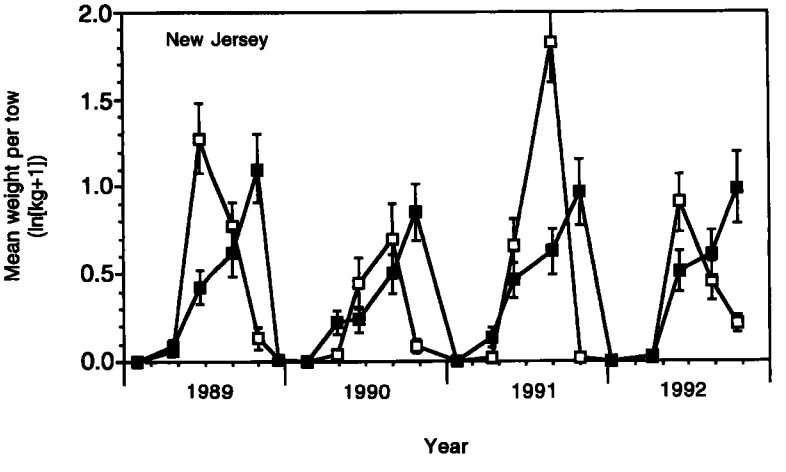


**Figure 9**

Seasonal abundance of northern searobins (open symbols) and striped searobins (filled symbols) based on all cruises (1989–92) for the New Jersey coastal survey (Table 2). Abundance is depicted as mean weight (± 1 standard error) of all tows per cruise. Cruises typically lasted one week, and a mean date value was used to plot each cruise.

*tenuis*), cusk (*Brosme brosme*), scup (*Stenotomus chrysops*), and ocean pout (*Macrozoarces americanus*) (U.S. Dep. Commerce, 1993). In contrast, population declines have been characteristic of traditional groundfish and flounder species, and aggregate biomass of principal pelagic species, skates, and spiny dogfish have increased in the western North Atlantic (U.S. Dep. Commerce, 1993).

Fishery landings, value, and catch rates for mid-Atlantic states have all declined over the past several decades (McHugh and Conover, 1986), and underused species such as searobins have limited potential to counter these trends. Our survey results, for New Jersey in particular, show that searobins are seasonally abundant in areas amenable to inshore commercial and recreational fisheries during summer and autumn. Trawlers can also find large aggregations offshore during winter and spring. Searobins are also a large proportion of pound-net landings during summer, although this fishing method is now reduced in comparison with historical levels (McHugh and Conover, 1986). Striped searobins may be a more marketable species because they are larger on average. Efforts to expand the marketability of searobins, such as has occurred recently by selling them live in restaurants (Lynch[1]), may lead to increased total landings and a more diverse fishery resource for the mid-Atlantic region.

## Acknowledgments

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# Abundance, growth, and mortality of young-of-the-year pinfish, *Lagodon rhomboides*, in three estuaries along the gulf coast of Florida

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**Abstract.**—Fixed-station and random-sampling data from 1989–94 were used to examine spatial and temporal patterns in abundance and size structure of young-of-the-year (YOY) pinfish, *Lagodon rhomboides*, in three Florida estuaries. Young-of-the-year pinfish first appeared at shallow-water (<1.4 m) seine stations in November in Choctawhatchee Bay (Florida Panhandle), and in December in Tampa Bay and Charlotte Harbor, both along the southwest Florida peninsula. Pinfish were caught at deepwater (>1.6 m) trawl stations within one month after their initial appearance at shallow-water (<1.4 m) sites in Choctawhatchee and Tampa bays. However, YOY were absent in the deep water of Charlotte Harbor until 1–3 months after their first appearance in shallow water. Most YOY pinfish were caught in waters <3.5 m. Young-of-the-year pinfish in shallow-water areas were associated with bottom vegetation, mostly seagrasses, in all bays. Annual variation in YOY abundance was correlated with variations in adult abundance in Tampa Bay and with temperature in Charlotte Harbor. Instantaneous growth rates were rapid (0.10 to 0.26/month) and were similar to published rates for other Florida and gulf coast populations. Similar rates of total instantaneous mortality (0.021 to 0.023/day) were estimated for all bay populations.

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Young-of-the-year pinfish, *Lagodon rhomboides*, play important ecological roles in the northeastern Gulf of Mexico as prey for fish (Carr and Adams, 1973; Seaman and Collins, 1983) and as predators on a range of invertebrates, often to a degree where entire assemblages of macrobenthic fauna are affected (Young et al., 1976; Young and Young, 1977; Nelson, 1978). In addition, YOY pinfish are an important link between primary and secondary production because they consume seagrasses (Stoner, 1982; Weinstein et al., 1982; Montgomery and Targett, 1992).

Despite the ecological importance of pinfish, their population dynamics have been inadequately examined. It is unknown if seasonal changes in abundance or movements occur throughout entire estuaries, if growth rates are similar among populations, or if abundances fluctuate annually because past studies have had limited spatial coverage (usually 1–4 seagrass sites were sampled in waters <2 m) and short sampling durations (<2 yr)(Reid, 1954; Caldwell, 1957; Hellier, 1962; Hoese and Jones, 1963; Cameron, 1969; Hansen, 1970; Stoner, 1983). In addition, factors that may influence year-class strength have not been examined, and mortality rates have not been estimated.

In this study, I use two to six years of data to document seasonal changes in abundance, distribution, and movements within shallow- and deepwater areas to identify factors that may influence spatial and annual abundance and to estimate and compare growth and mortality rates among three estuarine populations of YOY pinfish along the gulf coast of Florida, USA.

## Methods

Young-of-the-year pinfish were studied in 1) Choctawhatchee Bay and Santa Rosa Sound (surface area: ca. 450 $km^2$), located in the western Florida Panhandle, 2) Tampa Bay (ca. 886 $km^2$), and 3) Charlotte Harbor (ca. 575 $km^2$), the latter two located on the gulf side of the Florida peninsula (Fig. 1). All three bay systems are characterized by average depths of <5 m, salinities of 0–36 ppt, freshwater inflow from rivers, and expanses of bottom vegetation, primarily seagrasses (*Halodule wrightii* and *Thalassia testudinum*), in shallow areas. Seasonal mean water temperatures range from 10 to 29°C in Choctawhatchee Bay and Santa Rosa

Sound, from 15 to 30°C in Tampa Bay, and from 18 to 32°C in Charlotte Harbor.

Pinfish were sampled monthly from 1989 to 1994 at fixed seine and trawl stations. Fixed stations were approximately evenly distributed throughout shallow- and deepwater areas and included sites in major rivers in Tampa Bay and Charlotte Harbor. Monthly sampling began in 1992 in Choctawhatchee Bay, in 1989 in Tampa Bay, and in 1991 in Charlotte Harbor. Samples were collected with a 21.3-m × 1.8-m, 3.2-mm stretched-mesh seine, or a 6.1-m, 38-mm stretched-mesh otter trawl containing a 3.2-mm stretched-mesh codend liner. At beach stations, seines were set adjacent to the shoreline and hauled onshore; at offshore stations (<1.4 m), seines were set in open-water habitats away from the shoreline and retrieved offshore. In rivers, seines were set from the shoreline in a semicircular pattern from a boat. In deep water (>1.6 m), trawls were towed 1 knot for 5 min at river sites and for 10 min at bay sites. Three hauls or tows were made at each fixed station during daylight hours. Sampling occurred during the first two weeks of each month.

Pinfish were also sampled in spring (March to June) at randomly selected sites to provide more accurate estimates of YOY abundance. To coordinate sampling logistics, each bay was subdivided into 5–6 arbitrarily lettered, permanent zones (bay: zones A–E; rivers: zone F). All bay zones encompassed about equal area. Within each zone, 1' latitude × 1' longitude microgrids, representing the sites to be sampled, were randomly selected within randomly selected 1° latitude × 1° longitude grids. Sampling entailed randomly selecting a zone and then sequentially sampling all sites within each zone. At each site, three hauls were made with the same gears and deployment techniques used at fixed stations. Random sampling began in Choctawhatchee Bay in 1993 and in Tampa Bay and Charlotte Harbor in 1989 and occurred over eight, twelve, and ten weeks, respectively.

For all hauls, total numbers of pinfishes were counted, standard lengths were measured (±1 mm) for 20 randomly selected individuals per sample, and all fish were released. When large numbers of individuals (>1,000) were captured, the total number was estimated by fractional expansion of subsampled portions of the total catch split with a modified Motoda splitter (Motoda, 1959). Salinity (ppt), temperature (°C), depth (m), and bottom types were also recorded at all sites. Dominant vegetation types were recorded at seine sites only.

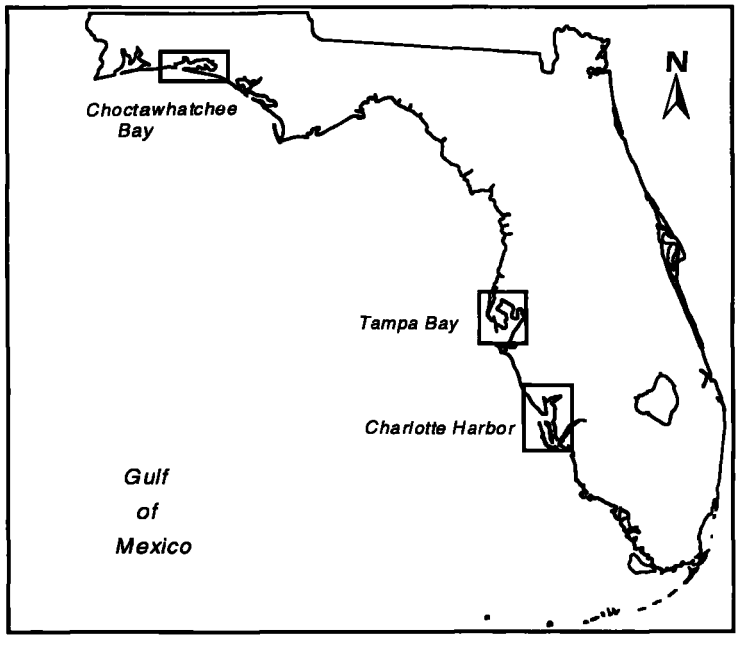


**Figure 1**

Map of Florida showing the locations of Choctawhatchee Bay, Tampa Bay, and Charlotte Harbor.

## Seasonal changes in YOY abundance and size structure

To examine seasonal changes in YOY abundance in shallow- and deepwater areas, comparable monthly mean number of individuals per 100 $m^2$ were calculated from fixed station data by year. I separated YOY data used in all analyses from data on older individuals by using maximum size limits selected from monthly length-frequency plots. Monthly length frequencies based on proportions of fish found in each length class were combined over years to describe within-year trends rather than year-to-year variability. Length maximum size limits used for Choctawhatchee Bay data were in agreement with the maximum lengths of scale-aged YOY pinfish from Pensacola Bay (Hansen, 1970).

## Depth distribution

To determine whether YOY were restricted to depth ranges during the period surrounding peak abundance, the cumulative frequency distributions of trawl and YOY pinfish depth occurrences were compared by using the Kolmogorov-Smirnov test (Perry and Smith, 1994). The cumulative frequency distributions for YOY pinfish were constructed by weighting depth at each random site by the number of YOY pinfish captured at that site. Only spring data from the first

trawl made at each random site were used to ensure independence of observations. Data from 1989–94 were combined to examine within-year trends rather than year-to-year variability.

### Factors influencing spatial YOY abundance

I examined variation in YOY pinfish abundance in shallow-water areas for year, deployment technique, month, zone, sediment type (mud or sand), absence or presence of bottom vegetation (mostly seagrasses), temperature, and salinity effects by bay. Spring catch data (transformed by using $\ln(x+1)$ prior to analysis) from the first seine haul at each randomly selected site were analyzed with general linear models (GLM; Hilborn and Walters, 1992) and PROC GLM (SAS Institute, 1988). Year, month, deployment technique, zone, sediment type, and bottom vegetation were treated as main effects, and temperature and salinity (transformed by using $\ln(x+1)$ prior to analysis) as covariates. All first-order interactions of the main effects were also tested. Any variable or first order interaction not significant at $\alpha = 0.05$ with type-III (partial) sum of squares was dropped from the initial GLM model and the analysis was repeated. In addition, least squares means and their 95% confidence intervals (Searle et al., 1980; SAS Institute, 1988) from the GLM's were back-transformed (Sokal and Rohlf, 1981) to examine significant abundance and main effect relationships.

Initial analyses revealed that the only significant first-order interactions were related to the random selection of zones for sampling. Because these interactions were not considered relevant to this study, they were absorbed in the error term, and the main effects and covariates were retested.

### Factors influencing YOY annual abundance

To determine if annual variations in YOY abundance were correlated with variations in temperature, I compared annual relative abundance indices (least squares means for the effect of year) to monthly means of sea-surface temperature before and during the first appearance of YOY pinfish, using Pearson product moment correlation (Sokal and Rohlf, 1981; Tyler, 1992). Temperature data were obtained from the National Oceanic and Atmospheric Administration's (NOAA) oceanographic monthly summary series.

I also used Pearson product moment correlation to determine if annual variations in YOY relative abundance were correlated with variations in adult abundance. Adult (>80 mm SL) pinfish abundance indices were derived from data collected in the Marine Recreational Fisheries Statistics Survey (MRFSS on Florida's west coast in 1988–93)(U.S. Dep. Commer., 1990; 1992). The GLM approach was used only to derive annual least-squares mean catch-per-intercept estimates (relative abundance) by adjusting the total number of fish caught per intercept for the classification variables of two-month sampling wave, fishing mode (party or charter boat, private or rental boat, or shore-based fishing boat), area fished, counties where interviews were conducted, and for the covariates of number of anglers per intercept and hours fished by anglers. All variables were significant contributors to the overall variation in catch rates in Tampa Bay (model: $F_{[28,3853]}=11.55, P<0.001$, $r^2=0.08$), but only year, sampling wave, county, and hours fished by anglers were significant for Charlotte Harbor (Model: $F_{[20,1060]}=5.74, P<0.001, r^2=0.10$).

### Growth

I examined annual growth of YOY by estimating instantaneous growth rates ($G$) using mean lengths for each bay and year. Growth was estimated with the following model:

$$\ln L_t = \ln L_0 + G \times t,$$

where $G$ = the instantaneous growth rate (per month);
$L_t$ = monthly mean length (mm);
$L_0$ = the theoretical length at which pinfishes recruit to each bay; and
$t$ = time in months (Ricker, 1975; DeAngelis et al., 1980).

### Mortality

Daily instantaneous total mortality rates were estimated for each bay population of pinfish by means of the relationship

$$Z = \frac{-\ln\left(\frac{N_{t+1}}{N_t}\right)}{30},$$

where $Z$ = the daily instantaneous total mortality; and
$N$ = the index of relative abundance at months $t$ and $t+1$ (Ricker, 1975).

Monthly indices of relative abundance from fixed seine stations were used in the equation. Although immigration and emigration in the shallow-water areas can bias the rate of decline in abundance used

to estimate mortality, I used data only from months over which these processes appeared low.

## Results

### Seasonal changes in YOY abundance and size structure

Young-of-the-year pinfish appeared first as post-larvae (9–12 mm) at shallow-water fixed seine stations during early November in Choctawhatchee Bay and early December in Tampa Bay and Charlotte Harbor, one to two months before mean temperatures were lowest (Fig. 2). In Choctawhatchee Bay and Tampa Bay, pinfish were first collected at deepwater trawl stations in the same month or one month after their initial appearance at seine stations (Fig. 2). In Charlotte Harbor, however, YOY were absent at trawl stations until January–March, one to three months after their first appearance at seine stations (Fig. 2).

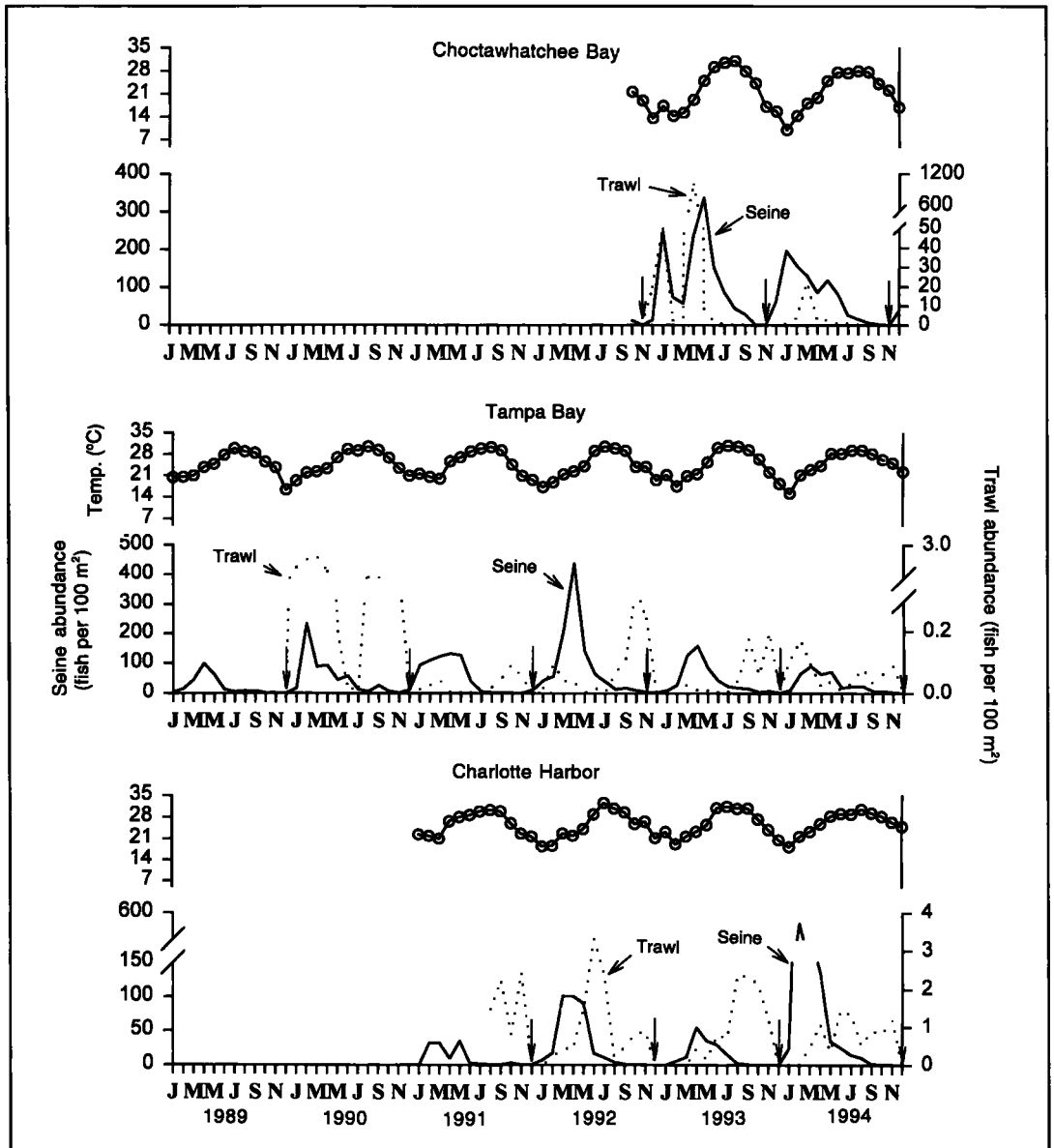


**Figure 2**

Monthly relative indices of young-of-the-year pinfish abundance (no. of fish) and mean monthly water temperature at fixed seine and trawl stations from 1989–94 for Choctawhatchee Bay, Tampa Bay, and Charlotte Harbor. Vertical arrows indicate the month of initial recruitment.

Relative abundance at fixed seine stations peaked in January and May in Choctawhatchee Bay, generally during March–April in Tampa Bay and Charlotte Harbor, and declined thereafter (Fig. 2). In Choctawhatchee Bay and Tampa Bay, relative abundance at trawl stations generally followed fluctuations in seine catches, but usually peaked one to two months before the peak at seine stations (Fig. 2). A second peak in trawl abundance was observed in Tampa Bay from August to October (Fig. 2). In Charlotte Harbor, relative abundance at trawl stations peaked during June–September, two to five months after the peak in seine abundance (Fig. 2).

In all bays, smaller pinfish were generally captured at fixed trawl stations during November to March than at fixed seine stations (Figs. 3–5). Progression of the smallest fish size beyond the minimum size measured during the months of first capture indicated that settlement of postlarvae to fixed stations ended by March–April in all bays (Figs. 3–5). In Tampa Bay, catch proportions of YOY <40 mm decreased at trawl stations in March. In July, YOY >60 mm were captured in higher proportions at trawl stations in all bays than during the preceding months (Fig. 3–5). Pinfish overwintering at shallow-water seine stations in Choctawhatchee Bay tended to be smaller than those remaining at seine stations in Tampa Bay and Charlotte Harbor (Figs. 3–5).

## Depth distribution

About 80% of the trawl catches of YOY pinfish in spring occurred in waters <3.1 m, <3.5 m, and <2.8 m in Choctawhatchee Bay, Tampa Bay, and Charlotte Harbor, respectively. Few fish (<1% of total catches) were captured in waters >5 m. The Kolmogorov-Smirnov test showed that cumulative frequency distributions for YOY pinfish depth were significantly different from those for trawl depth in all bays (Choctawhatchee Bay: $D$=0.51, $n_{depth}$=80, $n_{fish}$=34, $P$<0.001; Tampa Bay: $D$=0.44, $n_{depth}$=373, $n_{fish}$=76, $P$<0.001; Charlotte Harbor: $D$=0.48, $n_{depth}$=268, $n_{fish}$=59, $P$<0.001).

## Factors influencing YOY spatial abundance

The final GLM's accounted for proportions of 0.33–0.44 of the total variation in spring catches, depending on bay system (Table 1). Pinfish abundance was associated with the presence of bottom vegetation in all bays (Table 1; Fig. 6A), with rivers (zone F) and zones near bay mouths in Tampa Bay (D and E) and

**Table 1**

Final results of the general linear model analyses of pinfish catches for Choctawhatchee Bay, Tampa Bay, and Charlotte Harbor in spring. Partial (type-III) mean squares are shown. * = $P$<0.05, **= $P$<0.01, and *** = $P$<0.001.

| Location | Source | df | Mean square | $F$-value | $r^2$ |
|---|---|---|---|---|---|
| Choctawhatchee Bay | Model | 3 | 71.120 | 23.70*** | 0.436 |
| | Year | 1 | 0.097 | 0.03 | |
| | Deployment | 1 | 42.637 | 14.21*** | |
| | Bottom vegetation | 1 | 179.747 | 59.89*** | |
| | Error | 92 | 3.001 | | |
| | Corrected total | 95 | 5.152 | | |
| Tampa Bay | Model | 11 | 67.312 | 19.84*** | 0.334 |
| | Year | 5 | 14.041 | 4.14** | |
| | Zone | 5 | 65.287 | 19.25*** | |
| | Bottom vegetation | 1 | 193.316 | 56.99*** | |
| | Error | 425 | 3.392 | | |
| | Corrected total | 436 | 5.005 | | |
| Charlotte Harbor | Model | 13 | 59.461 | 15.85*** | 0.421 |
| | Year | 5 | 24.823 | 6.62*** | |
| | Zone | 4 | 33.193 | 8.85*** | |
| | Bottom vegetation | 1 | 24.406 | 6.51* | |
| | Bottom sediment | 1 | 43.380 | 11.56*** | |
| | Salinity | 1 | 62.795 | 16.74*** | |
| | Temperature | 1 | 22.778 | 6.07* | |
| | Error | 283 | 3.752 | | |
| | Corrected total | 296 | 6.198 | | |

Charlotte Harbor (B and C) (Table 1; Fig. 6B), with beach seine sets in Choctawhatchee Bay (Table 1; Fig. 6C), and with mud bottom in Charlotte Harbor (Table 1; Fig. 6D). Young-of-the-year pinfish catches were related to salinity and temperature in Charlotte Harbor only (Table 1).

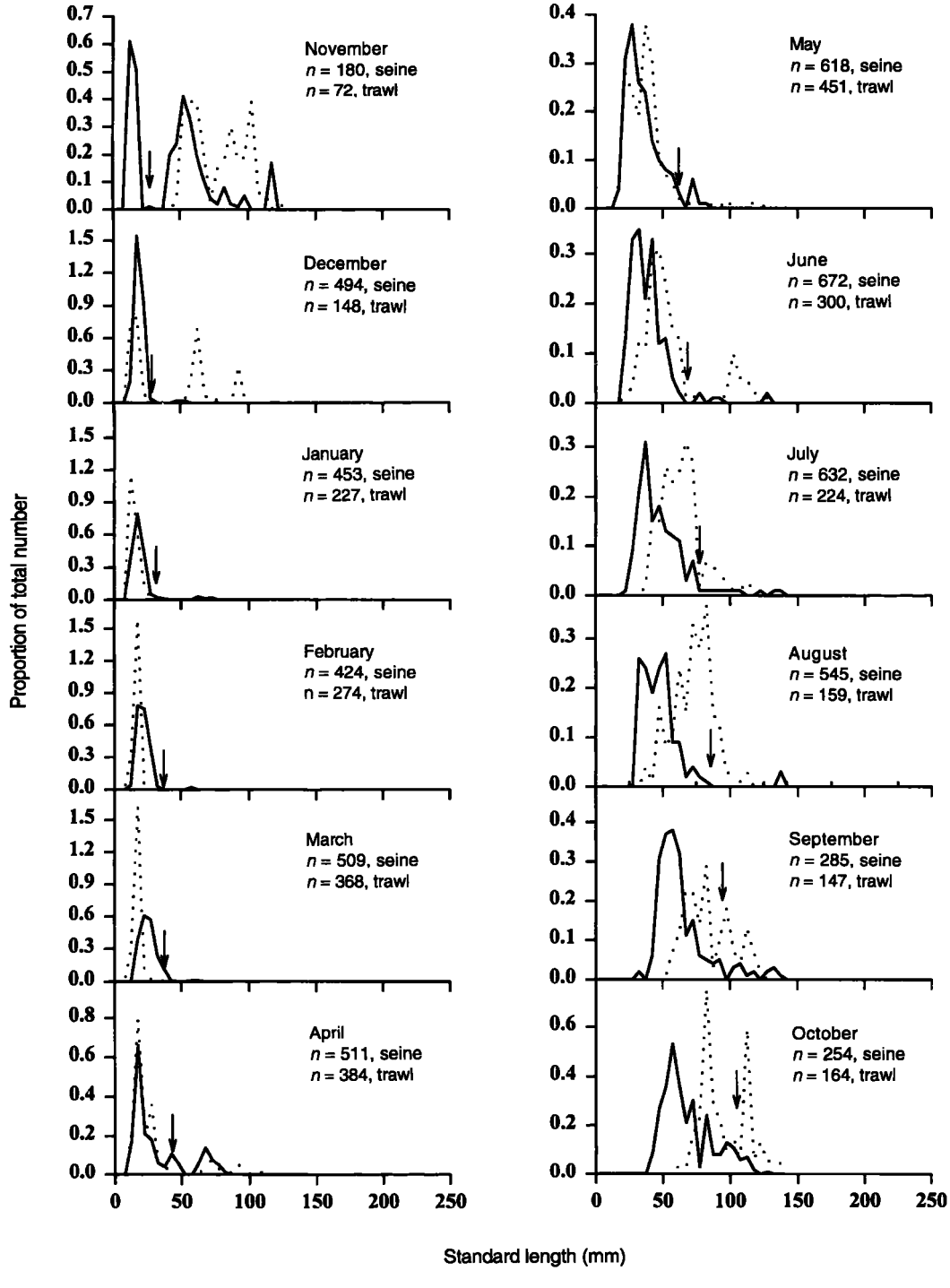


**Figure 3**

Monthly length-frequency distributions of pinfish captured at fixed seine (—) and trawl (· · ·) stations in Choctawhatchee Bay from 1989 to 1994. Vertical arrows indicate the monthly maximum size limits for young-of-the-year data. *n* is the number of pinfish measured.

Young-of-the-year pinfish abundance varied significantly between years in Tampa Bay and Charlotte Harbor (although not significant, year was included in the model for Choctawhatchee Bay to compute least squares means)(Table 1; Fig. 7). Pinfish abundance was also generally highest in Choctawhatchee

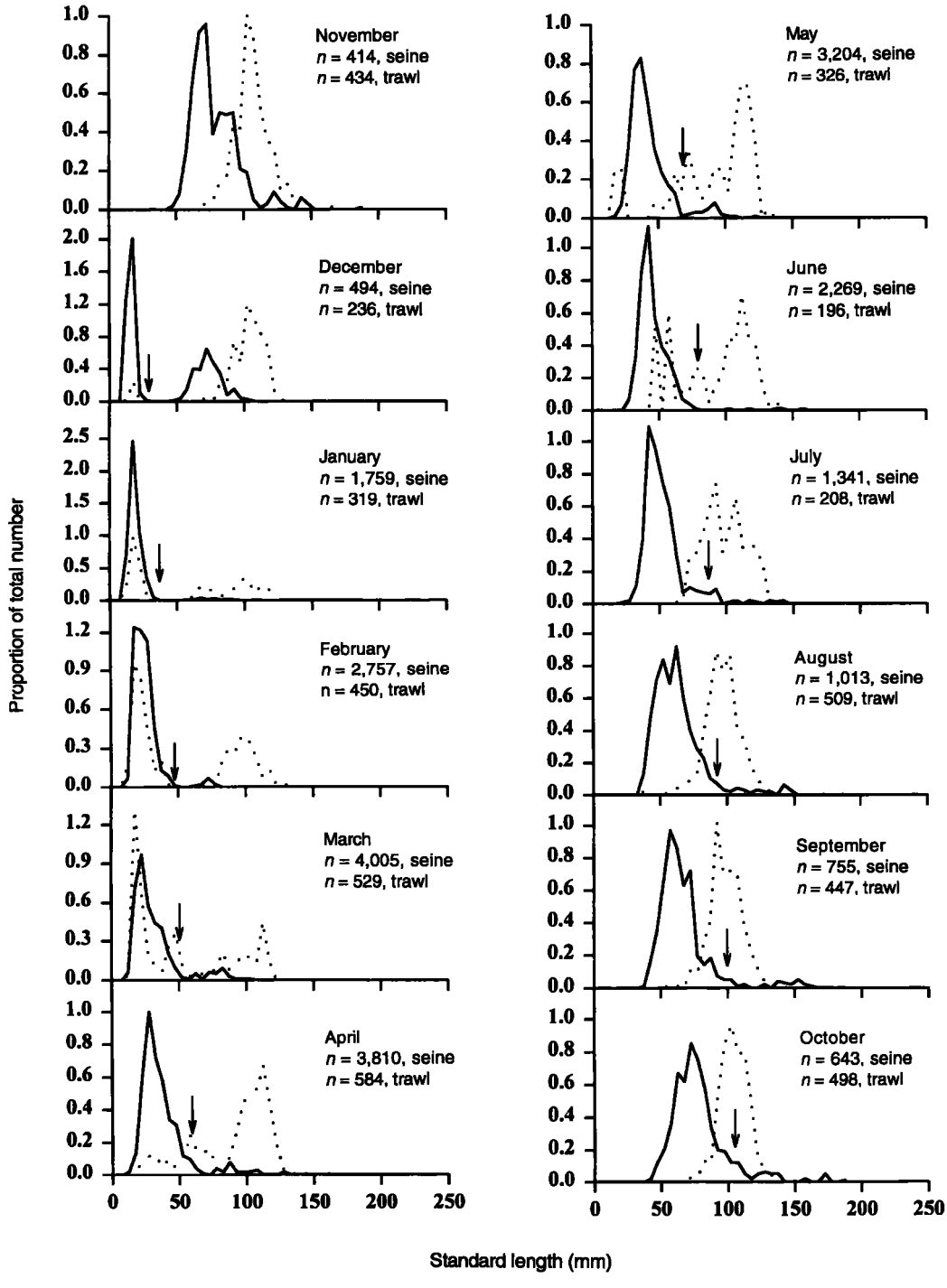


**Figure 4**

Monthly length-frequency distributions of pinfish captured at fixed seine(—) and trawl (· · ·) stations in Tampa Bay from 1989 to 1994. Vertical arrows indicate the monthly maximum size limits for young-of-the-year data. *n* is the number of pinfish measured.

Bay (range: 55.0–59.8 fish/haul), followed by Charlotte Harbor (5.5–50.4 fish/haul) and Tampa Bay (7.8–27.8 fish/haul)(Fig. 7).

## Factors affecting YOY annual abundance

Relative abundance of YOY pinfish was significantly

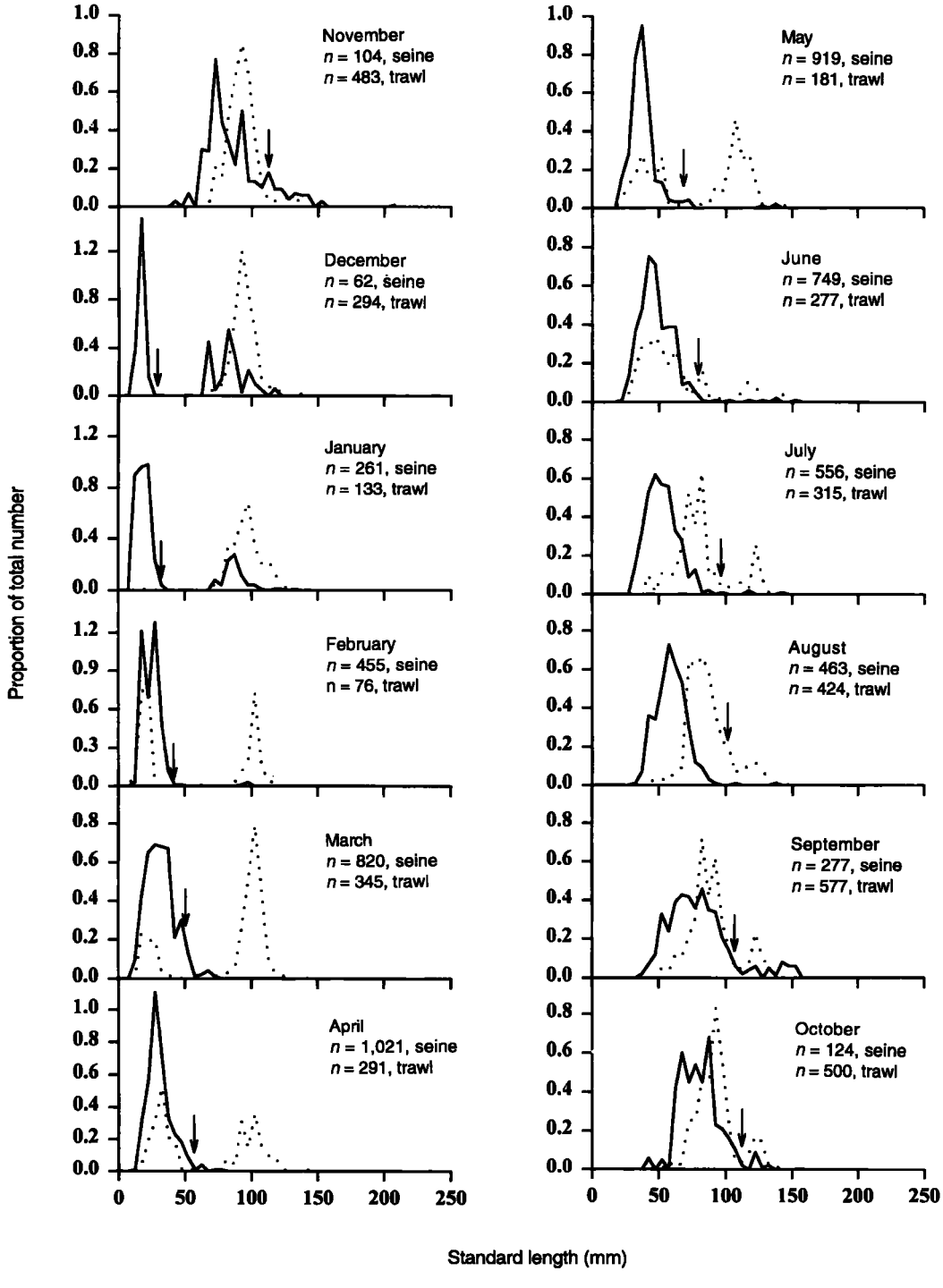


**Figure 5**

Monthly length-frequency distributions of pinfish captured at fixed seine(—) and trawl (· · ·) stations in Charlotte Harbor from 1989 to 1994. Vertical arrows indicate the monthly maximum size limits for young-of-the-year data. *n* is the number of pinfish measured.

and positively correlated with mean sea-surface temperatures in November (the month before first appearance) in Charlotte Harbor and with indices of adult abundance from 1988 to 1993 in Tampa Bay (Table 2).

## Growth

Growth rates were estimated with mean length data from fixed seine stations only from April through July to minimize biases associated with potential movements of YOY pinfish. Year-class growth rates were similar among bays. Instantaneous growth coefficients ranged from 0.18 to 0.26/month for Choctawhatchee Bay, 0.06–0.21/month in Tampa Bay, and 0.14–0.26/month for Charlotte Harbor, indicating that monthly growth of YOY pinfishes is rapid during late spring and mid-summer months (Table 3). Comparisons among bays revealed no consistent interannual patterns in growth except from 1993 to 1994 when rates declined in all bays (Table 3).

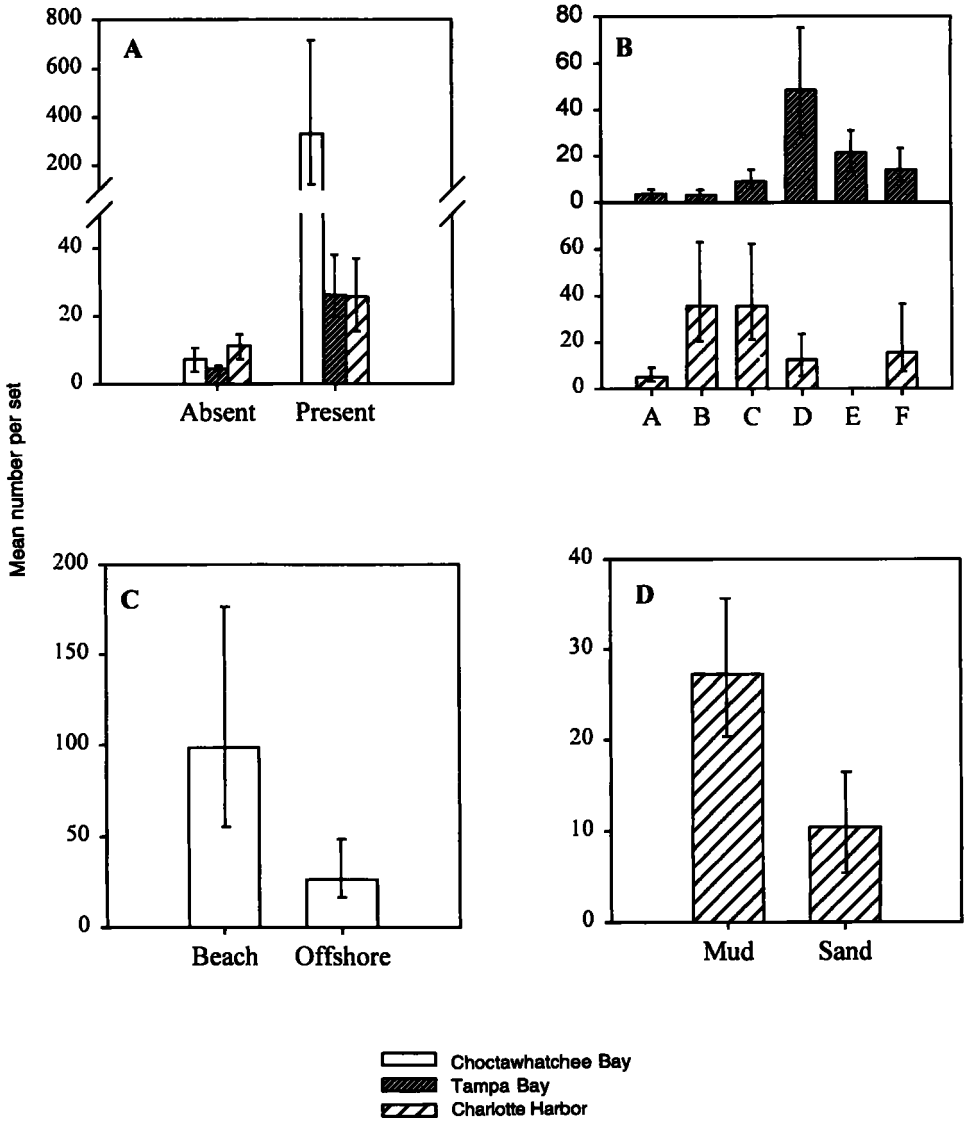


**Figure 6**

Least-squares means and 95% confidence intervals for main effects of (**A**) presence or absence of bottom vegetation, (**B**) zones, (**C**) deployment techniques, and (**D**) sediment type. Zones A–E encompass bay areas, whereas zone F encompasses rivers.

### Mortality

The estimates of $Z$ were calculated from the decline in indices of relative abundance at shallow-water fixed stations from May (month of secondary peak in abundance) to June for Choctawhatchee Bay, and April (month of peak abundance) to May for Tampa Bay and Charlotte Harbor. Relative abundance indices were averaged over all years prior to calculation in order to reduce the effects of interannual variability. Estimates of Z were 0.022/d, 0.021/d, and 0.023/d for Choctawhatchee Bay, Tampa Bay, and Charlotte Harbor, respectively (Table 4).

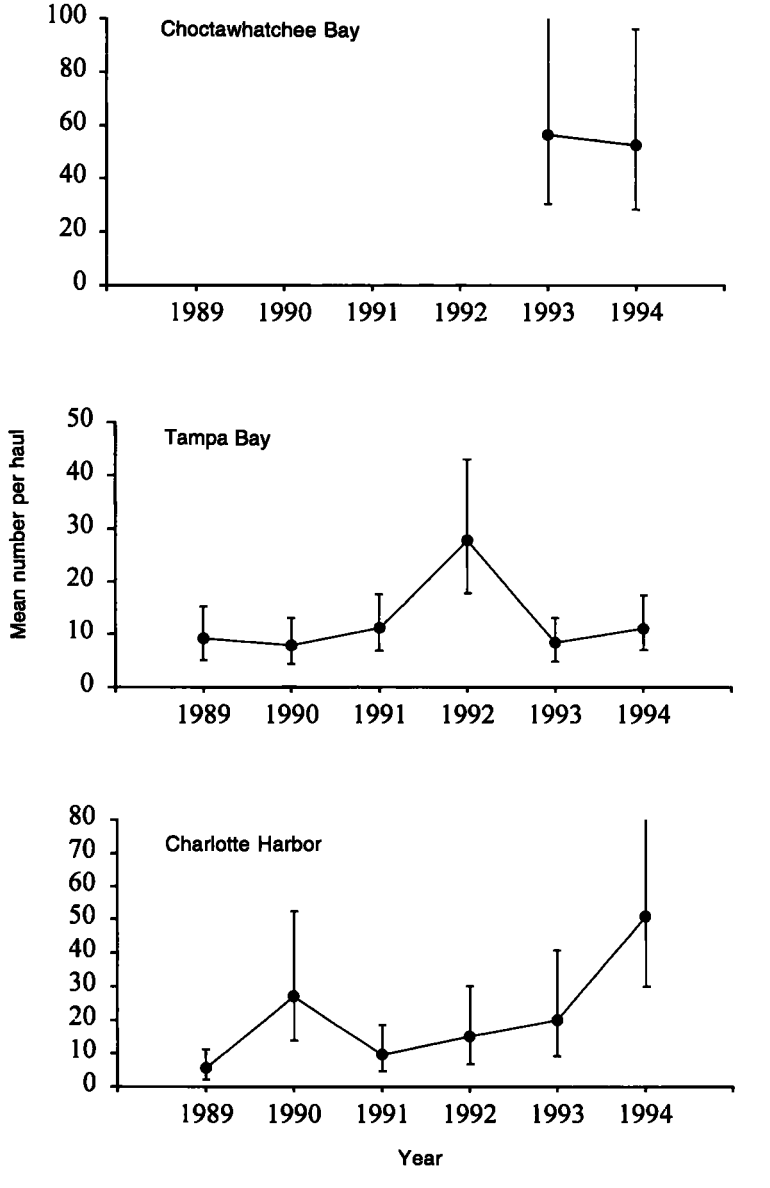


**Figure 7**

Annual indices of young-of-the-year abundance and 95% confidence intervals for Choctawhatchee Bay, Tampa Bay, and Charlotte Harbor from 1989 to 1994.

## Discussion

### Seasonal changes in YOY abundance and size structure

Pelagic pinfish larvae are transported from oceanic spawning areas and dispersed into estuaries via near-surface water currents (Darcy, 1985). After metamorphosis, postlarvae settle more or less near the bottom in estuaries (Hildebrand and Cable, 1938; Caldwell, 1957). Initial appearance of postlarvae (9–12 mm) and larger YOY (<28 mm) in shallow and deep water within a one-month period suggests pinfish settle to both areas in Choctawhatchee Bay and Tampa Bay. In Charlotte Harbor, settlement appears to occur first to shallow water, and then to deep water, because YOY pinfish were absent in trawls until 1–3 months after their first appearance at fixed seine stations. One explanation for these different patterns of settlement may lie with the bathymetry of each bay: more shallow-water area with seagrass beds (YOY pinfish are dependent on seagrass for protection from predators and food [Stoner, 1980; 1983]) is available in Charlotte Harbor (seagrass area=202 $km^2$) than in Choctawhatchee Bay (33 $km^2$) or Tampa Bay (83 $km^2$)(Sargent et al., 1995).

The occurrence of YOY pinfish mostly in water <3.5 m suggests that pinfish distribution is depth-restricted. The propensity of YOY pinfish to limit their depth is probably due to their dependence on seagrasses for cover (seagrasses are generally restricted to waters <2.3 m in Choctawhatchee Bay, Tampa Bay, and Charlotte Harbor [Durako[1]]), the distribution of pelagic and mobile epibenthic prey (Stoner, 1980), and light intensity (Gulbrandsen, 1996) (YOY pinfish must see their prey

[1] Durako, M. 1996. Florida Marine Research Institute, 100 Eighth Avenue SE, St. Petersburg, FL 33701-5095. Personal commun.

**Table 2**

Results of the Pearson product moment correlation tests for indices of recruit abundance from 1989 to 1994 versus mean sea-surface temperature during the months before and during initial recruitment from 1988 to 1993 and for indices of adult abundance from 1988 to 1993 for Tampa Bay and Charlotte Harbor. $r$ is the Pearson product moment correlation coefficient, $P$ is the significance probability, and $n$ is the sample size. MRFSS = Marine Recreational Fisheries Statistical Survey.

| | | Tampa Bay | | Charlotte Harbor | | |
|---|---|---|---|---|---|---|
| | Month | r | *P* | *r* | *P* | *n* |
| YOY indices-temperature | October | –0.05 | 0.92 | 0.67 | 0.15 | 6 |
| | November | –0.78 | 0.11 | 0.84 | 0.03 | 6 |
| | December | 0.15 | 0.78 | –0.21 | 0.67 | 6 |
| YOY indices–MRFSS adult indices | | 0.86 | 0.02 | –0.15 | 0.78 | 6 |

**Table 3**

Regression statistics for mean length (ML) versus month (m) for young-of-the-year pinfish captured at fixed seine stations. The regression takes the form: $\text{Ln}(ML) = \ln(L_0) + G \times m$ where $\ln(L_0)$ is the intercept and $G$ is the instantaneous growth rate or slope. Only data from April to July were used. All slopes and intercepts were significantly different from zero.

| Year | $\ln(L_0)$ | SE | *G*-value | SE | $r^2$ | *n* |
|---|---|---|---|---|---|---|
| Choctawhatchee Bay | | | | | | |
| 1993 | 2.03 | 0.217 | 0.26 | 0.038 | 0.956 | 4 |
| 1994 | 2.61 | 0.162 | 0.18 | 0.029 | 0.954 | 4 |
| Tampa Bay | | | | | | |
| 1989 | 2.77 | 0.078 | 0.18 | 0.014 | 0.988 | 4 |
| 1990 | 3.53 | 0.116 | 0.06 | 0.021 | 0.818 | 4 |
| 1991 | 3.17 | 0.030 | 0.10 | 0.005 | 0.994 | 4 |
| 1992 | 2.64 | 0.072 | 0.20 | 0.013 | 0.992 | 4 |
| 1993 | 2.49 | 0.274 | 0.21 | 0.049 | 0.904 | 4 |
| 1994 | 2.98 | 0.175 | 0.14 | 0.031 | 0.905 | 4 |
| Charlotte Harbor | | | | | | |
| 1991 | 2.38 | 0.095 | 0.26 | 0.017 | 0.991 | 4 |
| 1992 | 2.96 | 0.123 | 0.14 | 0.022 | 0.954 | 4 |
| 1993 | 2.46 | 0.243 | 0.21 | 0.043 | 0.920 | 4 |
| 1994 | 2.81 | 0.266 | 0.16 | 0.047 | 0.857 | 4 |

**Table 4**

Relative abundance (no. of fish/100 $m^2$) for April to June averaged over all years and estimates of total instantaneous mortality ($Z$) for young-of-the-year pinfish (*Lagodon rhomboides*) in Choctawhatchee Bay, Tampa Bay, and Charlotte Harbor. Data used to estimate $Z$ are boldface.

| Month | Choctawhatchee Bay | Tampa Bay | Charlotte Harbor |
|---|---|---|---|
| April | 163.6 | **164.2** | **97.2** |
| May | **228.2** | **88.5** | **48.9** |
| June | **119.2** | 39.1 | 18.7 |
| –Z | 0.022 | 0.021 | 0.023 |

and therefore feed little at night [Kjelson and Johnson, 1976]).

Young-of-the-year pinfish that settle to deep water move to shallow-water areas in early spring. Evidence for this is the peak in trawl abundance of YOY pinfish in all years, followed by a rapid decline before the peaks in abundance at seine stations in Choctawhatchee Bay and Tampa Bay (Fig. 2). This movement to shallow water may be due to YOY seeking food and refuge from predators because it coincides with seasonal increases in seagrass biomass and prey abundance in shallow waters (Thoemke, 1979; Lewis et al., 1985) and because the shallow water and structural complexity of seagrasses may provide protection from predation (Savino and Stein, 1982; Stoner, 1983; Ruiz et al., 1993).

Young-of-the-year pinfish move from shallow-water to deepwater areas in mid- to late summer, and this movement appears to be related to YOY size. Evidence for this is the shift to larger sizes in trawls in July (Figs. 3–5) concurrent with increasing catches in trawls in Tampa Bay and Charlotte Harbor (Fig. 2). This movement may represent the initiation of their fall spawning migration (Caldwell, 1957; Hansen, 1970) because gonadal recrudescence begins as early as July (Cody and Bortone, 1992) and because the modal lengths observed in trawls in July were about 80 mm, which is the minimum size observed for YOY pinfish with developing gonads (Hansen, 1970).

## Factors affecting YOY spatial abundance

Without meaningful, significant first-order interactions in the GLM analyses, the YOY abundance and main effect (zones, deployment technique, and bot-

tom type) relationships were difficult to assess. However, because pinfish abundance was associated with vegetation (seagrasses) in this and other studies (Stoner, 1980; Stoner, 1983), the significance of the main effects can be proposed in relation to seagrass distribution. Higher YOY pinfish abundances may have occurred in zones located near bay mouths because the largest areas of seagrass are located within these zones (Sargent et al., 1995). The absence of large expanses of seagrasses in Choctawhatchee Bay (Sargent et al, 1995) may have caused YOY pinfish to populate shallow-water beach areas abundantly to avoid predation (Ruiz et al., 1993). Because mud is commonly associated with seagrass beds in shallow-water areas of Charlotte Harbor (Mitchell[2]), higher abundances of YOY over mud may be expected.

It was surprising that more YOY pinfish were captured in Choctawhatchee Bay because there is less seagrass in this bay than in Tampa Bay or Charlotte Harbor (Sargent et al., 1995). Higher abundances of YOY pinfish may occur in Choctawhatchee Bay because *Halodule wrightii*, a thin-blade seagrass preferred by YOY pinfish for refuge and amphipod foraging (Stoner, 1982; 1983), occurred more frequently (62%) at vegetated sites in Choctawhatchee Bay than at vegetated sites in Tampa Bay (46%) and in Charlotte Harbor (40%).[3] The patchily distributed seagrass beds in Choctawhatchee Bay may also support higher abundances of pinfish than the continuously distributed seagrass beds in Tampa Bay and Charlotte Harbor because the ecotone between seagrasses and unvegetated areas may provide greater habitat complexity, offering protection from predators while providing close access to alternative feeding areas (Holt et al., 1983).

## Factors influencing YOY annual abundance

Although this study is an exploratory analysis, the positive correlation between YOY abundance and sea-surface temperatures in Charlotte Harbor suggests that oceanographic or biological events that occur before settlement may be important factors contributing to the annual variability in pinfish abundance. Higher temperatures may favor increased hatching success (Postuma, 1971) or increased growth of larvae, or both (Hunter, 1981; Miller et al., 1985; Pepin, 1991), or they may affect transport mechanisms (Lasker, 1984; Rothschild, 1986). For pinfish, both explanations are plausible given that adults spawn in offshore Gulf waters.

Direct spawning stock-recruitment relationships are often masked by variability in recruitment (Fogarty et al., 1991). The lack of correlation between YOY and adult abundances in Charlotte Harbor suggests that temperature may be a more influential factor for this bay. The significant correlation between YOY and adult indices at such a low sample size does suggest that for Tampa Bay, the relationship may not be markedly masked, and identification of the actual spawning stock-recruitment patterns may be possible with additional years of data.

## Growth

To compare growth rates for YOY pinfish from this study with those found for pinfish from Cedar Key, FL, Redfish Bay, TX, and the Laguna Madre, TX, I fitted the same growth equation to mean length data of YOY pinfish estimated from graphical plots shown in Caldwell (1957) for Cedar Key, Cameron (1969) for Redfish Bay, and Hellier (1962) for Laguna Madre, for April–July. Instantaneous growth rates were 0.10/month for YOY pinfish from Redfish Bay, TX, 0.17/month from the Laguna Madre, TX, and 0.25/month from Cedar Key, FL, indicating that growth in these bays was similar to growth of YOY pinfish in the three bays studied (Table 4). Similar growth rates were expected given that temperatures experienced by YOY pinfish among the Gulf coast estuaries were alike during the April to July growth period (Caldwell, 1957; Cameron, 1969; Hellier, 1962).

## Mortality

Daily mortality of YOY pinfish in shallow-water areas of the three Florida estuaries was low. My estimates of mortality (0.021–0.023) were similar to those made for other estuarine-dependent species such as juvenile gulf menhaden (*Brevoortia patronus*) in Fourleague Bay, Louisiana (0.017–0.021)(Deegan, 1990), spot (*Leiostomus xanthurus)* in York River, Virginia (0.017) (Weinstein, 1983), and Atlantic croaker (*Micropogonias undulatus*) in Rose Bay, North Carolina (0.023) (Currin et al., 1984). Unfortunately, I could not estimate mortality of YOY pinfish in deep water because emigration and immigration appeared to occur continuously over the spring–summer period at fixed trawl stations.

In summary, YOY pinfish first appeared in shallow-water areas during November in Choctawhatchee Bay and during December in Tampa Bay and Charlotte Harbor. In Choctawhatchee Bay and Tampa Bay, they were captured in deep water within one month

[2] Mitchell, M. E. 1997. Florida Marine Research Institute, Charlotte Harbor Field Laboratory, 1481-A Market Circle, Port Charlotte, FL 33953. Personal commun.

[3] Percent occurrence for seagrasses was estimated from random sampling data in spring.

after their shallow-water appearance. In Charlotte Harbor, YOY pinfish were absent in deep water until 1–3 months after they first appeared in shallow water. Young-of-the-year pinfish were generally restricted to depths <3.5 m in all bays. Two general movements were evident: from deep water to shallow water in spring, and from shallow water to deep water in mid- to late summer, the latter movement being size-dependent. High abundances of pinfish were commonly associated with the presence of seagrasses. Despite differences in abundance among bay populations, growth and mortality rates of young-of-the-year pinfish were similar in all bays.

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# Low-frequency acoustic measurements of Pacific hake, *Merluccius productus*, off the west coast of the United States

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**Abstract.**—Low-frequency volume scattering measurements were conducted by the Naval Research Laboratory (NRL) on the upper slope, slope base, and abyssal plain along the U.S. west coast between the Strait of Juan de Fuca, Washington, and Cape Mendocino, California. Comparisons of swimbladder radii estimated from resonances with those estimated from fish lengths obtained from quasisynoptic National Marine Fisheries Service (NMFS) trawl catches of Pacific hake, *Merluccius productus*, strongly suggest that the major source of the low-frequency scattering were Pacific hake. Estimates of hake density from the NRL low-frequency measurements and the NMFS acoustic, midwater trawl survey on the slope gave comparable values of 195–439 kg/ha and 91–369 kg/ha respectively. However, NRL measurements, up to 50 km offshore of the outer limit of the NMFS survey, found densities of 270–300 kg/ha in layers peaking at 225 to 450 m depth. This finding suggests that high densities of hake may occur farther offshore of the traditional limit of NMFS surveys and at depths which may be difficult to survey with conventional fisheries sounders.

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Pacific hake, *Merluccius productus*, are the most abundant large midwater fish on the continental shelf and slope of the west coast of the United States during summer (Ware and McFarlane, 1989). Hake winter between Point Conception, CA, and Baja California. In spring they migrate northward to feed in the productive waters along the continental shelf from northern California to Vancouver Island. They remain in this area from May through October. The migration between the winter spawning grounds and the summer feeding grounds is size structured, i.e. related to fish length and optimum swimming velocity (Francis, 1983; Smith et al., 1992), with the larger fish swimming faster and farther. Large fish migrate farthest north to near Vancouver Island, smaller fish reach only as far as southern Oregon and northern California (Stauffer, 1985).

A midwater trawl fishery targets hake occurring in dense feeding aggregations along the shelf break in midsummer (Stauffer, 1985). Since 1977, the National Marine Fisheries Service (NMFS) has conducted a triannual acoustic, midwater trawl survey to determine hake distribution and abundance (Dorn et al., 1994). During the 1992 survey, NMFS integrated volume scattering with a high-frequency (38-kHz) echo sounder and corroborated fish identity and size with midwater trawls. Volume scattering was converted to fish biomass with a volume scattering to biomass regression (Dorn et al., 1994).

Coincident with the 1992 fishery survey, the Naval Research Laboratory (NRL) conducted an acoustic survey of volume scattering using a broad-band low-frequency measurement system (Thompson and Love, 1996). Because the NRL survey was conducted quasisynoptically with the fisheries survey, comparisons were possible between the two surveys.

Although echo sounders at relatively high frequencies (>20 kHz) are a standard tool in fisheries surveys (MacLennan and Simmonds, 1992), a broad-band low-frequency sound at the natural resonance of the population of fish swimbladders at depth have been used as an alternative tool (Holliday, 1972; 1977a). A variety of acoustic models has been developed to help predict and understand various aspects of this resonance (Anderson, 1950; Andreeva, 1964; Love, 1978; Stanton, 1989; Clay, 1991, Feuillade and Werby, 1994). With these models, the acoustic resonance of a population of fish swimbladders at depth can provide quantitative information about the fish population. The spectrum of the resonance is depen-

dent on swimbladder size, depth, and fish behavior (Sand and Hawkins, 1973; Love, 1993). The scattered sound at resonance is almost completely omnidirectional, independent of fish aspect (Feuillade and Werby, 1994). As a result, resonance measurements are useful for inferring the size and abundance of the swimbladders. An inverse solution of measured scattering levels can be used to generate a size-frequency distribution of swimbladders (Holliday, 1977b), from which fish size can then be inferred.

On the U.S. west coast, Pacific hake, measuring 45 cm in fork length and occupying depths of 50 to 500 m, are expected to be resonant near 500 to 1,500 Hz (Love, 1978). Midwater trawls show that no other large pelagic fish are as abundant as hake (Dorn et al., 1994). Other fishes expected to contribute to scattering are anchovy and mesopelagic fishes (Kalish et al., 1986). Both are much smaller than hake and at depths of 50 to 500 m should only contribute to scattering above 2 kHz.

This study reports on low-frequency volume scattering measurements from what are assumed to be Pacific hake at depths of 50 to 500 m over the continental slope off the Strait of Juan de Fuca and the Oregon–California coasts. Bioacoustic models are used to estimate the number and size of swimbladders at depth. These results are compared with estimates of swimbladder size and abundance obtained from quasisynoptic acoustic data and midwater trawl catches collected by the National Marine Fisheries Service.[1] A comparison of swimbladder size is problematic. Fish can either let their swimbladders compress according to Boyle's law during descent, or they can actively add gas to the swimbladder to maintain neutral buoyancy. In addition, the relation between fish size and swimbladder volume is also highly variable within a group of fish and is affected by feeding and other aspects of fish behavior (Ona, 1990). We consider these possibilities and suggest several hypotheses about the swimbladder behavior of Pacific hake.

[1] 1992. Alaska Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way N.E., Seattle, WA 98115-0070. Unpubl. data.

## Materials and methods

### Measurements

The NRL low-frequency acoustic measurements were made from 14 to 29 August 1992 aboard the USNS *Wilkes* (T-AGS-33) in conjunction with a Naval Oceanographic Office (NAVOCEANO) survey. The NRL conducted measurements at 9 stations located on the continental slope and abyssal plain between the Strait of Juan de Fuca and Cape Mendocino (Table 1; Fig. 1). Stations 2 and 3 off the Washington coast were missed owing to heavy seas. Because we expected a north–south trend in the size composition of the hake, stations at similar latitude were grouped and named according to their proximity to geographic features: station 1—La Perouse; 4 and

**Table 1**

Volume reverberation stations conducted by the Naval Research Laboratory.

| Station no. | Date | Time (local [h]) | Day or night | Lat. N | Long. W | Bottom depth (m) |
|---|---|---|---|---|---|---|
| 1 | 14 Aug | 1836–1920 | day | 48°26' | 126°20' | 900 |
| 4 | 18 Aug | 0120–0223 | night | 44°44' | 125°04' | 1,100 |
| 5 | 19 Aug | 1325–1420 | day | 44°45' | 125°42' | 2,800 |
| 5 | 20 Aug | 0145–0240 | night | 44°38' | 125°43' | 2,900 |
| 6 | 21 Aug | 0000–0105 | night | 43°28' | 125°40' | 3,100 |
| 6 | 21 Aug | 0925–1032 | day | 43°27' | 125°38' | 3,100 |
| 7 | 23 Aug | 0025–0109 | night | 43°26' | 125°04' | 1,070 |
| 7 | 23 Aug | 0858–0935 | day | 43°30' | 125°06' | 1,245 |
| 8 | 24 Aug | 0905–0936 | day | 42°18' | 124°54' | 1,025 |
| 9 | 25 Aug | 2212–2248 | night | 42°19' | 125°40' | 2,800 |
| 9 | 26 Aug | 0856–0927 | day | 42°23' | 125°39' | 2,800 |
| 10 | 27 Aug | 0925–1001 | day | 40°15' | 125°35' | 2,400 |
| 11 | 28 Aug | 0117–0200 | night | 40°04' | 125°09' | 1,465 |
| 11 | 29 Aug | 0931–1006 | day | 40°03' | 125°08' | 1,500 |

5—Heceta North; 6 and 7—Heceta South; 8 and 9—Sebastian; and 10 and 11—Mendocino.

Just prior to the NRL survey, NMFS conducted a high-frequency acoustic-midwater trawl survey of Pacific hake. The survey began just south of San Francisco and ended off Cape Scott, Vancouver Island (Dorn et al., 1994). Generally, trawls were located inshore of the NRL stations. The NRL and NMFS surveys were separated by 43 days in the south (station 11, trawl 8), but only 5 days in the north (station 1, trawl 45)(Fig. 1). The NMFS survey provided information on fish size and abundance that could be compared with the results of the low-frequency acoustic analysis. Comparisons were restricted to midwater trawls located close to the NRL stations within each of the above named latitudinal regions. A north–south trend in fish size was evident, although a gap occurred in the size distributions between 38 and 40 cm (Fig. 2). Trawls appeared to catch fish on either side of this gap; only a few trawls contained both size classes. This finding suggests that, at sea, different size classes remain spatially separate (Fig. 1).

The NRL sound scattering measurements used an explosive sound source and a directional acoustic receiver. A 0.23-kg TNT charge detonated at 0.5 m depth provided a high source level over a wide frequency range. The shallow detonation depth allowed the gas bubble created by the explosion to vent to the surface and prevented the multiple sound pulses caused by bubble oscillations characteristic of charges detonated at greater depth. Measurement sequences consisted of 4 to 6 shots over a 30-min period. Because the ship typically drifted at 1–2 knots, the distance over which data were collected was on the order of a mile.

The acoustic receiver used for these measurements consists of a thirty-two element line hydrophone, 0.9 m long, mounted along the axis of a conical reflector that had a height of 0.9 m and an open base with a diameter of 1.8 m. The purpose of the reflector was to map an annular area of the opening to each hydrophone element for sound entering the reflector parallel to the axis and to decrease sensitivity to sound entering the reflector from other directions. The receiver was originally designed for use at frequencies between 2.5 and 20 kHz. By varying the number of active hydrophone elements, the receiver's 3-dB beam width can be maintained between 10° and 20° in that frequency range. The eight elements nearest the vertex of the cone form a 45-cm aperture and are used for frequencies from 10 to 20 kHz. By doubling the active length with eight additional elements, a 90-cm aperture is formed that can be used for frequencies between 5 and 10 kHz, and all 32 elements form a 180-cm aperture that can be used below 5 kHz. Between 2.5 and 5 kHz, measured beam patterns of the receiver show a main lobe with shape and 3-dB beam width similar to the main lobe of theoretical beam patterns (Urick, 1983) for a plane circular array 1.8 m in diameter, whereas the side lobes are lower than those for a plane circular array. Below 2.5 kHz, the main beam widens beyond 20°, reaching 38° at 1,600 Hz, 58° at 800 Hz, and 74° at 500 Hz.

Received signals from each TNT shot were amplified, high- and low-pass filtered

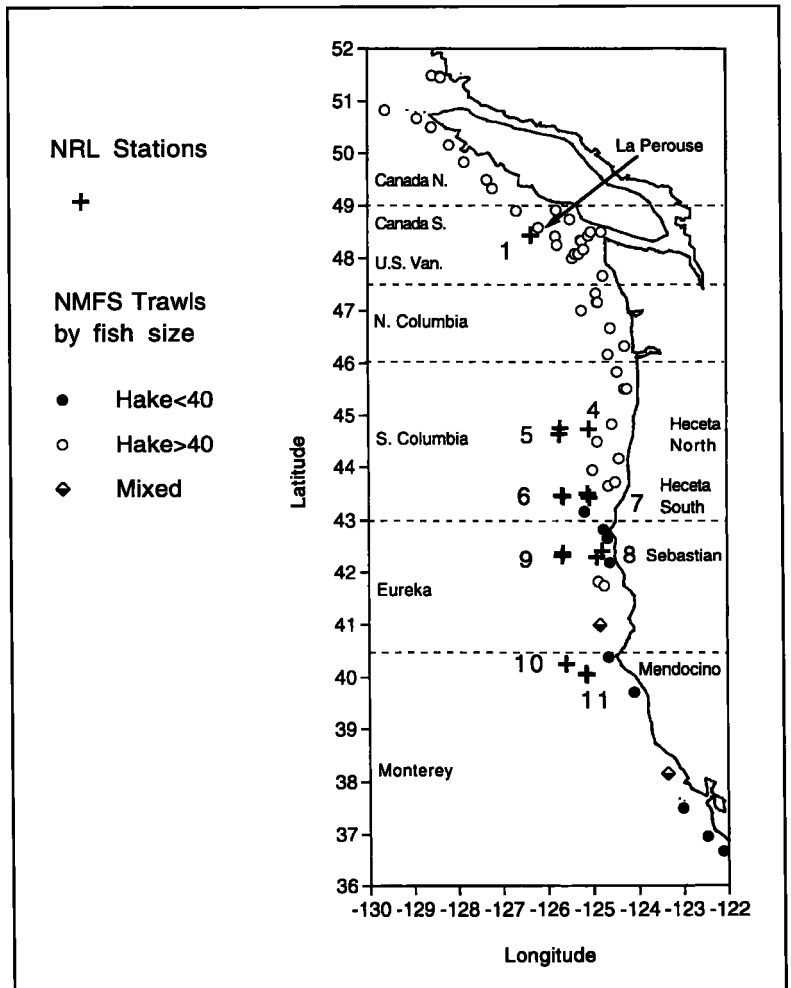


**Figure 1**

Map of the U.S. west coast showing Naval Research Laboratory (NRL) stations and locations where pertinent National Marine Fisheries Service (NMFS) midwater trawls were undertaken.

at 400 and 6,000 Hz, respectively, digitized at a 20-kHz sampling rate, and stored. Digitally stored signals were subsequently filtered into 21 1/6 octave bands from 500 to 5,000 Hz and amplitude versus time envelopes calculated for each band. There was little variation between shots in a sequence. Envelopes of all shots in a sequence were averaged to obtain a single set that was representative of scattering during that sequence, and this averaged data was used to calculate volume scattering strength, $S_v$, the scattering strength of a unit volume of water, as a function of depth. Data were displayed as 2-dimensional images showing $S_v$ in dB on a color scale as a function of frequency and depth. Scatterer depths were determined from the $S_v$ images; integration over these depths produced a series of layer scattering strength ($S_L$) versus frequency curves. On the basis of the distinct nature of the $S_L$ curves, scatterers were assumed to be swimbladder-bearing fish. Hence, $S_L$ curves were used to determine swimbladder size with a swimbladder scattering model. Fish swimbladders are not spherical, nonetheless their size may be conveniently expressed in terms of equivalent spherical radii (ESR) (i.e. the radii of spheres of equivalent volume). Thus ESR can be derived independently from acoustic data and trawl data and compared to evaluate each method for assessing population statistics.

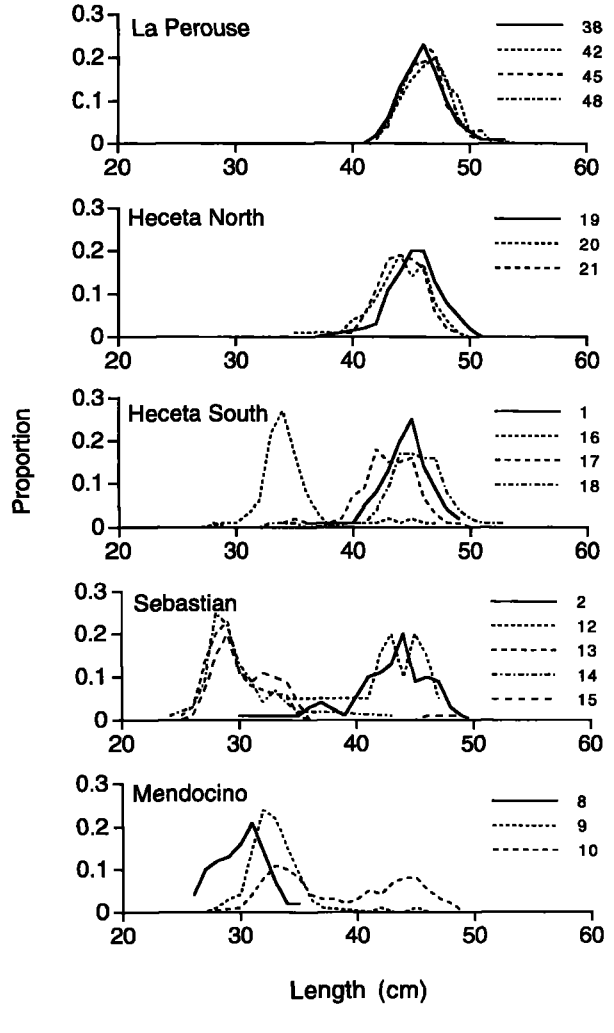


**Figure 2**

Length of hake taken in the 1992 NMFS acoustic-midwater trawl survey. Lengths are shown for trawls grouped by geographic region. Numbers indicate NMFS trawl number.

## Inverse solution

The ESR of the scatterers were obtained from the $S_L$ curves of the acoustic data with the nonnegative least squares solution of

$$\mathbf{S} = \sigma\mathbf{n}, \tag{1}$$

(Holliday, 1977b) for $\mathbf{n}$, a column vector containing the number of scatterers in each of $p$ size classes of swimbladder radii. $\mathbf{S}$ is a column vector of measured layer backscattering cross sections $\sigma_{bs_L}$ ($S_L = 10 \log \sigma_{bs_L}$) for the $q$ frequencies at which measurements were made. The matrix $\sigma$ is of dimension $q \times p$ and contains individual backscattering cross sections $\sigma_{bs_i}$ that are calculated over each of the $q = 21$ measurement frequencies (1/6 octaves from 500 to 5,000 Hz) and $p = 18$ semilogarithmically spaced radii ($r$=0.25, 0.3, 0.35, 0.4, 0.45, 0.5, 0.6, 0.7, 0.8, 0.9, 1.0, 1.2 1.4, 1.6, 1.8, 2.0, 2.25, and 2.5 cm) with a model of swimbladder resonance (Eq. 3 below). In solving Equation 1, the number of measurement frequencies varied from station to station depending on data quality, with from 4 to 6 of the lower 1/6 octaves excluded. This variation was usually due to lower-frequency data that were low level and affected by noise. The inverse solution was also restricted to exclude radii smaller than the radius expected to be resonant at 5,000 Hz at the depth of each layer. These radii were calculated with the subsequent Equation 4 for the resonance frequency, $f_0$. The quality of the inverse solution of Equation 1 for $\mathbf{n}$ was examined by comparing the original data, $\mathbf{S}$, to an estimate of the layer strength obtained from the forward calculation $\hat{\mathbf{S}} = \sigma\mathbf{n}$.

Solution of Equation 1 above assumes that the $\sigma_{bs_L}$ are the backscattering cross sections of a unit horizontal area of a layer of dispersed acoustically noninteracting scatterers, such that

$$\sigma_{bs_L} = \sum_{i=1}^{\Phi} \sigma_{bs_i}, \quad (2)$$

where $\sigma_{bs_i}$ is the backscattering cross section of the $i^{th}$ scatterer and $\Phi$ is the number of individuals within a 1-m$^2$ vertical column that extends over the depth of the layer. At some stations, usually at night, several layers were evident. In these cases, Equation 1 was solved for each individual layer, and the subsequent distributions of ESR were summed.

## Swimbladder model

The matrix $\sigma$ of individual backscattering cross sections $\sigma_{bs_i}$ was calculated with Love's model (1978) which models a fish swimbladder as an air-filled viscous spherical shell. The acoustic cross section in the back-scattered direction, $\sigma_{bs}$, for a single swimbladder of radius $r$ is given by

$$\sigma_{bs} = \frac{r^2}{\left(\frac{f_0^2}{f^2 H^2} + \left(\frac{f_0^2}{f^2} - 1\right)^2\right)}, \quad (3)$$

where $\sigma_{bs}$ is in m$^2$;
$r$ is in m;
$f$ = the insonifying frequency in Hz;
$f_0$ = the swimbladder's monopole resonance frequency in Hz; and
$H$ = a damping factor.

The resonance frequency is

$$f_0^2 = \frac{3\gamma_a P}{4\pi^2 r^2 \rho}, \quad (4)$$

where $\gamma_a$ = the ratio of specific heats of air ($\gamma_a$=1.4);
$P$ = the ambient pressure in Pa; and
$\rho$ = the density of fish flesh in kg/m$^3$.

The damping factor is

$$\frac{1}{H} = \frac{2\pi r f^2}{f_0 c} + \frac{\xi}{\pi r^2 f_0 \rho}, \quad (5)$$

where $c$ = the speed of sound in water in m/sec; and
$\xi$ = the viscosity of fish flesh in Pa sec.

Love's model includes a term in Equation 4 that accounts for the effects of swimbladder wall tension on $f_0$ and a thermal damping term in Equation 5. However, Love (1978) shows that these terms are negligible for the present case, therefore they were omitted for clarity. The physical properties of fish used here were taken from Love (1978): $\rho$ = 1050 kg/m$^3$ and $\xi$ = 50 Pa sec.

Swimbladders are not spherical but resemble prolate spheroids or cylinders with major-to-minor axis (length-to-diameter) ratios up to 10. However, it has been shown that spheroidal and cylindrical air bubbles have only a slightly higher resonance frequency than spherical bubbles (Weston, 1967; Feuillade and Werby, 1994; Ye, 1997). Love's model with Weston's correction to the resonance frequency has recently been used successfully to examine scattering from commercial-size fish in several ocean regions (Love, 1993; Thompson and Love, 1996) and what are presumed to be deep-water grenadiers off Oregon (Nero et al., 1997).

To model hake for this study, we assumed the swimbladder to be a prolate spheroid with a major-to-minor axis ratio of 8. This assumption is reasonable based on our at-sea measurements on Pacific hake (see below) and reported measurements on 13 pollack, *Pollachius pollachius,* from the North Atlantic (Foote, 1985), both of which gave major-to-minor axis ratios near 8. The resonance frequency of such a spheroid is about 20% higher than for a sphere of equal volume (Weston, 1967); this correction factor was taken into account by increasing $f_0$ given in Equation 4 by a factor of 1.2. Recently, Feuillade and Werby (1994) have shown that the broadside target strength of such spheroids is about 0.5 dB less than that of a sphere. Because this difference is well within the expected error of our measurements, it was not incorporated into our model calculations.

## Fish length and bladder size

We made direct comparisons of ESR derived from the NRL acoustic data with estimates of ESR from the lengths of fish obtained in NMFS trawls. However, the process of deriving swimbladder size from fish length is problematic. Because one of the primary functions of a swimbladder is to act as a hydrostatic organ, making a fish neutrally buoyant, one can assume ratios of swimbladder volume to fish volume near 0.05 (Jones and Marshall, 1953). However, many fish are frequently less than neutrally buoyant. In addition, food and gonadal products can crowd the abdominal cavity and reduce swimbladder volumes. Repeated measurements indicate values near 0.03 are common for gadoids (Foote, 1985; Ona, 1990) but that they are highly variable (Sand and Hawkins, 1973; Jones and Scholes, 1985; Foote, 1985; and Ona, 1990). Our field measurements on five hake

caught by angling at the surface at night gave values ranging from 0.03 to 0.09 (rough approximations from fish length and swimbladder dimensions). Because these fish had ascended several meters to take artificial bait at the surface, we chose to use the more accurate determination of 0.03 for pollack and saithe, *Pollachius virens*, calculated from data in Foote (1985). For converting fish length to weight we used $W = 0.0057L^{3.026}$, determined from lengths and weights of hake captured in the 1992 NMFS trawls, males and females combined.

Calculated swimbladder size distributions were modified to account for two sources of variability expected in the natural hake population. First, for variability of bladder radii due to the above mentioned effects of food and gonadal products, we approximated the distribution of swimbladder volume to fish volume as follows: 30% of the fish had the mean value of 0.03 whereas 10% of the fish had swimbladders 50% smaller, 20% had swimbladders 25% smaller, 30% had swimbladders 25% larger, and 10% had swimbladders 50% larger than the mean. These values were based on rough approximations of information contained in Ona (1990). Second, for variability in the fish weight ($W$) to length ($L$) relationship, we approximated a normal distribution of $W$ on $L$, where 20% of the fish had the mean $W$ given by the regression equation $W = 0.0057L^{3.026}$, and 17% were 10% heavier (lighter), 12% were 20% heavier (lighter), 7% were 30% heavier (lighter), and 4% were 40% heavier (lighter) than the mean.

### Abundance and biomass estimates

Abundance data for hake were determined by summing **n**, the column vector of fish number to obtain $\Phi$. Biomass was determined by summing the product of **n**, the column vector of fish number, and the expected weight of each fish ($r$ to $L$ and $L$ to $W$, relationships above). Biomass values were averaged for the NRL stations, grouped according to NMFS fisheries assessment regions: Canada South (Sta. 1); Southern Columbia (Sta. 4, 5, 6, and 7); and Eureka (Sta. 8, 9, 10, and 11) and compared with reported surface biomass of hake obtained from the NMFS high frequency acoustic survey (Fig. 10 in Dorn et al., 1994).

## Results

### Volume scattering data

Stations 1 (Fig. 3), 7 (Fig. 4), and 11 (Fig. 5) were selected to show representative volume scattering because they are on the slope in 900 to 1500 m of water and encompass the latitudinal range of stations covered by the NRL survey (Fig. 1). Stations 7 and 11 had day and night data; station 1 had only day data. In each image, $S_v$ is shown as a function of frequency and depth. For shallow stations, bottom echoes are black. In all images, what appears to be intense scattering near the surface is actually the direct blast from the shot and close-in surface scatter. Most stations show three layers of scatterers.

All stations had a strong scattering layer between 100 and 500 m both day and night. During the day the layer was strongest at 200 to 300 m with a resonance peak at about 1,000 Hz. This layer becomes progressively deeper to the south, being centered at 200 m at station 1, 220 m at station 7, and 320 m at station 11. This layer was presumed to be composed of Pacific hake on the basis of a prior consideration of the most likely abundant scatterers.

A second layer occurred at about 50 to 200 m at night and scattered sound at 3 to 5 kHz, frequencies well above the strongest (peak) scattering from the hake (Figs. 4B and 5B). The depth and frequency of occurrence of this layer matches the findings of Kalish et al. (1986) who provide a detailed study of the composition and scattering strengths of mesopelagic fish off Oregon. Therefore, we conclude this nighttime layer to be mesopelagic fishes that, during the day, should be deeper (near 200 to 300 m), resonant above 5,000 Hz, and not detectable by our measurements. This is supported by weak daytime scattering above 4,000 Hz at 250 m (Fig. 5B), which may be the low-frequency end of this daytime mesopelagic layer.

A third layer, beginning at about 1,000 m and extending to the end of the data record was evident in all data extending beyond 1,000 m. On the basis of this layer's resonance near 2,000 Hz and its location in depth, Nero et al. (1997) concluded that this scattering layer was caused by pelagic grenadiers. In subsequent analysis we considered only the low-frequency scattering from the hake—those scattering layers that are above 600 m and have a resonance below 2 kHz.

The acoustic resonance of the hake swimbladders is evident in the layer strength data for both day and night (points, Figs. 6 and 7). During the day, the majority of the scattering occurred in a fairly narrow depth range (Figs. 3–5); therefore only one set of layer strength data was calculated at each station (Fig. 6). During the night, the fish were more dispersed, and therefore the hake layer was separated into sublayers, and layer strengths were calculated for each (Fig. 7). Day layer strengths in the north at station 1 peaked at a slightly lower frequency (1,050

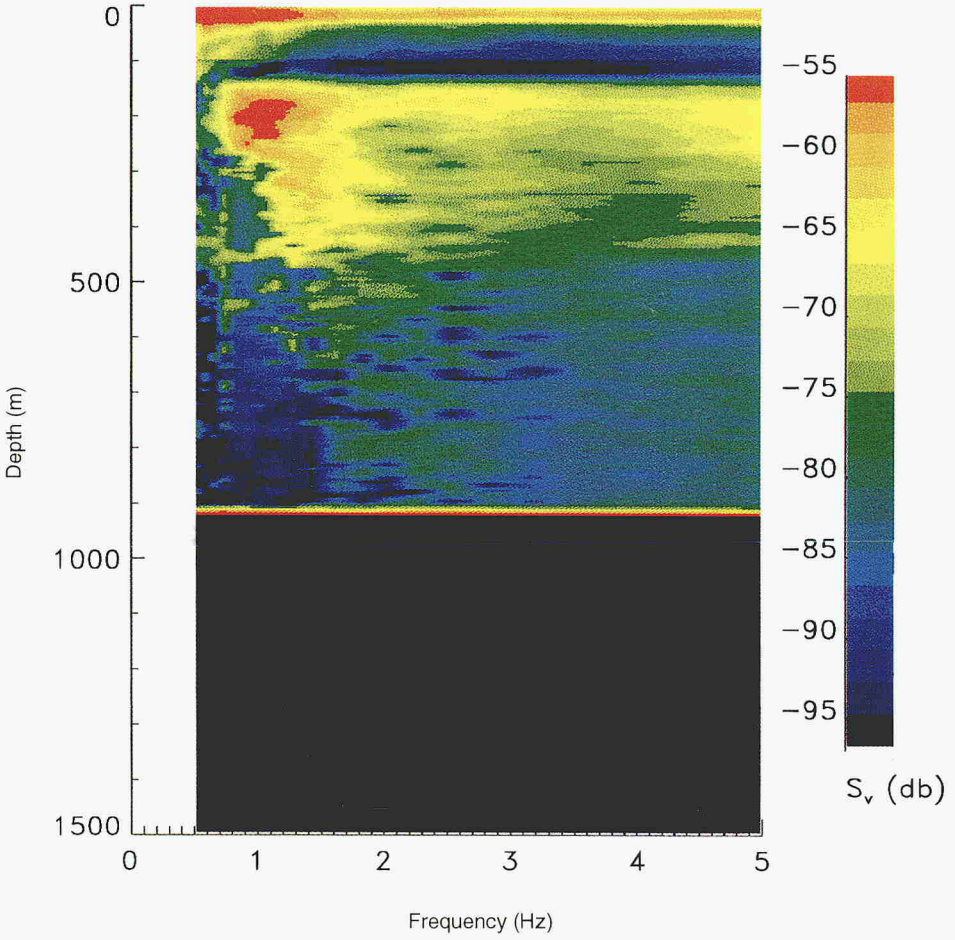


**Figure 3**
Volume reverberation at NRL station 1, during the day.

Hz) than at station 11 in the south (1,400 Hz). At night the resonance peaks of the individually integrated layers differed, with the peaks of the shallow sublayers occurring at about 1,000 Hz and the resonance peaks of the deep sublayers occurring at about 1,500 Hz.

### Bladder size and number

The inverse analysis resulted in the determination of a distribution of ESR for each station grouped by geographic area (Fig. 8). The inversion gave an almost exact fit to the scattering data (curves and points in Figs. 6 and 7) indicating that the estimates of the distributions of ESR were quite good. Overall, the largest radii are near 2.2 cm, peaks occur between 1.2 and 1.8 cm, there is a dip at 0.8 cm, and smaller peaks occur between 0.5 and 0.7 cm. With the weight-length regression for hake given earlier, a swimbladder volume to fish volume ratio of 0.03, and if variabilities in either are ignored, $L = 28r$. Thus, the inversion tells us that, if the larger scatterers are hake, they are between 22 and 62 cm long with the greatest number between 34 and 50 cm (ignoring that variabilities increase the size range slightly). Figure 2 indicates that NMFS caught hake between about 25 and 55 cm length, with the greatest number between 28 and 46 cm length. Hence, we believe the estimated size range agrees well with trawl data, and we feel confident in our assumption that the scatterers with ESR of 0.8 to 2.2 cm are, indeed, Pacific hake.

Scatterers with ESR below 0.8 cm were present at all stations with the greatest numbers occurring between 0.5 and 0.7 cm (Fig. 8). According to their ESR, these fish are probably a mixture of mesopelagic fish and northern anchovy. This is consistent with findings of Kalish et al. (1986) who caught several spe-

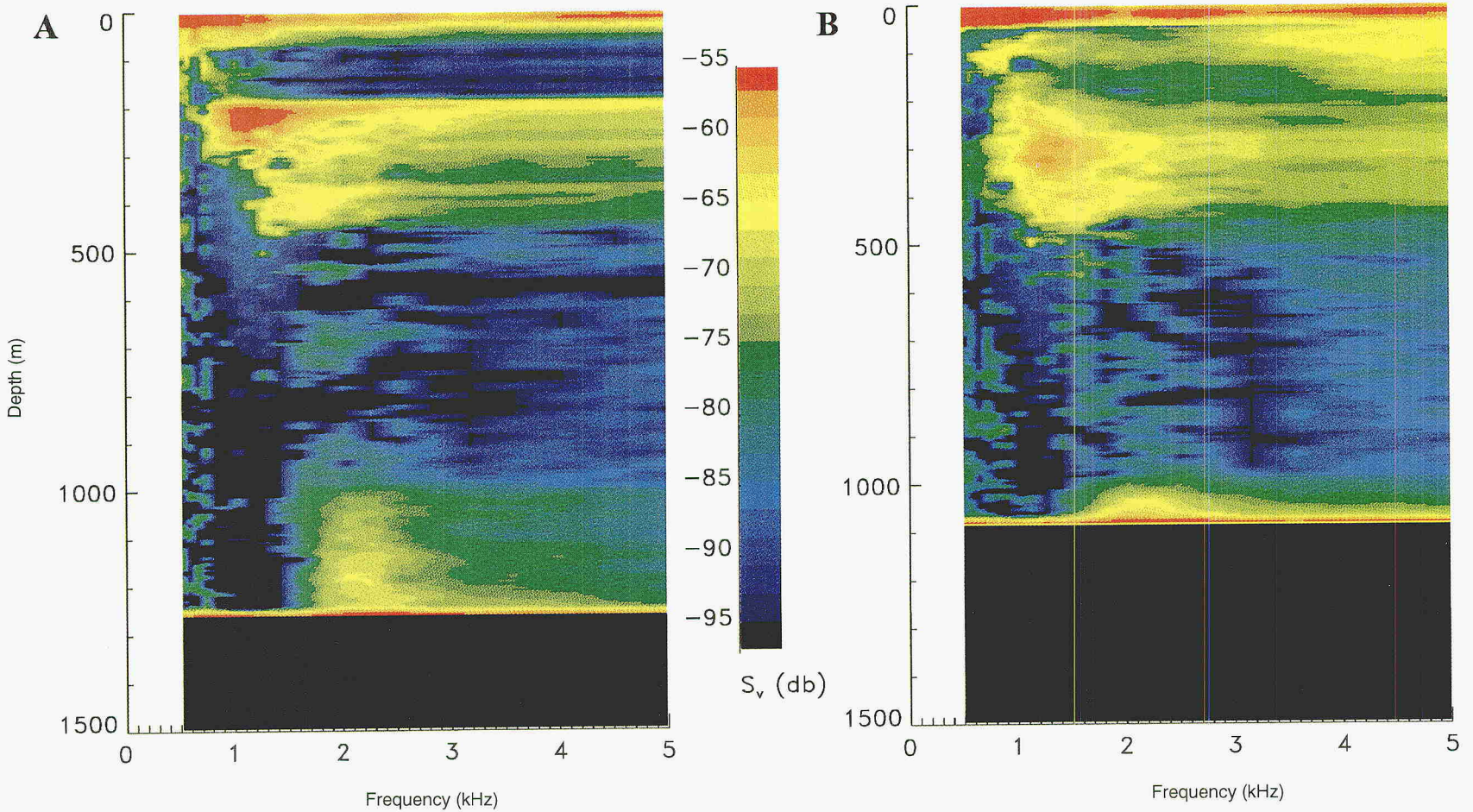


**Figure 4**

Volume reverberation at NRL station 7; (**A**) during the day, and (**B**) during the night.

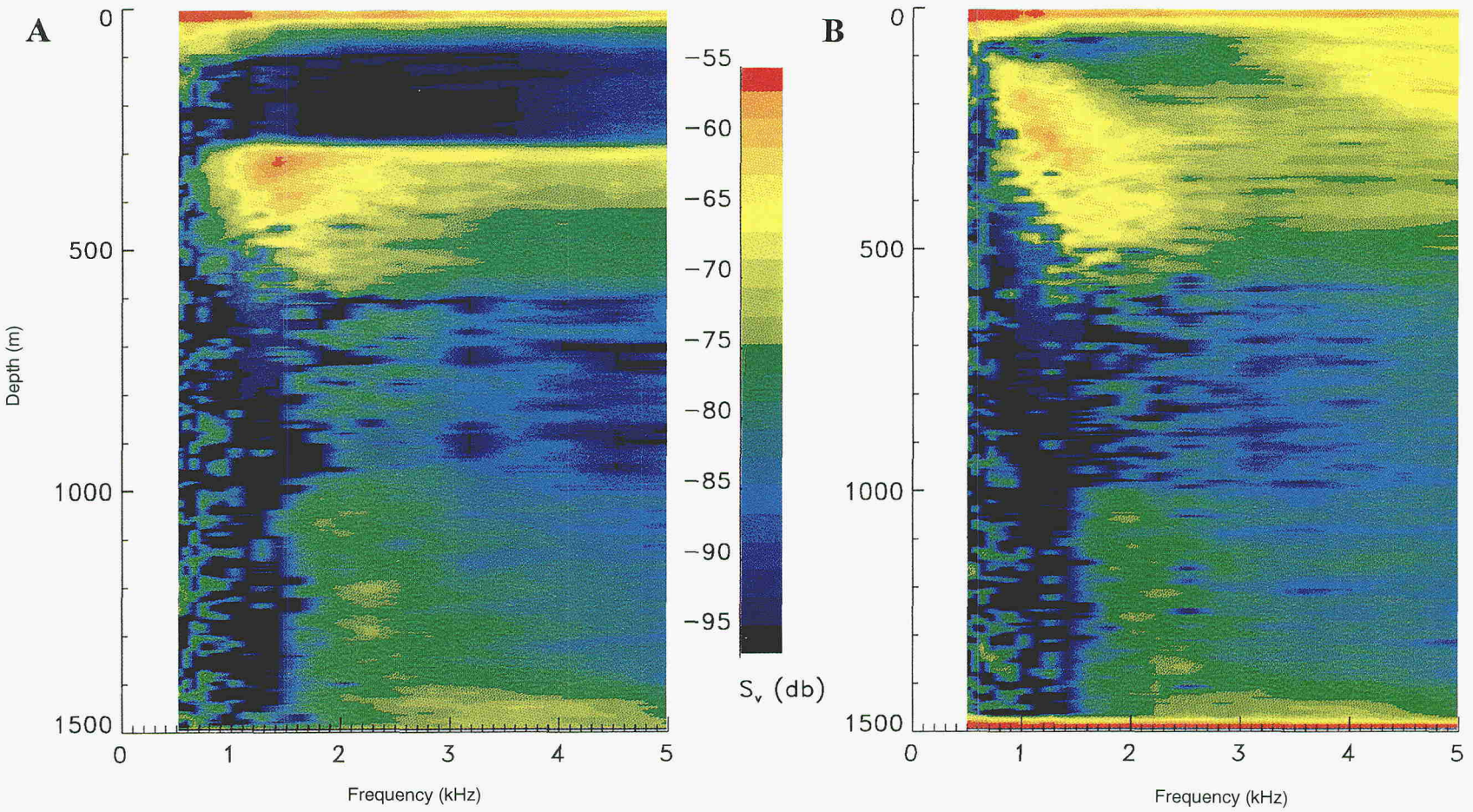


**Figure 5**

Volume reverberation at NRL station 11; (**A**) during the day, and (**B**) during the night.

cies of mesopelagic fish (*Symbolophorus californiensis*, *Tarletonbeania crenularis*, and *Diaphus theta*) and northern anchovy (*Engraulis mordax*) off the coast of Oregon at depths corresponding to our acoustic layer depths and had ESR between 0.1 and 0.7 cm. Thus, we expect that the fish with ESR between 0.25 and 0.7 cm in the present study are most likely these species.

For a more complete comparison of the trawl and low-frequency acoustic data, the lengths of hake caught in trawls were converted to ESR by using the previously mentioned weight-length regression and the swimbladder-volume-to-fish-volume ratio. The conversion included the variability in both relationships so that these ESR would be equivalent to the measured ESR. Figure 9 shows the resulting trawl estimates of ESR. The estimated distributions agree well with the measured ESR in the north at La Perouse, Heceta North, and Heceta South but not at the southern stations of Sebastian and Mendocino. The trawl data show a clear north–south trend in fish size (Figs. 2 and 9), whereas the acoustic data (Fig. 8) indicate that ESR, and presumably hake body size, do not change with latitude. The NRL low-frequency acoustic measurements did not show the same north–south trend in fish size that was apparent in the trawl data.

A summary of the number of swimbladders for small, 0.25–0.7 cm, and large fish, 0.8–2.5 cm, determined from the low-frequency acoustic data is given in Table 2, which includes information on the peak depth at which scattering occurred and the depth range of each layer. The density of small fish was much greater at night than during the day because these fish probably migrated to below 200 m during the day where they were resonant well above 5 kHz. For the large fish (presumably hake), at all stations where day–night measurements were made, densities were determined to be higher during day than at night. These higher daytime densities likely occurred because some hake migrated above 50 m depth at night and were missed because of the signal saturation caused by the explosion. (Measurements with an upward-looking system indicated that hake migrated to within several meters of the surface at some stations at night[2]).

The quasi-synoptic NRL and NMFS measurements provided an opportunity to compare two independent measures of the surface density of hake for several large regional areas of the U.S. West Coast. Only daytime density estimates were compared because data suggested that hake near the surface at night were missed by NRL acoustic measurements. Daytime surface density estimates for both surveys are given in Table 3. The estimates differ most for Canada South (NRL station 1) where NRL saw an abundance of fish over bottom depths near 1,000 m whereas the NMFS acoustic-midwater trawl survey saw approximately 1/4 that number. NRL station 1 was within the region covered by the NMFS survey tracklines (Dorn et al., 1994) and was sampled by NRL 5 days

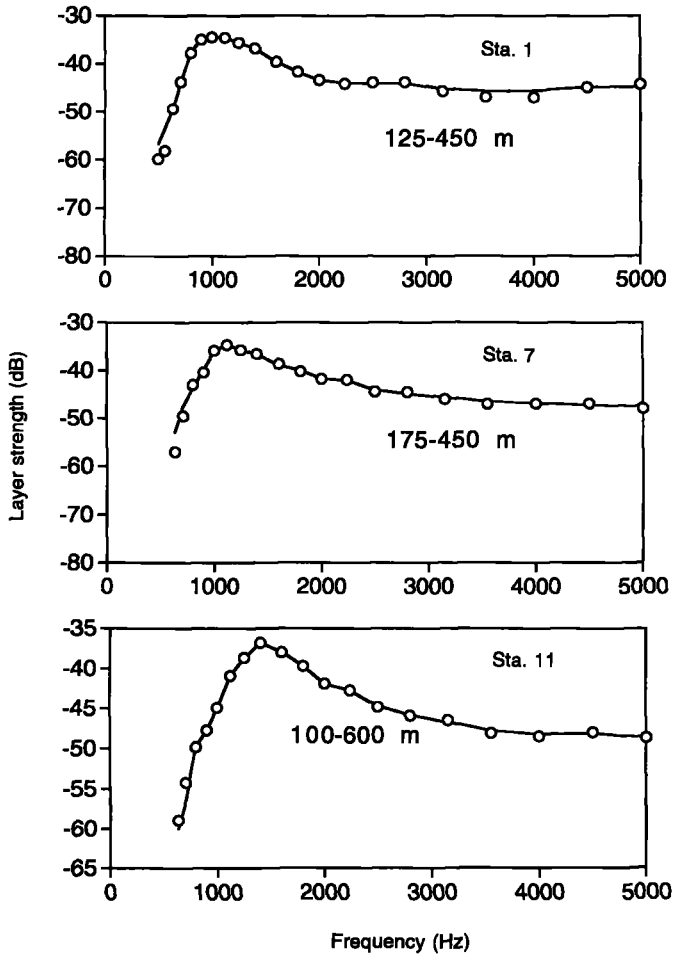


**Figure 6**

Layer strength data (open circles) for the daytime. Curves show inverse analysis fit to the data.

[2] 1992. Naval Oceanographic Office (NAVOCEANO), Acoustics Div., Stennis Space Center, MS, 39522-5001. Unpubl. data.

after the NMFS survey. At all other NRL inshore stations, densities were similar to the NMFS survey estimates. At all offshore NRL stations, densities remained high. Comparisons between the offshore NRL station data and the NMFS data were not possible because the NMFS survey did not extend beyond bottom depths of approximately 1,200 m. The offshore NRL measurements, approximately 50 km beyond the NMFS survey, gave densities as high as 300 kg/ha in layers at 300 to 400 m depth.

An examination of swimbladder behavior in hake was conducted on the NRL data by determining the relation between the acoustically measured swimbladder radii and depth for all stations (Fig. 10). In this analysis, it was assumed that hake at one station do not exhibit a size-dependent stratification in the water column. At night, hake were spread throughout the water column, allowing estimates of average ESR for several distinct layers at some stations. During the day, the hake were in a more compact single layer, resulting in only one estimate.

In Figure 10 curve, "A" depicts the shape of the relation between swimbladder radii and depth that is expected if the gas volume changed according to Boyle's Law and the bladder radius decreased with increasing depth. If hake maintain a near constant volume of gas in their bladders by adding or removing gas, then they would have a constant swimbladder radius, as depicted by line "B" in Fig. 10. There are no clear trends in the data. However, several weak relationships are worth noting. First, data taken from less than 100-m depth at stations 5 and 7 show unusually small radii suggesting some size-dependent stratification. Excluding these two values gives a weak but significant correlation for the remaining data (correlation coefficient=–0.373). In addition, two sets of data, from stations 9 and 11, and possibly from station 5, exhibit a decrease in bladder radius with depth. Stations 6 and 7 show an increase in radius with depth whereas station 4 shows maximum radius at middepth.

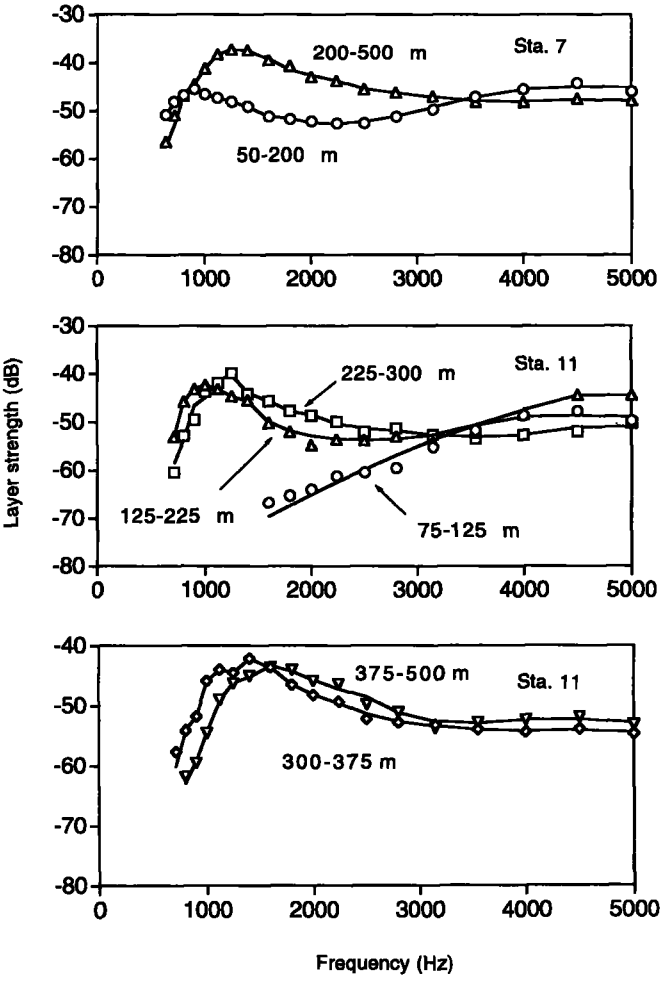


**Figure 7**

Layer strength data (symbols) for the nighttime. Curves show inverse analysis fitted to the data (note: no data were collected during night at station 1 and station 11 is separated into two panels for clarity).

## Discussion

Pacific hake are believed to be the main cause of midwater scattering at frequencies of 1–2 kHz along the continental shelf and slope of the west coast of the United States (Figs. 6–7). No other large bodied midwater fishes are as abundant as hake (Ware and McFarlane, 1989). In addition, hake made up 97% of the catch in midwater trawls taken during the NMFS triennial acoustic-midwater trawl survey in the summer of 1992.[3] Other small fishes, mesopelagic fish, and northern anchovy may be abundant but will resonate well above 2 kHz. They are believed to be the source of scattering above 3 kHz in the upper 200 m at night (Fig. 7).

[3] 1992. Alaska Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA 98115-0070. Unpubl. data.

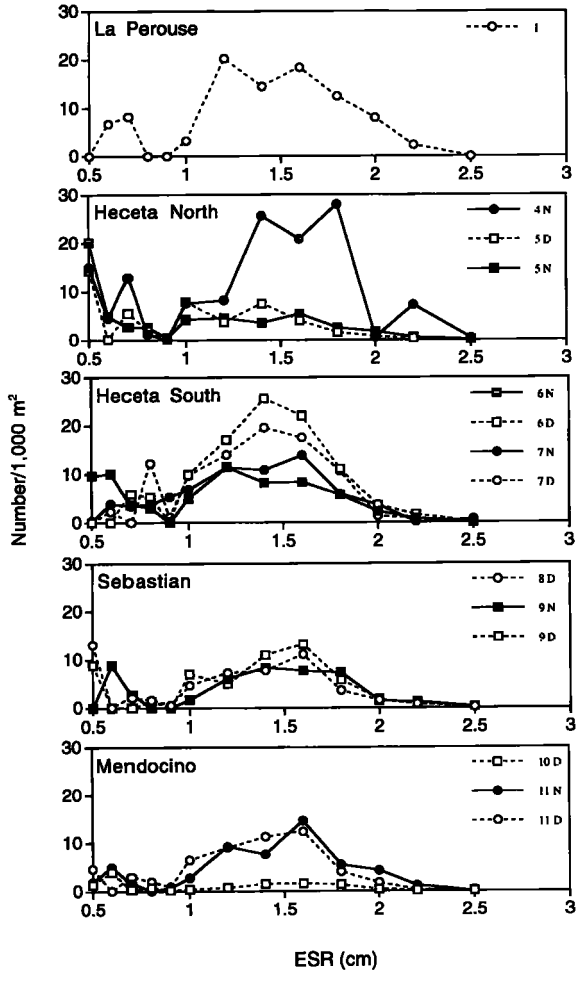


**Figure 8**

The equivalent spherical radius (ESR) of swimbladders for the NRL stations.

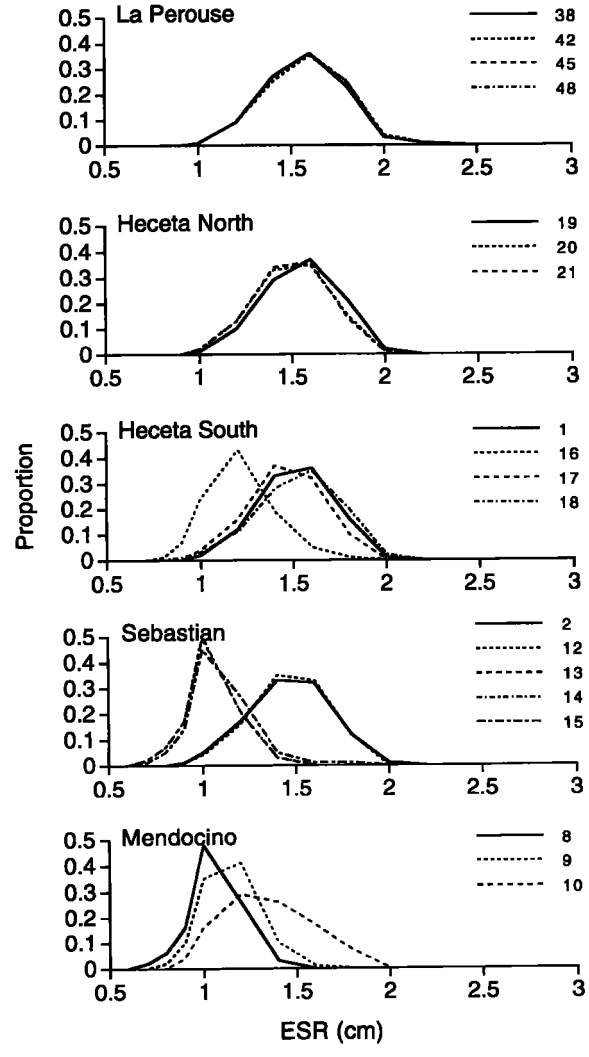


**Figure 9**

The equivalent spherical radius (ESR) calculated from the length of hake obtained from NMFS midwater trawls. Numbers indicate trawl number.

Discrepancies exist between the NMFS trawl estimates of hake size and our acoustic estimates at stations in the south of the study area. Only the larger size class of hake was detected acoustically whereas both large and small size classes of hake were caught in the trawls. Several explanations are suggested.

One possibility is that large hake mask the scattering from small hake. However, if ratios of small to large hake are anywhere close to those seen in the Sebastian and Mendocino trawls (Fig. 2), our inverse solution of the acoustic data would easily have detected both size classes.

Another possibility is that a physiological phenomenon caused the observed absence of a north–south trend in swimbladder size even though the southern fish were smaller. Such a phenomenon would have to cause the swimbladder-volume-to-body-volume ratio to increase in smaller hake. Differences in stomach fullness could cause such a trend. Food evacuation times are different for different food types: large hake eat fish that are evacuated slowly, small hake eat crustaceans that are evacuated quickly (Durbin et al., 1980, *in* Livingston, 1983) In addition, hake swimbladders could regress slightly in the larger fish. Although these hypotheses are possible, they would need to result in a complete cancellation of the north–south trend in fish size. This result is unlikely.

**Table 2**

Volume reverberation estimates of the density and depths of occurrence of probable fish swimbladders at stations along the Washington–California coast. Numbers in parentheses following densities in the 0.25 to 0.7 cm radius category are the smallest radii included in the estimates. ind. = individuals.

| Station no. | Day | | | Night | | |
|---|---|---|---|---|---|---|
| | Depth (m) | | Density (ind./1,000 $m^2$) | Depth (m) | | Density (ind./1,000 $m^2$) |
| | Peak | Range | | Peak | Range | |
| 0.25–0.7 cm radius | | | | | | |
| 1 | 200 | 125–450 | 162 (0.35) | — | — | — |
| 4 | — | — | — | 70 | 50–550 | 4,855 (0.25) |
| 5 | 380 | 250–525 | 21 (0.45) | 70 | 50–550 | 7,974 (0.25) |
| 6 | 225 | 125–475 | 30 (0.4) | <50 | 100–525 | 393 (0.3) |
| 7 | n/a | 175–450 | 6 (0.4) | 75 | 50–500 | 1,440 (0.25) |
| 8 | 325 | 150–550 | 17 (0.4) | — | — | — |
| 9 | 400 | 200–600 | 10 (0.45) | 75 | 50–550 | 1,695 (0.25) |
| 10 | 325 | 150–550 | 6 (0.45) | — | — | — |
| 11 | 300 | 100–600 | 14 (0.4) | 175 | 125–500 | 648 (0.3) |
| 0.8–2.5 cm radius | | | | | | |
| 1 | 200 | 125–450 | 79 | — | — | — |
| 4 | — | — | — | 245 | 100–550 | 99 |
| 5 | 380 | 250–525 | 28 | 375 | 50–550 | 25 |
| 6 | 225 | 125–475 | 96 | 200 | 100–525 | 45 |
| 7 | 220 | 175–450 | 87 | 300 | 50–500 | 62 |
| 8 | 350 | 150–550 | 39 | — | — | — |
| 9 | 400 | 200–600 | 46 | 425 | 100–550 | 34 |
| 10 | 450 | 375–550 | 7 | — | — | — |
| 11 | 325 | 100–600 | 48 | 275 | 125–500 | 46 |

More likely possibilities are biogeographic effects of species composition and fish size. One possibility is that the NRL measurements were not on hake but another fish such as jack mackerel or chub mackerel, which may not have exhibited a north–south trend in fish size. However, the predominant fish in the area sampled were hake. Trawls close to the NRL stations contained only 1% jack and chub mackerel.[4] Another possibility is that large hake migrated southward with the NRL survey. This is also unlikely. The NRL survey took place in the last two weeks of August. At about the same time (17 Aug) NMFS was still collecting large hake in trawls near 51°30'N (Queen Charlotte Sound). Furthermore, the commercial fishery caught large hake off Washington as late as September and October (Dorn et al., 1994).

**Table 3**

Surface density estimates (kg/ha) of Pacific hake as determined by NMFS acoustic-midwater trawl survey and NRL measurements (day only). Data are grouped by NMFS geographic regions. Numbers in parentheses indicate the number of stations included in the averages for the NRL stations.

| Region | Bottom depth (m) | | |
|---|---|---|---|
| | NMFS 1,000–1,200 | NRL inshore 900–1,500 m | NRL offshore 2,400–3,100 |
| Canada South | 91 | 439 (1) | — |
| Southern Columbia | 369 | 348 (1) | 270 (2) |
| Eureka | 238 | 195 (2) | 300 (2) |

The most reasonable hypothesis to explain the discrepancy between trawl and acoustic estimates in hake size in the south of the study area is that the same cohort of hake was encountered at all NRL sta-

[4] 1992. Alaska Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA 98115-0070. Unpubl. data.

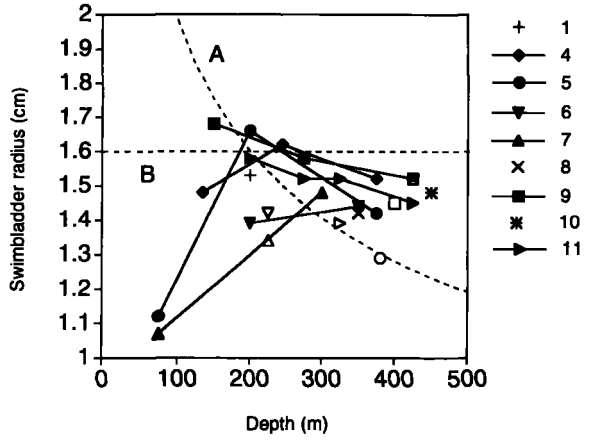


**Figure 10**

Mean equivalent spherical radius (ESR) in sublayers at night (dark symbols) and daytime (open symbols with same shape) for NRL stations. Stations 1, 8 , and 10 are daytime only. Dashed lines are (**A**) the calculated ESR for a swimbladder exhibiting constant mass of gas (decreases over depth), and (**B**) constant volume of gas (level with depth).

tions. There is some evidence that different cohorts stay together and remain separate from other size classes along the same section of coast. In the NMFS trawl data, most trawls show two predominant size groups, large hake (modal size >40 cm) and small hake (modal size <40 cm). These two groups rarely occurred in the same trawls. Where the two size groups overlapped (between 38°N and 43.5°N), two trawls caught large numbers of both size groups, two trawls caught large fish, and six trawls caught small fish. Some of the trawls with small fish were made near NRL stations 7 and 8. We hypothesize that at the time of the NRL survey (35 to 39 days after the NMFS survey), these small hake may have moved slightly inshore or south of the NRL stations and were replaced by larger fish.

Our interpretation of resonance and calculation of swimbladder size and fish size required assumptions of the relation of swimbladder radius, $r$, to fish length, $L$. We also assumed that this relation was constant with depth. As gadoids migrate they do adjust the gas volume of the swimbladder (Sand and Hawkins, 1973). Unfortunately our examination of swimbladder behavior in hake is inconclusive. The results of examining radius as a function of depth suggest that hake do compensate somewhat for pressure changes by adding and removing gas; however, they do not appear to compensate completely. We caution that this conclusion is conjectural and could be an artifact of size-dependent stratification of hake in the water column. Overall, bias introduced in our estimates by not accounting for the possible addition and removal of gas to the swimbladders of fish descending and ascending could have resulted in, assuming the worst case, an underestimate of length and biomass by 10% and 35%, respectively. This bias would not have affected our estimates of fish numbers because they were dependent on the number of radii independent of associated fish size.

Comparison of the NMFS survey estimates of surface density with the NRL estimates of surface density produced several important findings. First, although there were spatial and temporal differences in the surveys and although different acoustic techniques were used, the similarities between the surveys were encouraging and suggest that good accuracy is obtained with both techniques. Second, an NRL measurement at one station (one-mile drift) may be influenced by local minima or maxima in hake density. This hypothesis is suggested by the high values at station 1 where only a few days previously, in NMFS samples, much lower values were obtained. By chance at station 1, NRL may have made a measurement over an isolated concentration of fish. Third, relatively high densities of fish were seen at offshore stations in NRL sampling. Some NMFS acoustic transects suggest a high abundance of fish near the offshore limit of several transects taken near 43°N (Dorn et al., 1994). This high abundance would indicate that, at times, high densities of hake occur offshore, probably as a result of a particular set of as-yet-unknown oceanographic conditions.

This study has two important implications for fisheries surveys. First, hake may occur in high numbers, up to 300 kg/ha, approximately 50 km offshore of the outer edge of traditional fisheries acoustic surveys. Second, at these offshore sites the peak in the main scattering layer of hake may at times occur at depths of 400 to 450 m. At these depths hake could be difficult to assess by conventional 38-kHz fisheries sonars; therefore underestimates of the abundance of hake over deep water are possible.

## Acknowledgments

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**Abstract.**—Annual fluctuation in the number of newly settled juveniles and in the stock size of the sunray surf clam, *Mactra chinensis*, were examined from 1987 to 1994 off the coast of Tomakomai, southwest Hokkaido. Stock size was estimated with a model based on two known population parameters, juvenile density and age composition. Juvenile density and the stock size (or mass) ranges were 1.3 to 157.0 ind./$m^2$ and 249.8 to 1,127.4 metric tons, respectively; a time lag between the relative fluctuations of both agreed with age-at-recruitment to the stock. Our results suggest that population dynamics are directly influenced by the number of juveniles. The predicted stock size approximated the measured value and, consequently, a long-term prediction of stock size was deemed possible, provided age composition and juvenile density are determined.

# Population dynamics and stock size prediction for the sunray surfclam, *Mactra chinensis*, at Tomakomai, southwest Hokkaido, Japan

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The sunray surfclam, *Mactra chinensis*, is a commercially important bivalve belonging to the family Mactridae and is widely distributed on the upper subtidal sandy bottom off the coast of Japan, China, Korea, Sakhalin, and the maritime province of Siberia (Habe, 1977). This clam has been harvested from marine waters off Hokkaido as incidental catch in the fishery for Japanese surfclam, *Pseudocardium sachalinensis*, which is the most commercially important bivalve in northern Japan (Kinoshita and Terai, 1954).

Recently, the demand for *M. chinensis* caught off Hokkaido has increased owing to decreasing catches on Honshu Island (Kurata, 1991). However, from 1985 to 1994, the annual Hokkaido catch fluctuated between 705 and 1,310 metric tons. In response to this wide fluctuation, stock management plans are now required. Although there are some studies of the breeding season (Miyazaki, 1957; Tomita, 1974), growth (Hanaoka and Shimazu, 1949), spatial distribution (Hayashi et al., 1965, 1967), increase in the number of juveniles (Inoue and Ozu, 1960; Yoshimatsu, 1977), and catch fluctuation (Saito et al., 1982), these studies have provided only fragmentary information. Of necessity, several temporary stock management measures, similar to those used for *P. sachalinensis*, have been implemented by several fisheries cooperative associations in Hokkaido to regulate the fishery for *M. chinensis* . These measures include limiting allowable catch and imposing a minimum harvestable shell length and period or area for fishing. We have systematically studied the life history of *M. chinensis* and have already reported on its reproductive cycle (Sakurai et al., 1992), age at first maturation (Sakurai et al., 1992), relation between

age and growth (Sakurai, 1993), spatial distribution pattern (Sakurai, 1994), and annual mortality rate (Sakurai, 1996) off the coast of Tomakomai, southwest Hokkaido, Japan.

The aim of this study is first to examine the fluctuation in density of newly settled and harvestable-size *M. chinensis* at Tomakomai and to predict the stock size according to the population parameters that we have already reported.

## Materials and methods

### Study area

The study was conducted on a subtidal sandy bottom off Tomakomai (42°36'N, 141°32'E), where *M. chinensis* with shells longer than 60 mm are harvested commercially. Figure 1 shows the survey area in relation to the entire fishing ground, which is about 32 km$^2$ in area. The survey area is situated on the fishing grounds within 6 km of shore and covers depth ranges from 3 to 11 m. The sediment in the area is fine or very fine sand with low organic carbon content, less than 0.3% of dry weight (Sakurai et al., 1991). The bottom water temperature at 10-m depth ranges between 3.0°C in March and 20.2°C in September (Sakurai, 1993).

### Sampling and processing of clams

The breeding season of *M. chinensis* occurs between July and September at Tomakomai (Sakurai et al., 1992), the planktonic larval period lasts for 14–21 days (Tsurui, 1980; Kobayashi and Ujima, 1983), and shells of newly settled juveniles grow to 1–3 mm long between September and November (Sakurai, 1994). The density of newly settled juveniles was therefore

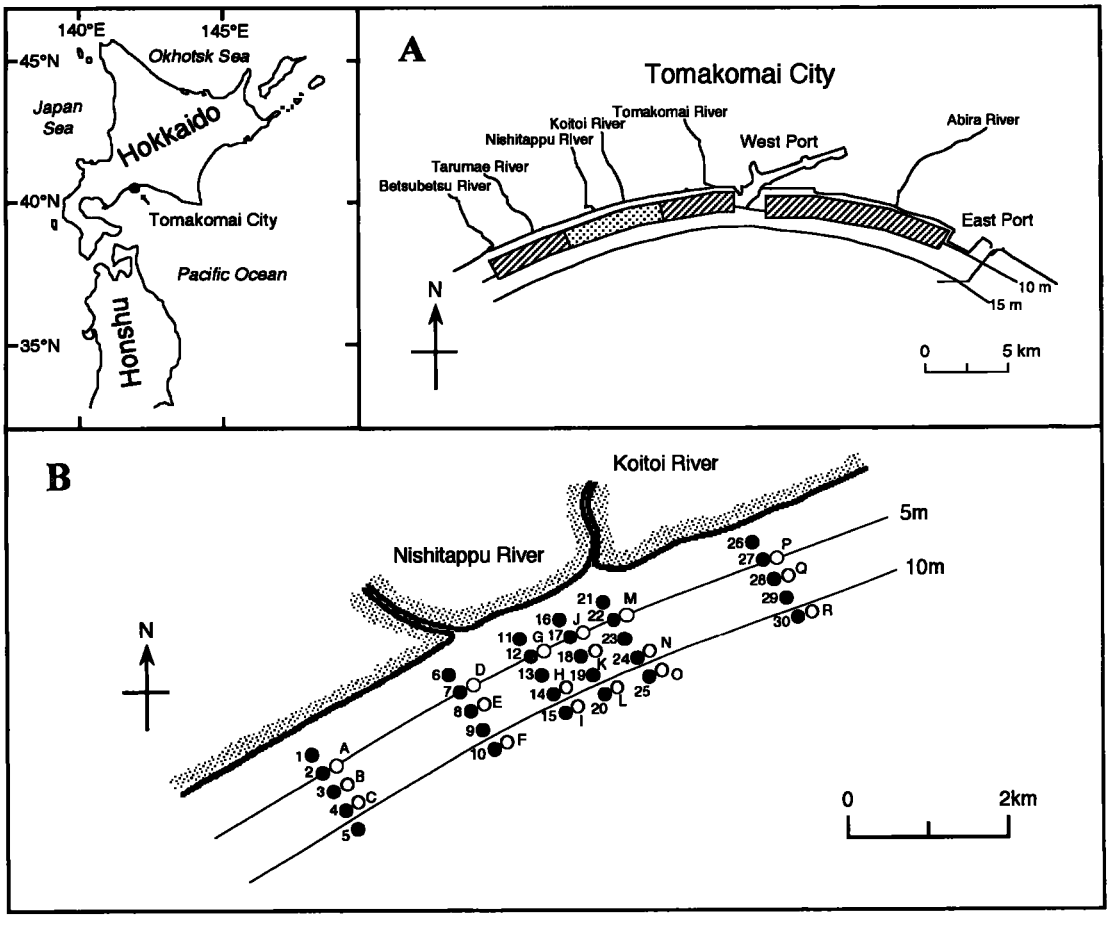


**Figure 1**

Location of the survey area off the coast of Tomakomai, southwest Hokkaido, Japan. (**A**) Shaded and dotted portions represent the entire fishing ground of *M. Chinensis*; dotted portion represents the survey area. (**B**) Solid and open circles indicate stations sampled by a Smith-McIntyre grab sampler and Japanese surfclam hydraulic jet dredge, respectively.

investigated during September and November in 1987–94 as tabulated in Table 1. Thirty sampling stations used for the collection of juveniles were arranged as shown in Figure 1. Each of the stations was set up at six transects including depths of 3, 5, 7, 9, and 11 m for evaluating the average density of juveniles in the fishing ground. The distribution of juveniles had been previously observed at 9 m, parallel to the shoreline in Tomakomai (Sakurai, 1994). Two samples were collected at each station with a Smith-McIntyre grab (sampling area: 0.05 $m^2$), sieved through a 1-mm mesh, and preserved immediately in 5% buffered formalin in the field. Sorting, identification based on morphological characteristic of the shell (Habe, 1977), and counting of juveniles were done in the laboratory.

Harvestable-size clams with shells >60 mm long were collected at 18 sampling stations in April, 1987–94 (Fig. 1; Table 1). Samples were collected with a hydraulic jet dredge (width=1.2 m, mesh size of net bag=70 mm, spacing of teeth=36 mm, and angle of tooth=60°) normally used for collecting *P. sachalinensis*. The dredge was towed parallel to shore for 50–100 m at each station. Distance of each tow was estimated by measuring the length of the dredge-connected rope wrapped by a winch. Sorting was conducted in the field. Shell lengths were measured to the nearest 0.1 mm with a sliding caliper in the laboratory. Clams with shells >60 mm long were grouped into 5-mm intervals and counted at each station. These counts were subsequently adjusted on the basis of catch efficiencies of the dredge for the different 5-mm-long intervals (60–65 mm to 0.75, 65–70 mm to 0.82, 70–75 mm to 0.88, 75–80 mm to 0.95, and >80 mm to 1.00), which were based on the selectivity curve of *M. chinensis* (Nashimoto, 1984), before density (ind./sample area) was estimated. The density was then converted to biomass (g/sample area) by using the weight (g) equivalent for the median shell length of each size interval. The length-weight equivalent was determined from 107 clams with shells 57.8–83.4 mm long sampled at station N (Fig. 1) in April 1991 as follows:

$$\log W = 3.16 \log L - 4.071, \quad (r = 0.9728, P < 0.01) \quad (1)$$

where $W$ = the weight (g); and
$L$ = the shell length (mm).

Next, the stock size ($N_e$; unit: $t$ [age in years]) in the survey area was estimated with the following equation:

$$N_e = 18^{-1} A \sum_{i=1}^{18} b_i l_i^{-1} w^{-1} \times 10^{-6} \quad (2)$$

where $A$ = survey area (72 × 105 $m^2$);
$b_i$ = biomass (g/sample area) at each station;
$l_i$ = tow distance (m) at each station; and
$w$ = width of the dredge (1.2 m).

In *M. chinensis*, an external growth ring with a light penetrable band, as shown in Figure 2, is formed annually on the shell during declining water temperature, November–January, and is able to be distinguished from other rings (Sakurai, 1993). For the stock size prediction, therefore, the age of clams was determined by counting these rings. Clams with shells >60 mm long sampled at station N (Fig. 1) in April 1991 were used for age determination because the distribution of harvestable-size *M. chinensis* was observed at 9 m parallel to the shoreline in Tomakomai (Sakurai, 1996) and because specimens were considered typical of age composition in the survey area. Age determination was conducted by first washing out the shell periostracum of the specimens with a chlorine bleaching agent and by drying it in the shade. Next, the specimens were put on a light box, and external growth rings with light penetrable bands were counted.

Age-determined clams were grouped into 5-mm intervals at each age and counted. These counts (ind./sample area) were adjusted by using the above efficiencies, and then density (ind./$m^2$) was estimated at each age by multiplying the counts by tow distance and width of the dredge.

**Table 1**

Sampling dates of newly settled juveniles and harvestable-size clams of *M. chinensis*.

| Year | Newly settled juveniles | Harvest-size clams |
|---|---|---|
| 1987 | 20 Nov | 2–5 Apr |
| 1988 | 15 Nov | 1–4 Apr |
| 1989 | 21 Nov | 2–5 Apr |
| 1990 | 4 Sep | 11, 12 Apr |
| 1991 | 26 Nov | 10, 11 Apr |
| 1992 | 15 Oct | 16, 18 Apr |
| 1993 | 20 Sep | 12, 13 Apr |
| 1994 | 29 Nov | 20, 21 Apr |

## Stock size prediction

The predicted stock size ($N_{pi}$; $i$=1992,1993, . . . , 1997; unit: $t$), based on the age composition in April 1991, was estimated for each year class as follows:

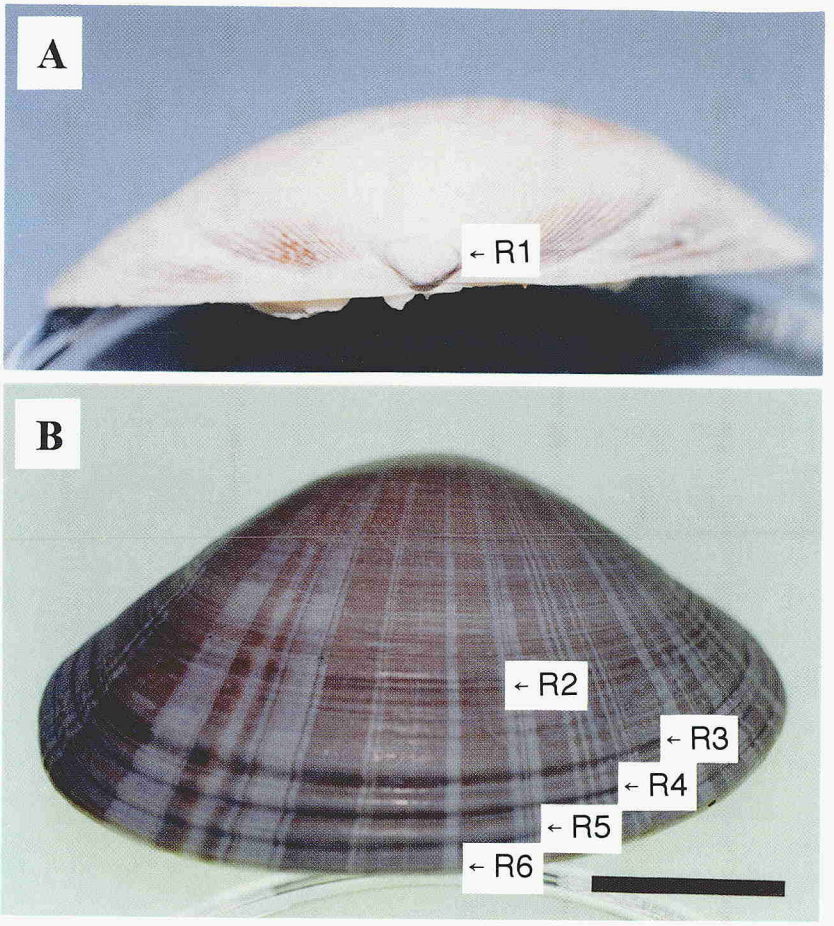


**Figure 2**

*Mactra chinensis*. Dorsal view (**A**) and outside view (**B**) of the right valve of a clam from Tomakomai in June 1992. $R_n$ ($n$=1–6) indicates the $n$th external growth ring with a light penetrable band as clear rings could be distinguished from other innumerable fine rings. Scale bars represent 20 mm length.

$$N_{pi} = A\left\{\sum_{t=tc}^{t_{\lambda-1}} n_{t,i-1} S_t W_{t+1} + n_{0,i-3} S_{0-tc} W_{tc}\right\} \times 10^{-6} \quad (3)$$

where $n_t$ = density (ind./m$^2$) at age $t$;
$t_{c,}$ = age at first capture; and
$t_\lambda$ = longevity.

Although *M. chinensis* attains a commercial size at age 2.3 yr (i.e. in November of the second year) at Tomakomai (Sakurai, 1993), we assumed $t_c$ to be 2.7 yr (i.e. in April of the second year) because the real stock size and the age composition in this study were investigated during April. $S_t$ represents the survival rate at age $t$ and was calculated from the following equation:

$$S_t = 1 - 100^{-1} m_t, \quad (4)$$

where $m_t$ is the annual mortality rate at age $t$ (age 0 yr: 94.0%; 1 yr: 53.1%; 2 yr: 44.8%; 3–9 yr: 42.7%) calculated with data from Sakurai (1996) with the assumption that annual mortality is constant. In April 1992–97, $n_t$ was estimated in turn by multiplying the previous year by each $S_t$ and by adding density of recruitment which was estimated by multiplying each $n_{0,i-3}$ by $S_{0-tc}$. Density at age 10 yr and older ($n_t \geq 10$) was not considered in the estimated age composition because the longevity ($t_\lambda$) of *M. chinensis* is 10 yr (Sakurai, 1993). The weight at age [$t$+0.7] yr, $W_t$, was calculated according to Equation 1 and the following equation from Sakurai (1993) :

$$L = 78.31\left\{1 - e^{-0.67(t-0.34)}\right\}, \quad (5)$$

where $L$ = shell length (mm); and
$t$ = age (years) of *M. chinensis*.

## Results

The densities of newly settled juveniles, as shown in Figure 3, ranged from 1.3 to 157.0 ind./m$^2$ in 1987–94. The densities and the measured stock size of harvestable-size clams ranged from 0.7 to 3.1 ind./m$^2$ and from 249.8 to 1127.4 tons in 1987–94, respectively (Fig. 4).

The age composition of sunray surfclam in April 1991 is shown in Figure 5. The 2-year age group predominated with a share of 33.9%; the 6-, 7- and 3-year groups accounted for 17.3%, 12.2%, and 11.1%, respectively, and the other age groups represented less than 10% of the whole composition. Clams older than 9 years were not found in the survey area. The predicted stock size at each age in April 1992–97 calculated from Equation 3 is shown in Figure 6. It was predicted that the age groups spawned in 1988 and 1991 would predominate from age 2 to 5 in the harvestable-size clams.

Although bivalve fishing was prohibited in 1985–91 at depths of 5 to 10 m off the coast of Tomakomai, including the survey area, in order to protect *P. sachalinensis* juveniles, fishing resumed there in July 1992. Therefore, the catch of *M. chinensis* from 1992 to 1994 in the survey area was estimated by multiplying the annual catch at Tomakomai (Hokkaido, 1994, 1995, 1996) by the ratio of the survey area to the whole fishery area (Table 2). Subsequently, stock size was estimated by subtracting the value of the survey area in Table 2 from the sum of the age composition in Figure 6. The results are shown in Figure 7 together with the real stock sizes from Figure 4. The predicted values were within about 10% of the real values (Table 3).

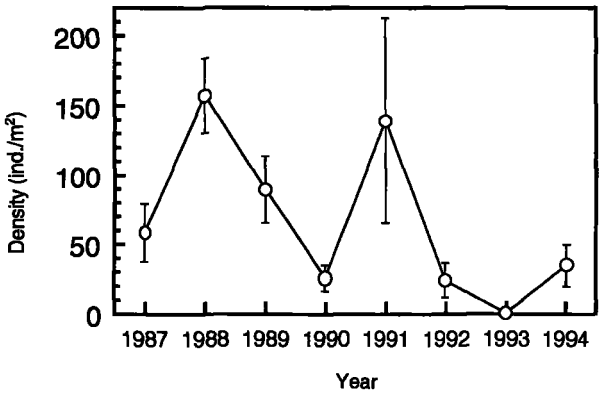


**Figure 3**

Annual fluctuation of the mean density of newly settled juvenile sunray surfclams. Vertical bars represent standard deviations.

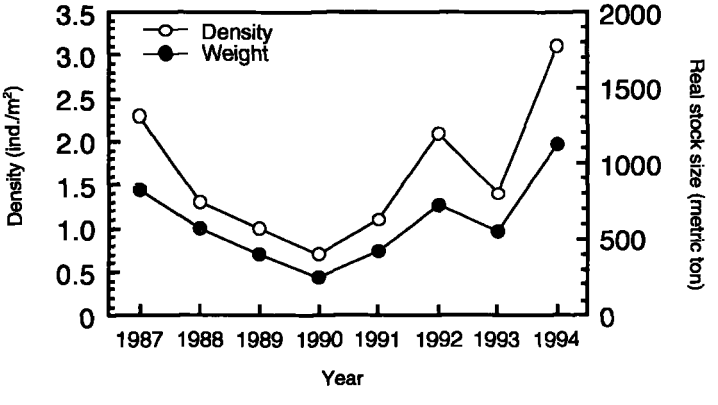


**Figure 4**

Annual fluctuation of the density (open circles) and the measured stock size (solid circles) of sunray surfclams.

## Discussion

It is well known that marine invertebrates with planktonic larval stages show considerable fluctuations in numbers of recruits; sudden increases in numbers of juveniles occur occasionally (Hanaoka, 1972). Nakaoka (1993) noted that it is necessary for these populations to experience such sudden increases in order to maintain their populations. Sudden increases of *M. chinensis* have been reported from many of the fishing grounds in Japan. For example, a maximum density of about 980 ind./m$^2$ for clams with 60-mm-long shells was reported off the coast of Miura, Kanagawa Prefecture (Inoue and Ozu, 1960). In the present study, densities of newly settled juveniles ranged from 1.3 to 157.0 ind/m$^2$ (Fig. 3); during our study we did not find such a remarkable fluctuation in recruitment off the coast of Tomakomai compared with that observed for the population off Miura. Additionally, there were no dominant or vacant age groups in the age composition (Fig. 5); thus, it appears that the population of *M. chinensis* is maintained by comparatively stable recruitment occurring off the coast of Tomakomai.

*Mactra chinensis* grows to harvestable size at age 2.3 yr at Tomakomai (Sakurai, 1993); consequently newly settled juveniles spawned in the years 1987 through 1991 are presumed to have recruited to the

stock in April 1990–94. As Figures 3 and 4 show, juvenile densities in 1988, 1989, and 1991 were relatively high, causing the real stock sizes in 1991, 1992, and 1994 to increase in comparison with each previous year. In contrast, the lower juvenile densities in 1987 and 1990 caused the real stock size in 1990 and 1993 to decrease in comparison with each previous year. Therefore, it is suggested that the population dynamics at Tomakomai are directly influenced by the number of newly settled juveniles. The number of juveniles is determined by the settlement and mortality of early benthic stages (Günther, 1992). We think that it is necessary to examine the factors that cause fluctuations in the number of juveniles to gain a full understanding of the population dynamics of *M. chinensis*.

In the present study, we define a model using two known population parameters, juvenile density and age compositions, to predict the stock size of *M. chinensis*. It has been shown that the age groups that have relatively higher densities at the juvenile stage predominate for four years from age 2 to 5 in harvestable-size clams. Saito et al. (1982) reported that a large catch of *M. chinensis* continued for a few years off the coast of Ishikari, Hokkaido, because the dominant age group was maintained. This was the case in our study. Therefore, we consider that our model is appropriate for predicting the population dynamics of *M. chinensis* at Tomakomai and other sites. Furthermore, the predicted stock size of our model was close to the measured value (Fig. 7), and consequently accurate long-term prediction of stock size is possible with this model, provided age composition and juvenile density are determined.

On the other hand, analysis of age and growth based on external growth rings has been conducted for various bivalves including *Placopecten magellanicus* (e.g. Stevenson and Dickie, 1954; Claereboudt and Himmelman, 1996), *Pecten maximus* (e.g. Dillon and Clark, 1980), *Megangulus venulosus* (Goshima et al., 1991), *Mesodesma mactroides* (Defeo et al., 1992), *Clinocardium californiense* (Goshima and Noda, 1992), and *Abra tenuis* (Dekker and Beukema, 1993). However, it is suggested that age determination based on external growth rings of bivalves would be unreliable because it is difficult to distinguish the growth rings from other rings owing to several stimuli (Dillon and Clark, 1980). Nevertheless, the growth rings of *M. chinensis* have been distinguished clearly from other innumerable fine rings by checking the rings with light penetrable bands (Sakurai, 1993). These bands are regarded as nacreous layers. Therefore, age determination in the present study would be as reliable as that based on microgrowth analysis with acetate peels or thin sections (Lutz and Rhoads, 1980), and we consider that our model would be able to predict the stock size without over- or underestimates. In our model, however, annual mortality is assumed to be constant; therefore, age com-

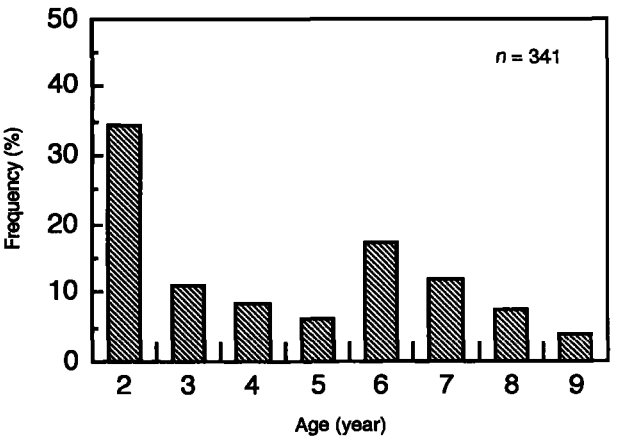


**Figure 5**

Age composition of the harvestable-size sunray surfclams sampled at station N (Fig. 1) in April 1991.

**Table 2**

Estimated catch of *M. chinensis* in the survey area and whole fishery ground off the coast of Tomakomai.

| | Catch (metric ton) | |
|---|---|---|
| Year | Survey area | Whole fishery ground[1] |
| 1992 | 7.2 | 36.0 |
| 1993 | 14.6 | 73.0 |
| 1994 | 22.0 | 108.0 |

[1] Based on data from Hokkaido Fisheries Statistics in 1994, 1995, and 1996.

**Table 3**

Comparison of the real ($R$) and predictive ($P$) stock size for *M. chinensis*.

| Year | $R$ (metric ton) | $P$ (metric ton) | $(R-P) \times 100/R$ (%) |
|---|---|---|---|
| 1992 | 728.3 | 651.8 | 10.5 |
| 1993 | 550.3 | 586.0 | –6.5 |
| 1994 | 1,127.4 | 1,015.8 | 9.9 |

position would need to be reinvestigated if there was an unexpected change in mortality, such as that resulting from clams being washed ashore by a large typhoon or other storms (Sakurai et al., 1996).

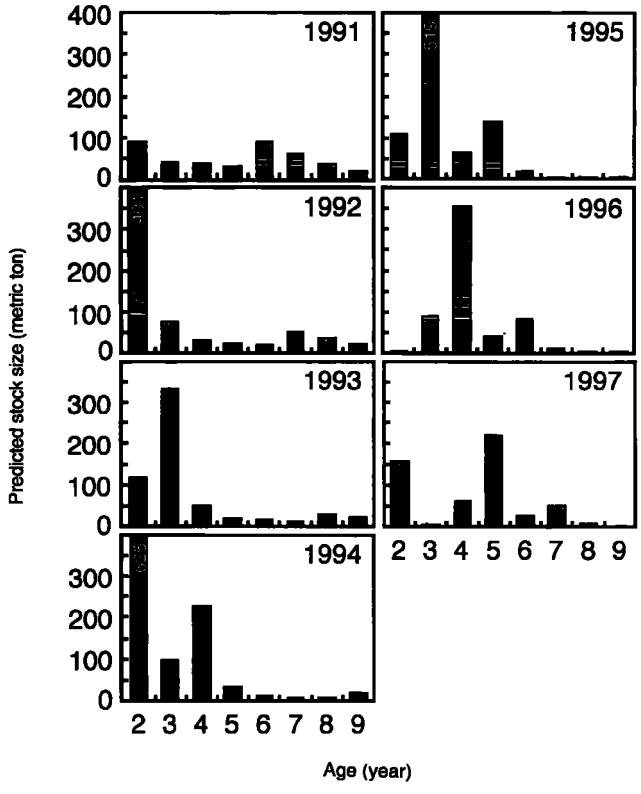


**Figure 6**
Predicted age compositions for the harvestable-size sunray surfclams in April from 1991 to 1997.

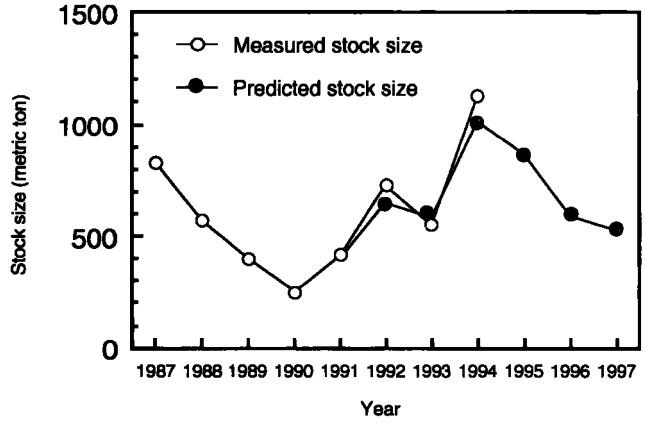


**Figure 7**
Annual fluctuation of the measured (open circles) and predicted (solid circles) stock size of sunray surfclams.

## Acknowledgments

We wish to express our appreciation to Y. Kanno and S. Goshima, Faculty of Fisheries, Hokkaido University, for their helpful advice and discussion. We are also grateful to the staff of Tomakomai Fisheries Cooperative Association for their kindness during this work.

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# Reproductive biology, growth, and natural mortality of Puget Sound rockfish, *Sebastes emphaeus* (Starks, 1911)

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In spite of being one of the most common rockfish in the rocky nearshore region of the Strait of Georgia, relatively little is known about the early life history, ecology, recruitment, and reproductive biology of Puget Sound rockfish, *Sebastes emphaeus*.

In rockfish, fecundity at 50% maturity ranges from 2,000 (*S. dalli*) to 417,000 (*S. paucispinis*) eggs per female (Haldorson and Love, 1991). Parental care in this genus is essentially lecithotrophic, characterized by primitive, unspecialized viviparity at an evolutionary stage when eggs, embryos, and early larval stages are protected inside the female body rather than born live as fairly advanced young (Wourms, 1991). Although most other northeastern Pacific *Sebastes* release their young between January and July (Westrheim, 1975), parturition occurs in August and September for Puget Sound rockfish (Moulton, 1975; Beckmann, 1995).

The goals of this study were to delineate the spawning season more closely and to determine the age and length at first maturity, the growth and mortality rates, and the length-fecundity relationship for Puget Sound rockfish.

## Materials and methods

A total of 362 Puget Sound rockfish older than age 0 were collected during 23 sampling trips in coastal waters of the San Juan Islands, from 26 June 1994 to 12 March 1995 (Table 1). The fish were collected either by anglers using hook-and-line gear or by SCUBA divers using spears and hand nets. The average collection depth for these rockfish was 15 m to 21 m, with a maximum depth of 76 m.

In addition, 19 collection trips were made with hand nets for young-of-the-year (YOY) specimens. These trips extended from 26 February through 18 August 1994, and 424 YOY were obtained.

The spawning period was defined as occurring from the time when the first females with spent ovaries were caught to the time when no females with embryos were observed. A total of 253 females older than age 0, collected between June 1994 and March 1995, were classified by maturity stage according to the criteria described in Finckh McDermott (1994). Nonlinear least square regression was used to fit the data to the logistic model:

$$P_L = \frac{1}{1+e^{-(\alpha+\beta L)}},$$

where $P_L$ = proportion mature at length $L$ (mm FL);
$\alpha, \beta$ = constants; and
$-\frac{\alpha}{\beta}$ = length at which 50% of fish are mature ($=L_{0.5}$).

Sagittal otoliths were removed from the fish and stored in 50% ethanol. Readings prepared by the break-and-burn method were taken either from left or right otoliths, following the international convention of considering 1 January as the birth date. All final age determinations were made by the coauthor with extensive age-determination experience (B. Goetz), after examining the results obtained by the senior author and then examining edge type and annulus formation for the entire collection. A sample of 59 otoliths was read twice (with six months between readings) and showed 66% agreement (to the ex-

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Fishery Bulletin 96: 352–356 (1998).

**Table 1**

Date and sampling method for collections of Puget Sound rockfish older than age 0.

| Date | Number collected | Method | Date | Number collected | Method |
|---|---|---|---|---|---|
| 26 Jun 1994 | 6 | spear | 3 Aug 1994 | 41 | hook and line |
| 28 Jun 1994 | 4 | spear | 8 Aug 1994 | 19 | hook and line |
| 29 Jun 1994 | 12 | spear or hand net | 21 Aug 1994 | 11 | spear or hook and line |
| 5 Jul 1994 | 5 | hook and line | 26 Aug 1994 | 8 | hook and line |
| 6 Jul 1994 | 22 | spear | 29 Aug 1994 | 8 | hook and line |
| 7 Jul 1994 | 11 | spear | 30 Aug 1994 | 10 | hook and line |
| 7 Jul 1994 | 20 | hook and line | 2 Sep 1994 | 21 | hook and line |
| 13 Jul 1994 | 35 | hook and line | 6 Sep 1994 | 7 | hook and line |
| 22 Jul 1994 | 15 | hook and line | 10 Sep 1994 | 13 | hook and line |
| 24 Jul 1994 | 3 | hand net | 30 Dec 1994 | 21 | hook and line |
| 26 Jul 1994 | 6 | hand net | 12 Mar 1995 | 37 | hook and line |
| 28 Jul 1994 | 27 | hook and line | | | |

act year) between independent readings, with no obvious bias.

Age-length relationships were estimated from the mean length at age for age groups 1–13, derived from the otolith readings. The mean length of age-0 fish was estimated from the mean length of the YOY captured with nets during February–August 1994. Lengths for YOY were originally recorded as standard length, and were converted to fork length by using the relationship for shortbelly rockfish (*S. jordani*) reported by Echeverria and Lenarz (1984). The mean age of YOY (0.7 years) was estimated by assuming that parturition occurred on 1 September. Mean length at age for age groups 1–13 was estimated from fish collected during June–December, 1994. Data were fitted to the von Bertalanffy growth model (Ricker, 1975) with nonlinear least squares regression. Male and female fish were treated separately owing to the difference in sex-specific growth rates.

Mortality was estimated from the age composition of catches (281 fish aged successfully, sexes combined) made during June–December. Because Puget Sound rockfish are not the target of any fishery, the catch curve (Ricker, 1975) was used to estimate natural mortality (M) with linear regression of log (frequency) on age. Only fish 3 years and older were used to estimate M, because it was apparent (Fig. 1) that 1- and 2-year-olds were not fully available to our sampling gear.

Fork length (FL) to the nearest millimeter and wet gonad weight (GW) and wet somatic weight (SW) to the nearest milligram were measured for all adult females. Somatic weight was defined as the weight of the fish with the stomach emptied and the gonads removed. The gonadosomatic index ($GSI = GW/SW$) was used to determine relative reproductive effort for a mature female of average size. Allometric relationships between GW-body length and SW-body length were determined by using log-log linear regression (Gunderson and Dygert, 1988). Only fully mature females in the later stages of vitellogenesis were used in estimating GSI. Histological examination of a subsample of 12 individuals, representing a broad range of lengths and relative GSI values, showed that all of them were in the migratory nucleus stage of egg development just prior to ovulation (McDermott[1]).

Fecundity was estimated by counting all nonatretic oocytes in advanced vitellogenesis with subsamples from both ovaries of 16 fish ranging from 112 to 178 mm FL. From preliminary measurements it could be seen that vitellogenetic oocytes were at least twice the size of the resting and immature primary oocytes. All oocytes with the longest axis exceeding 250 µm were counted. A gravimetric subsampling method (Nichol and Pikitch, 1994) was chosen to estimate oocyte numbers.

Because of the nonuniform distribution of oocytes and connective tissue within the ovaries, ovarian sacs and ovarian stroma were removed prior to subsampling. Thin sections of the remaining egg mass were taken from five different transects equally spaced along the longitudinal axis of each ovary. Each subsample was weighed, pipetted into a plastic grid dish, and the eggs of each subsample were counted. Final fecundity estimates were made by multiplying

[1] McDermott, S. 1995. School of Fisheries, Univ. Washington, Seattle, WA 98195. Personal commun.

the mean oocytes/mg, averaged across all subsamples, by total egg mass weight. Fecundity data were fit to an allometric relationship with log length-log fecundity linear regression (Haldorson and Love, 1991).

## Results

Females with unfertilized eggs were caught from 26 June to 8 August 1994. Embryos without pigmented eyes were observed from 22 July to 29 August, and embryos with pigmented eyes from 24 July to 29 August. The first spent female was observed on 21 August, and all mature females caught from 31 August to 10 September showed spent ovaries. Only resting females were captured on 30 December. Mature females captured on 12 March 1995, were either resting or in the initial stages of vitellogenesis. Spawning occurred over a relatively short time period, with only 9 days between the time when the first spent female and the last gravid female were observed. Ovaries did not contain developing embryos and cleaving eggs at the same time, indicating that individual Puget Sound rockfish spawn only one brood per season.

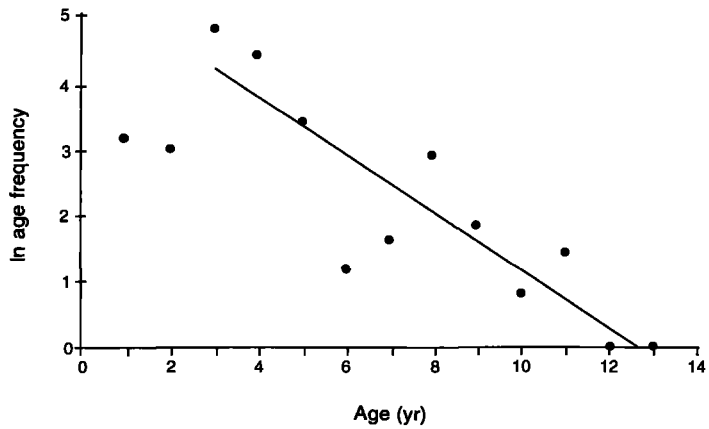


**Figure 1**

Estimation of natural mortality for Puget Sound rockfish (sexes combined) with a catch curve (predicted line).

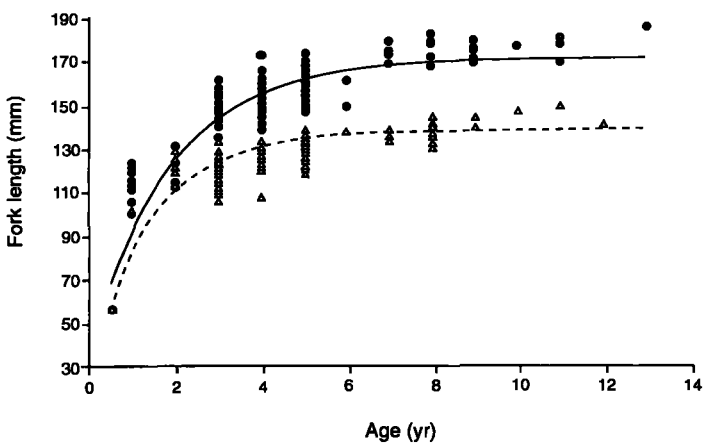


**Figure 2**

Comparison of female and male age-length (FL) relationships for Puget Sound rockfish. Solid line and filled circles show predicted relationship (von Bertalanffy growth model) and data for females; dashed line and open triangles show predicted relationship and data for males.

The oldest observed fish was a female 13 years old, followed by a 12-year-old male. The largest male caught was 145 mm FL and the largest female 178 mm FL (Fig. 2). The age-length relation (von Bertalanffy growth model) for male Puget Sound rockfish was $L_t = 137.39\ (1 - e^{-0.7042(t+0.3232)})$ and for females $L_t = 170.72\ (1 - e^{-0.5353\ (t+0.4603)})$. Based on the regression result of ln(frequency) = 5.554–0.44 (age), the instantaneous annual rate of natural mortality (M) for fish 3 years and older was estimated to be 0.44 (Fig. 1).

Female Puget Sound rockfish reached sexual maturity at a median length of $L_{0.5}$ = 121.71 mm *FL* (Fig. 3) corresponding to a predicted age of 1.87 years with the von Bertalanffy growth model. The length-maturity parameters derived from the logistic model were $\alpha = -39.678$ and $\beta = 0.326$. The average length of all mature females larger than $L_{0.5}$ was $L_{AV}$ = 150.93 mm.

The somatic weight-length relationship was $SW = 5.882 \times 10^{-5}\ L^{2.687}$ with the predicted somatic weight for $L_{AV}$ = 42.06 g. The gonad weight-length relationship was $GW = 5.869 \times 10^{-7}\ L^{3.151}$ with the predicted gonad weight for $L_{AV}$ = 4.30 g. From these two weights the GSI for Puget Sound rockfish was computed as 0.10.

The lowest fecundity was 3,295 eggs for a female of 112 mm FL and the highest was 57,787 for an individual 156 mm FL (Fig. 4). The length-fecundity (*F*) relationship was $F = 0.052\ L^{2.679}$, and the fecundity for a mature female of average length (150.93 mm) was estimated to be 35,723 eggs. The estimated fecundity per gram for a female $L_{0.5}$ cm long (Haldorson and Love, 1991) was 779 eggs.

Although egg size was variable, the majority of the eggs within an individual female were about the same size and at the same developmental stage. The time span between the capture of the first fertilized female and the first spent female yields a rough estimate of 30 days for the gestation period.

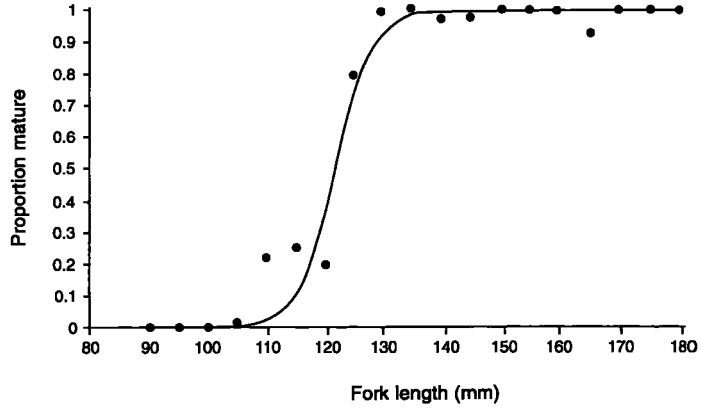


**Figure 3**

Length-maturity relationship predicted for female Puget Sound rockfish (predicted line). Solid circles indicate data.

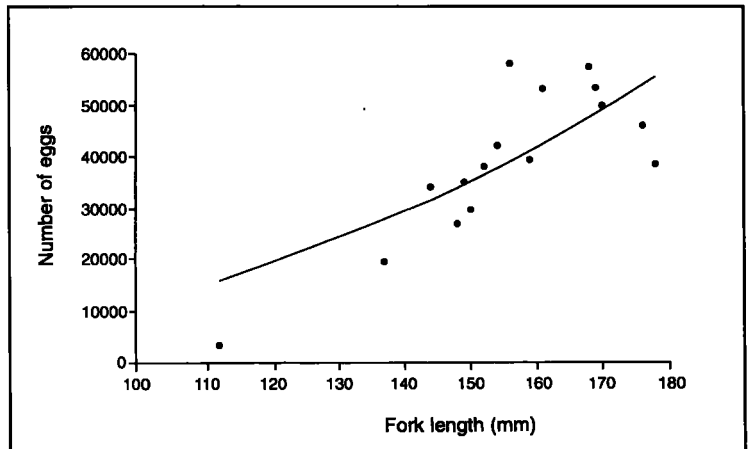


**Figure 4**

Length-fecundity relationship for female Puget Sound rockfish (predicted line). Solid circles indicate data.

## Discussion

Puget Sound rockfish show high fecundity per gram, early age at maturation, small body size, and a relatively short life expectancy compared with other rockfish of the genus. No other rockfish studied to date has a higher fecundity per gram at $L_{0.5}$ (Haldorson and Love, 1991). A high natural mortality would be expected to accompany these life history characteristics, and the estimated M of 0.44 is high compared with that of other rockfish .

Puget Sound rockfish have a GSI (0.10) close to that of other early maturing rockfish (e.g. shortbelly rockfish, GSI=0.07, M=0.26, maturation age=2 years; Gunderson, 1997). However, a comparison of the catch-curve estimate of M with empirically derived estimates suggests some possibility that the catch curve is based on an unrepresentative sample and has been overestimated. The maximum age observed in our study (13 years) corresponds to an M of 0.32 with Hoenig's (1983) empirical estimation technique, whereas the GSI (0.10) gives an estimate of M = 0.18 with Gunderson's (1997) estimator.

A constant recruitment is assumed if the catch curve is used, yet the data in Figure 2 suggest that the 1988 year class (age 6 in 1994) appears to have recruited at significantly lower levels than the others. Our catch-curve estimate of M should probably be regarded as provisional, and additional collections of age-composition data or tagging studies should be undertaken to validate it.

The fecundity of 3,300–57,800 eggs observed for Puget Sound rockfish is in the range of fecundities of similar-size rockfish. Shortbelly rockfish (18–31 cm TL) has a fecundity from 7,000 to 50,000 (Hart 1973). Our fecundity estimates for Puget Sound rockfish are comparable to those obtained by Moulton (1975).

The estimated gestation period for Puget Sound rockfish is similar to the 29-day gestation period reported for yellowtail rockfish (*S. flavidus*), a species which has been shown to be lecithotrophic, providing only a negligible amount of maternal energy during gestation (Hopkins et al. 1995). The high fecundity per gram and relatively brief gestation period suggest that parental care is limited in comparison to other rockfish.

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# Age, growth, and calving season of bottlenose dolphins, *Tursiops truncatus*, off coastal Texas

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Life history studies of bottlenose dolphins, *Tursiops truncatus*, in North America began over a century ago with observations by True (1890) on dolphins captured in a directed fishery along the coast of Cape Hatteras, North Carolina. He detected an approximately equal sex ratio but variability in size among individuals in almost every catch. He noted tooth development (eruption) and state of fissure of the umbilical cord in young dolphins, as well as reproductive state in females (i.e. lactating or pregnant). Furthermore, he suggested that calving took place primarily in the spring. Since then, much of the knowledge of life history of bottlenose dolphins in the western Atlantic has been obtained from dolphins captured incidentally during fishing operations or directly for research or display, and from stranded animals (Sergeant et al., 1973; Hohn, 1980; Hersh, 1987; Barros and Odell, 1990; Mead and Potter, 1990). More recent and extensive information on age, growth, and population biology has been obtained from a long-term study of free-ranging bottlenose dolphins in Sarasota Bay, Florida (e.g. Hohn et al., 1989; Scott et al., 1990; Wells and Scott, 1990; Read et al., 1993).

Equivalent life history studies have not been conducted on bottlenose dolphins from the north or western Gulf of Mexico, although this is the most common cetacean inhabiting the coastal waters of the northwestern Gulf (Barham et al., 1980; Fritts et al., 1983; Leatherwood and Reeves, 1983; Mullin et al., 1990). It also is the most commonly stranded species along the Gulf coast, particularly along the coast of Texas. Strandings of bottlenose dolphins have been recorded routinely in Texas since 1974 ( Jones, 1987; Schmidly and Shane[1]). Since late 1980, the Texas Marine Mammal Stranding Network (TMMSN) has recovered over 800 carcasses. In the spring of 1990 and 1992, the TMMSN documented the highest frequency of bottlenose dolphin strandings since the program began (Hansen[2]). Unusually high mortalities among bottlenose dolphins along the Texas coast have emphasized the need for baseline information on their life history to allow better interpretation of the impacts of these mortalities on the populations. The available source of data and samples to begin such studies is the strandings themselves. This study of stranded specimens was conducted to estimate 1) age structure of stranded specimens, 2) growth from length-at-age data, 3) mean length at birth, 4) calving season, and, where possible, 5) age and length at sexual and physical maturation. These data provided the material for a preliminary examination of the life history of bottlenose dolphins that inhabit the coastal waters of Texas.

## Materials and methods

From January 1981 through December 1990, 898 stranded bottlenose dolphins (373 males, 292 females, and 233 specimens of unknown sex) were recovered by members of TMMSN along the 715-km Texas coastline. Tooth sections were prepared for 205 specimens (Table 1), which comprised the entire sample of specimens from which teeth were collected. The teeth were fixed in 10% buffered formalin and processed following the decalcification, sectioning, and staining protocol described by Hohn et al. (1989). Age was estimated by counting the number of GLG's (growth layer groups, Perrin and Myrick, 1980) in dentine and cement without reference to data on the sex and length

[1] Schmidly and Shane. 1978. A biological assessment of the cetacean fauna of the Texas coast. Rep. U.S. Mar. Mamm. Comm., contract report MMC-74/05, 38 p.

[2] Hansen, L. J. 1992. Stranding rate and trends. *In* L. J. Hansen (ed.), Report on investigation of 1990 Gulf of Mexico bottlenose dolphin strandings, p. 15–20. National Marine Fisheries Service, Southeast Fisheries Center, Contribution MIA-92-93-21.

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**Table 1**

Sample sizes and sex ratios of bottlenose dolphins, *Tursiops truncatus*, stranded along the Texas coast from January 1981 through December 1990 and of the subsample for which age was estimated.

| Sample | Males | Females | Sex unknown | Sex ratio (M:F) |
|---|---|---|---|---|
| Total | 373 | 292 | 233 | 1.3 : 1 |
| Aged | 78 | 81 | 36 | 1 : 1.04 |
| <1.0 yr old | 22 | 10 | 7 | 2.2 : 1 |
| 1–20 yr old | 46 | 39 | 22 | 1.2 : 1 |
| >20 yr old | 10 | 32 | 7 | 1 : 3.2 |

of the animals. The age structure of males and females was compared by using the nonparametric Kolmogorov-Smirnov (K-S) test (Sokal and Rohlf, 1981).

Growth was determined by fitting the nonlinear, least-squares Gompertz model to length-at-age data (SAS Institute, 1985):

$$S(t) = A\left(\exp\left(-b\exp(-k)\right)\right), \quad (1)$$

where $S$ = a measure of size (cm);
$A$ = asymptotic length;
$b$ = the constant of integration;
$k$ = the rate of growth constant; and
$t$ = age (yr) (Laird, 1966).

Total body length was measured to the nearest centimeter in a straight line from the tip of the upper jaw to the notch of the fluke (Norris, 1961). Predicted asymptotic lengths for males and females were compared by using the approximate $t$-test (Sokal and Rohlf, 1981). These lengths were then compared with the corresponding asymptotic lengths for male and female bottlenose dolphins from Sarasota Bay, Florida (Read et al., 1993).

Length at birth was estimated in three ways: 1) as the mean length of 21 specimens from the entire data set ($n$=898) determined to be neonates on the basis of the presence of remains of the umbilical cord or folded dorsal or caudal fins; 2) as the mean length of 21 specimens (no overlap with the previous sample of 21) estimated to be <0.1 year old because the neonatal line in tooth sections had not yet formed or had just started to form (Hohn and Hammond, 1985); 3) as the predicted value from the Gompertz model. Calving season was also identified in three ways: as the date of stranding of 1) neonates, 2) specimens <0.1 year old, and 3) specimens measuring 90–120 cm in length.

Reproductive data were available for 57 females from the total sample of stranded females from which some data were collected ($n$=292). Teeth were available for 25 of these. Sexual maturity of females was determined by noting 1) the presence or absence of a corpus of ovulation from external examination of ovaries or 2) the presence of a fetus or an extended uterus, indicating a pregnancy. Sexual maturity of males could not be evaluated because few data or samples from testes were collected.

Vertebrae from 24 males, 25 females, and 12 dolphins of unknown sex were collected. All were examined for state of physical maturity. From this sample, teeth were available for only 11 males, 12 females, and 8 specimens of unknown sex. Physical maturity was determined by noting the degree of fusion of the epiphysis to the centrum of thoracic and lumbar vertebrae. Three categories were used to classify the specimens: a) not fused (immature), b) fusing (maturing), and c) fused (mature).

## Results

### Age and sex composition

Estimates of age were obtained for 78 males, 81 females, and 36 specimens of unknown sex (Table 1; Fig. 1). For an additional 10 dolphins (5 males, 3 females, and 2 dolphins of unknown sex), only minimum ages, ranging between 12+ to 20+ years, were obtained because poor-quality tooth sections precluded accurate age estimates. These 10 specimens were excluded from all analyses. Occlusion of the pulp cavity was not seen in any of the tooth sections.

The oldest male and the oldest specimen of unknown sex were 33 years old and the oldest female was 41 years old (Fig. 2). Age distributions for males and females were significantly different (K-S test, $P$<0.01). Specimens less than 1 year old accounted for a relatively large part (20%) of the aged sample and were skewed towards males, but with increasing age, the proportion of females in the sample increased significantly (chi-square ($\chi^2$) $P$=0.003, for data stratified by age group 0–0.9, 1.0–9.9, 10.0–19.9, and ≥20 years; Table 1). Because of the relatively large number of males less than one year of age, the K-S test was rerun with that age class excluded for both males and females. The difference was still significant (K-S test, $P$<0.01).

### Growth

The Gompertz model gave predicted asymptotic lengths of 263.5 cm for males and 244.7 cm for fe-

males. Trends in the residuals, however, showed that the fit was poor for a number of age classes (Fig. 3). To obtain a better predictor, the model was fitted to a data set that excluded all specimens less than 1 year of age, analogous to the procedure in Read et al. (1993) where the Gompertz model was found to describe well the growth of bottlenose dolphins from Sarasota Bay, Florida. With this subset of data, asymptotic length was slightly higher for males (268.0 cm) and for females (246.7 cm) but neither were significantly different from the predicted values from the total sample (approximate $t$-test, $P>0.05$, Table 2). Trends in the residuals showed that predicted length at age was a better fit for ages 1–9 years and was slightly overestimated at asymptote.

In an attempt to find a fit with evenly dispersed residuals, the Gompertz model was modified to fix length at birth at 109.5 cm, as calculated below by independent means, rather than by solving for the asymptotic value, $A$:

$$S(t) = 109.5\left(\exp\left(b\left(1-b\exp(-k)\right)\right)\right). \qquad (2)$$

Predicted asymptotic length was 261.7 cm for males and 244.4 cm for females. Predicted length from birth through age 2 years was very similar to that estimated from the total sample with the Equation 1 version of the Gompertz model. Length at age was still underestimated and this derivation of the model did not improve the fit.

Although none of the iterations produced a fit that represented all age classes well, the best overall predicted values occurred with Equation 1) when specimens <1 year of age were excluded (Fig. 3) and, for comparative purposes, predicted lengths were taken from this model (268 cm for males and 246.7 cm for females). Males were significantly larger than females at asymptotic length (approximate $t$-test, $P<0.05$). Asymptotic lengths of males and females were not significantly different (approximate $t$-test, P>0.05) between dolphins from Texas and Sarasota Bay, Florida (Table 2).

## Length at birth and calving seasonality

There was no difference in length at birth between male and female neonates or between males and females <0.1 year old ($t$-test, $P>0.05$). Therefore, data were combined to produce a single estimate with each method (Table 3). Mean length at birth from combined data was not significantly different between these two methods ($t$-test, $P>0.05$), therefore the total data set was combined (males, females, and sex unknown, $n=42$) to give an estimated length at birth of 109.4 cm (SD=8.5). Length at age 0 estimated from the Gompertz curve was greater than length at birth estimated from the more direct measures. In addition, because the best-fit version of the Gompertz

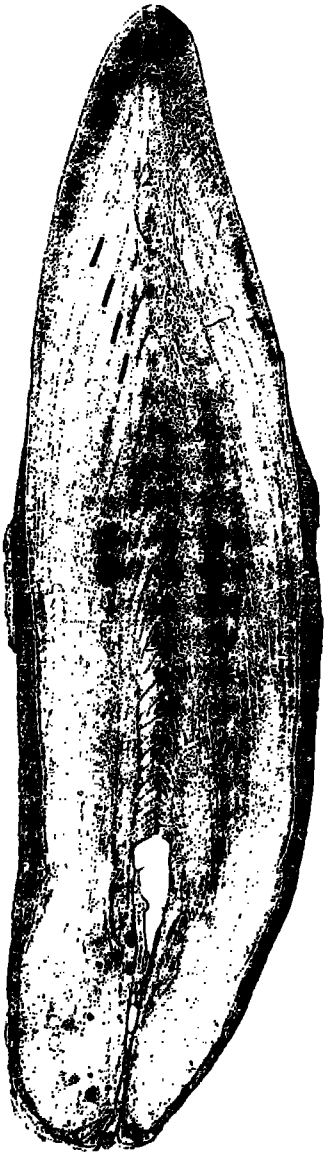

**Figure 1**

Midlongitudinal stained thin sections from the tooth of a 29-year-old, 261-cm female bottlenose dolphin, *Tursiops truncatus*, stranded in Texas. Growth layer group (GLG) boundaries were considered to be the relatively thin dark layers; most of these are easily visible. Boundaries between the first few layers are marked with a small black line on the upper left side of the section. The last few, very fine GLG's near the pulp cavity are difficult to see at this low magnification.

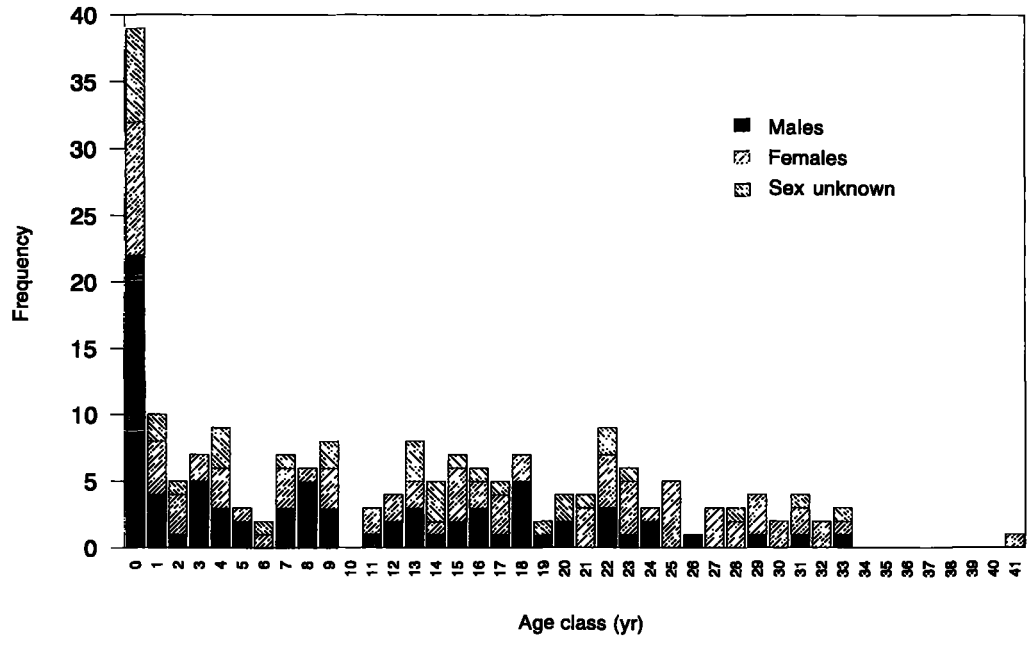


**Figure 2**

Age distribution of bottlenose dolphins, *Tursiops truncatus*, stranded along the coast of Texas from 1981 to 1990.

**Table 2**

Parameter values and their asymptotic standard errors (SE) from the Gompertz growth model fit to two sets of length-at-age data from bottlenose dolphins, *Tursiops truncatus*, stranded along the coast of Texas. The first set included all the available data; the second set was a subset of the first set that excluded specimens <1.0 yr of age. $A$ = asymptotic length, $b$ = the constant of integration, and $k$ = the rate of growth constant. $n$ = number of dolphins in each sample.

| | $n$ | $A \pm$ SE | $b \pm$ SE | $K \pm$ SE |
|---|---|---|---|---|
| Female length | | | | |
| All data | 78 | 244.7 ± 1.90 | 0.755 ± 0.0423 | 0.497 ± 0.0490 |
| Specimens of age <1.0 yr excluded | 68 | 246.7 ± 2.22 | 0.482 ± 0.0873 | 0.294 ± 0.0655 |
| Male length | | | | |
| All data | 75 | 263.5 ± 2.93 | 0.785 ± 0.0308 | 0.351 ± 0.0313 |
| Specimens of age <1.0 yr excluded | 54 | 268.0 ± 3.64 | 0.592 ± 0.0679 | 0.234 ± 0.0388 |

model excluded specimens less than 1-yr-old extrapolation to age 0 to estimate length at birth was inappropriate. The ratio of mean length at birth to asymptotic length was 40.8% for males and 44.4% for females.

The mode in strandings of neonates ($n$=12 of 21) and specimens <0.1 year of age ($n$=11 of 21) occurred in March (Fig. 4). In both data sets, 86% of the specimens stranded during March and April. Except for five specimens found in November and December, all neonates stranded from February through June.

## Sexual and physical maturation

Because reproductive data were collected from only 57 females (Table 4), the sample size was too small to estimate the mean age and length at sexual maturation. Only seven pregnant females were noted; the smallest was 233 cm and the longest was 335 cm. The latter, an extremely large female, also had the largest fetus (122-cm male) recorded in the TMMSN stranding database. Teeth were available for three of the seven pregnant females, and they were esti-

mated to be 9.8, 23, and 27 years of age. A 4.8-year-old pregnant female, 245 cm long, was excluded from this sample owing to possible mislabeling of samples. No reproductive data were available for males.

Mean age and length at physical maturation could not be calculated owing to the small sample sizes (Table 4). Two specimens, a 280-cm male and a 253-cm female, were notable because they were relatively large yet physically immature.

## Discussion

Despite the widespread distribution and high abundance of bottlenose dolphins along the Atlantic and Gulf of Mexico coasts of the United States, the majority of biological information for this species has come from a few locations, a relatively small number of studies, and small sample sizes. Basic questions still remain throughout much of the range. The current data provided the opportunity to begin to evaluate similarities and differences in bottlenose dolphin life history in relation to areas where previous studies had been conducted.

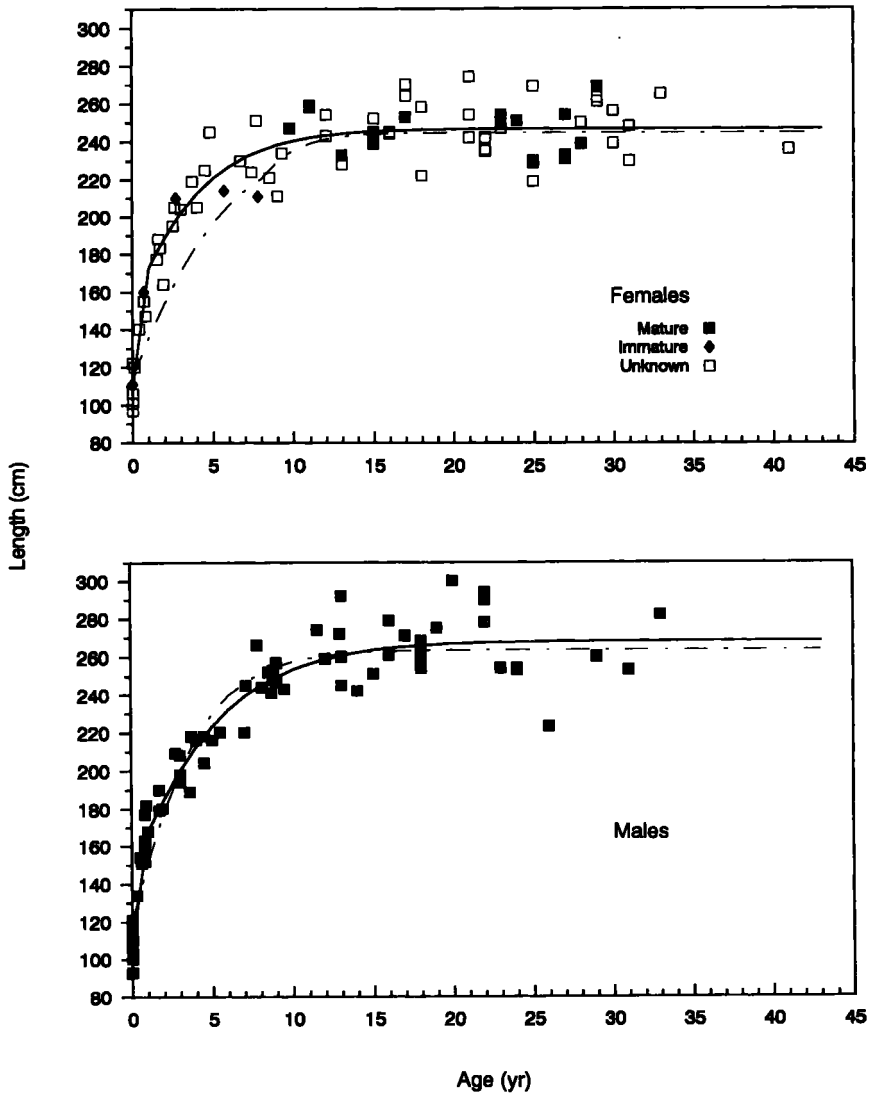


**Figure 3**

Scatterplots of length at age for female and male bottlenose dolphins, *Tursiops truncatus*, stranded along the coast of Texas. The solid lines represent the predicted growth trajectory from the Gompertz model when specimens less than 1 yr old are excluded; growth between birth and age 1 was determined by using the independently estimated length at birth and the predicted length at age 1. The dashed lines represent the predicted growth trajectory from the Gompertz model with the entire data set. Although the asymptotic lengths are similar, the growth trajectories are different, particularly for females.

Results from this study support the hypothesis that in bottlenose dolphins sexual dimorphism in body length is not exhibited at birth (Sergeant et al., 1973; Hohn, 1980; Kasuya et al., 1986; Cockcroft and Ross, 1990) but does occur in adults (Read et al., 1993). Although a number of studies have concluded that sexual dimorphism in adult size does not exist in bottlenose dolphins from the Atlantic and Gulf of Mexico coasts of the United States (for example, Hohn, 1980; Hersh, 1987; Hersh et al., 1990; Mead and Potter, 1990), the contradictory results could be explained partly because sample sizes in earlier studies were small but also because these other studies did not fit a growth curve to obtain predicted asymptotic lengths that could be directly compared (Read et al., 1993). The dimorphism at asymptotic length may result from females diverting energy to reproduction at the same ages that males are gaining girth and mass (Read et al., 1993) and thus would explain why sexual dimorphism occurs in adults, but not at birth.

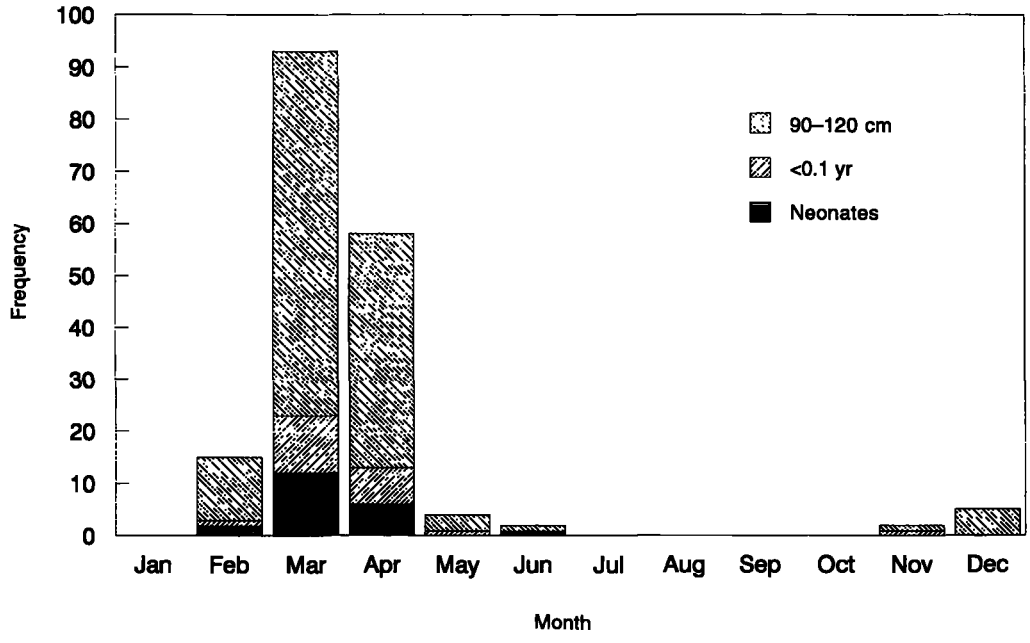


**Figure 4**

Calving seasonality illustrated as the monthly distribution of strandings of neonates, specimens <0.1 years old, and specimens 90–120 cm in length.

**Table 3**

Estimated length at birth (cm) for bottlenose dolphins, *Tursiops truncatus*, stranded along the coast of Texas. The two methods of defining a newborn animal ("neonates" and "specimens <0.1 yr") are described in the text. The Gompertz values were the predicted lengths at age 0 ($L_0$) from the Gompertz curve fitted to age-at-length data for males and females. The samples for neonates and specimens <0.1 yr are independent. *n* = number of dolphins in each sample.

| | Males | Females | Sex unknown | Total |
|---|---|---|---|---|
| Neonates | | | | |
| mean | 109.5 | 111.2 | 107.3 | 109.5 |
| SD | 9.3 | 13.6 | 5.0 | 9.3 |
| *n* | 12 | 5 | 4 | 21 |
| range | 94–124 | 91–128 | 102–112 | 91–128 |
| Specimens < 0.1 yr | | | | |
| mean | 109.7 | 107.4 | 113.7 | 109.7 |
| SD | 7.7 | 9.7 | 3.5 | 7.5 |
| *n* | 13 | 5 | 3 | 21 |
| range | 93–121 | 97–122 | 110–117 | 93–122 |
| Gompertz | | | | |
| mean | 128.2 | 115.1 | | |
| SD | 3.6 | 4.9 | | |
| *n* | | | | |
| range | | | | |

Bottlenose dolphins from the coast of Texas are not significantly different in adult size from those in Sarasota Bay, Florida (Read et al., 1993), the only other western Atlantic or Gulf of Mexico area for which growth curves have been fitted to length-at-age data. Contrary to the analysis of Read et al. (1993), however, we found that the Gompertz curve did not adequately describe growth across all age classes. The curve did not respond readily enough to simulate rapid growth during the first couple of years. The fit was improved by excluding specimens less than 1 year of age, the phase of growth where the rate and absolute incremental increase are greatest. Although this approach provided a data set comparable in range of ages to that used in Read et al. (1993), the Gompertz model proved a better predictor for the Sarasota Bay, Florida, sample where the predicted length of young animals was larger. The large and unbiased sample of live animals that represented most of the individuals in Sarasota Bay probably accounts for these differences. The fit might be further improved if the sample was large enough to allow for a two-stage Gompertz fit (e.g. see Perrin et al., 1976) that would accommodate the growth spurt occurring at maturation (Cheal and Gales, 1992; Read et al., 1993).

Estimates of length at birth are not available for the Sarasota Bay animals. Along the mid-Atlantic

coast of the United States, however, Mead and Potter (1990) estimated length at birth (117 cm) as the mean length of 13 specimens classified as neonates on the basis of a folded or flaccid dorsal fin. Using the equivalent data set from the Texas sample (neonates), we found that the length at birth of mid-Atlantic coastal bottlenose dolphins was significantly different ($t$-test, $P$=0.02) from the estimate of 109.4 cm for Texas animals, but this result should be considered preliminary until larger sample sizes are available.

Mean length at birth may best be estimated by using morphological characteristics. Tooth-layer deposition patterns proved to be accurate in comparison to results from morphological data and can be valuable when morphological characteristics are not recorded. The method, however, is more time consuming. In contrast, use of predicted lengths of 0-yr-old animals from a fitted growth curve may be inaccurate, as was the case with this sample.

Strandings of neonates along the Texas coast are highly seasonal, with a mode in March. Using stranding data, Urian et al. (1996) found a significant difference in calving season between bottlenose dolphins from the coast of Texas (citing this data set) and those from the central-west coast of Florida, including Sarasota Bay. Stranding patterns may not accurately reflect actual calving, however, because neonates that did not survive may be those that were born earlier or later than calves that did survive. In the Sarasota Bay area, Urian et al. (1996) found that the mean date of birth estimated from stranded neonates was 16 days earlier than that estimated from sighting records of females with new calves, although this difference was not significant. They suggested that the photo-identification data may also be biased owing to unequal and discontinuous distribution of survey effort, a finding also made by Caughley and Caughley (1974). Further error may arise from lack of detection of neonates that stay very close to the female. Photo-identification studies of calving season along the Texas coast identified a peak in number of neonates in May (Shane, 1977). This later detection of neonates, in comparison with stranded animals, is consistent with the results from the central-west coast of Florida and limitations of the photo-identification method.

The increase in proportion of females with age in the Texas sample is similar to a general pattern identified in delphinids, with a slight bias towards young males and old females (Ralls et al., 1980; Perrin and Reilly, 1984; Wells and Scott, 1990). Some authors have attributed this shift to higher natural mortality rates in males (Kasuya, 1976; Miyazaki, 1977; Wells and Scott, 1990). No direct or unbiased estimates of mortality are available for bottlenose dolphins from Texas, and patterns from stranded animals may not accurately reflect the population.

**Table 4**

Sample sizes and descriptions of sexual and physical maturity in bottlenose dolphins, *Tursiops truncatus*, stranded along the coast of Texas. Reproductive data were not collected for males.

| Sample | Females | Males | Sex unknown |
|---|---|---|---|
| Total stranded with at least minimum data collected | 292 | 373 | 233 |
| With reproductive data | 57 | | |
| Number immature | 17 | | |
| Number mature | 40 | | |
| Largest immature (cm) | 235 | | |
| Shortest mature (cm) | 225 | | |
| With reproductive and age data | 25 | | |
| Number immature | 6 | | |
| Number mature | 19 | | |
| Oldest immature (yr) | 7.8 | | |
| Youngest mature (yr) | 9.8 | | |
| Youngest pregnant (yr) | 9.8 | | |
| With vertebrae examined for physical maturity | 25 | 25 | 12 |
| Number immature | 10 | 16 | 8 |
| Number maturing | 2 | 2 | 0 |
| Number mature | 13 | 7 | 4 |
| Largest immature (cm) | 253 | 280 | 253 |
| Shortest mature (cm) | 219 | 237 | 231 |
| With physical maturation and age data | 12 | 11 | 8 |
| Number immature | 2 | 7 | 4 |
| Number maturing | 1 | 1 | 0 |
| Number mature | 9 | 4 | 4 |
| Oldest immature (yr) | 15 | 16 | 9.9 |
| Youngest mature (yr) | 13 | 18 | 20 |

The proportion of specimens less than 1 year of age in the sample of stranded animals is higher than expected. In bottlenose dolphins from Sarasota Bay, Florida, Wells and Scott (1990) calculated that animals in the same age class represented 3.4% of the population, and that the crude birth rate was 5.5% annually (range of 1.1–10.4% over eight years). The higher percentage (20%) of calves in the Texas sample most likely is due to the high rate of mortality in neonates and young calves. It is also interesting to speculate that cows with young calves may occupy more protected waters and, therefore, are more likely to wash ashore when they die, contributing to a stranding sample not representative of the population.

Some of the specimens in the sample were notably large, e.g. a 300-cm male, a 335-cm female, a 280-cm

physically immature male, and a 253-cm physically immature female. Although the sample is assumed to consist predominantly of the coastal form of bottlenose dolphins, it is possible that specimens from the larger offshore form (Duffield et al., 1983; Hersh and Duffield, 1990; Hersh et al., 1990) were included. These specimens remained in the sample because they were not specifically identified as offshore individuals from independent criteria. The inclusion of offshore individuals of various lengths may be responsible for some of the variability in length at age seen in this study.

Results from this study show that bottlenose dolphins from the coast of Texas have some similarities and some differences with bottlenose dolphins from the west coast of Florida and the mid-Atlantic coast of the United States. However, samples size are small, precluding, for example, any substantial reproductive analyses. We strongly encourage the routine collection of reproductive and other samples from stranded specimens. Such basic information as the average age at sexual maturation and calving interval remains unknown even though large numbers of bottlenose dolphins are found stranded each year.

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# Diet of dusky dolphins, *Lagenorhynchus obscurus*, in waters off Patagonia, Argentina

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The dusky dolphin, *Lagenorhynchus obscurus*, is probably the best known species of the genus *Lagenorhynchus* in the Southern Hemisphere. It is common in temperate waters of New Zealand, South Africa, Peru, northern Chile, and Argentina (Crespo, 1991; Van Waerebeek, 1992; Crespo et al., in press). Incidental catches have been recorded in coastal and offshore fisheries of Argentina (Corcuera et al., 1994; Crespo et al., 1994a, 1994b; Dans et al., in press), whereas directed captures have occurred off Peru (Read et al., 1988; Van Waerebeek and Reyes, 1990; Reyes, 1992).

The biology of dusky dolphins has been studied in Argentina since the 1970's (Würsig and Würsig, 1980; Würsig and Bastida, 1986; Dans et al., 1993). A detailed behavioral study was carried out at Península Valdés (Würsig and Würsig, 1980), and preliminary information about the reproductive biology of females was obtained by Dans et al. (1993, 1997).

Feeding habits have been briefly described for dusky dolphins from New Zealand (Gaskin, 1972), Patagonia (Dans et al., 1993; Crespo et al., 1994c), and Antarctic and sub-Antarctic waters (Goodall and Galeazzi, 1985). In Patagonia, the behavior of dusky dolphins feeding on Argentine anchovy, *Engraulis anchoita*, schools has been described by Würsig and Würsig (1980). A more recent and detailed study of their feeding habits by stomach content analysis was carried out in coastal waters of central Peru (McKinnon, 1994). The Peruvian sample consisted of animals caught mostly in gill nets (McKinnon, 1994). Peruvian anchoveta, *Engraulis ringens*, was the most important prey species for Peruvian dusky dolphins, accounting for 92.5% in number and 83.8% in weight of the total sample, and 97.8% frequency of occurrence (McKinnon, 1994). Differences in diet between lactating and nonlactating mature females were not found, and the anchoveta was almost the exclusive prey species in both sexes (McKinnon, 1994).

The objective of the present study is to describe the diet of the dusky dolphin in Patagonia in terms of both species composition and prey size. Seasonal and annual composition were not investigated because the sample size was small when subdivided along these lines.

## Materials and methods

The sample consisted of 25 dolphins (6 males and 19 females) caught incidentally between November 1989 and April 1994 by the trawling fishery that operates over the Patagonian Continental Shelf. All dolphins were caught in the area between 43°S and 46°30'S and between the coastline and the 100-m isobath. Most individuals were frozen onboard to –20°C when they were caught.

The total weight, standard length, and other body measurements (Norris, 1961) were recorded for each dolphin before dissections were made. Stomach contents were collected and then stored, either frozen or in 70% alcohol. They were separated with several sieves with a mesh size between 25 mm and 0.5 mm. Flesh material from the sieved contents was placed in a deep, water-filled plastic tray, enabling removal of the remaining flesh material. Otoliths, fish bones, and cephalopod beaks were identified with the aid of published catalogues (Clarke, 1962, 1980, 1986; Torno, 1976; Menni et al., 1984; Roper et al., 1984; Boschi et al., 1992; Gosztonyi and Kuba[1]) and a reference collection of otoliths, cephalopod beaks, and crustaceans belonging to the Marine Mammals Laboratory, Centro Nacional Patagónico, CONICET.

The number of individuals of a particular fish species (NF) found in a stomach was calculated as

[1] Gosztonyi, A., and L. Kuba. 1996. Atlas de huesos craneales y de la cintura escapular de peces costeros patagónicos. Plan de Manejo Integrado de la Zona Costera Patagonica (PMIZCP), Global Environmental Facility (GEF), Programa de las Naciones Unidas para el Desarrollo (PNUD), Wildlife Conservation Soc. (WCS), and Fundación Patagonia Natural (FPN) Informe Técnico 4, 29 p.

Manuscript accepted 6 August 1997.
Fishery Bulletin 96:366–374 (1998).

$$NF = LO + 0.5NO, \quad \text{if } LO > RO,$$

or as

$$NF = RO + 0.5NO, \quad \text{if } RO > LO,$$

where $LO$, $RO$, and $NO$ = the number of left, right, and not assigned otoliths respectively.

Minimal number of cephalopods was obtained with maximum count of upper and lower beaks for each species.

All complete and nondigested elements (otoliths and beaks) were measured with digital calipers. Some otoliths or beaks were digested, or broken, and could not be measured. Any otolith was considered too digested to be measured if it presented rounded borders and rostrum, and an ill-defined sulcus. Around 42% of the prey items were represented by broken or digested elements. Size values for these pieces were randomly assigned from sizes of items taken from the stomach and measured. When only broken or digested elements were found in the stomach, the average individual weight of the prey species in the whole sample was used to estimate the individual weight of the items.

The length of prey items was estimated by using regressions between total length (TL) and otolith length (OL) for fishes, and between dorsal mantle length (DML) and lower rostral length (LRL), or lower hood length (LHL), for squids. Wet weight (W) was estimated from regression-estimated length of prey by using regressions between W and TL for fishes, and between W and DML for squids. Regressions for most prey species were developed during this study on the basis of materials collected from commercial hauls. All regressions were calculated as simple linear regressions. Those variables that did not have linear relationships were made linear with natural logarithms (Table 1). The TL and W of *Notothenia* sp. was estimated with *Notothenia angustifrons* regressions (Table 1). The W of *Octopus tehuelchus* was estimated with *Octopus vulgaris* regression between W and LHL (Table 1). The W of each *Semirossia tenera* was assumed to be 3 g, as was the average individual weight recorded for this species in a sample taken onboard a commercial trawler by one of the authors (N.A.G.). In one stomach (that of LO22 dolphin), only fish eye lenses and a few beaks were found. In this case, eye lenses were similar in size to those of anchovy; therefore the an-

**Table 1**

Equation, sample size ($n$), and determination coefficient ($r^2$) of the regressions used to estimate size and weight of prey of dusky dolphins in Patagonia. The variables used in the regressions were otolith length (OL), lower hood length (LHL), lower rostral length (LRL), total length (TL), dorsal mantle length (DML) and wet weight (W). OL, LHL, and LRL are in mm, TL and DML are in cm, and W is in g.

| Scientific name | Common name | Equation | $n$ | $r^2$ | Source |
|---|---|---|---|---|---|
| *Engraulis anchoita* | Argentine anchovy | $TL = 2.368 + 3.56\ LO$ | 79 | 0.70 | This study |
| | | $W = 2.5\ 10^{-3}\ TL^{3.353}$ | 81 | 0.93 | |
| *Merluccius hubbsi* | Argentine hake | $TL = 1.823\ LO^{1.072}$ if $OL<15$ | 447 | 0.93 | |
| | | $W = 4.76\ 10^{-3}\ TL^{3.061}$ if $OL<15$ | 469 | 0.92 | This study |
| | | $TL = 1.984\ LO^{1.05}$ if $OL>15$ | 693 | 0.91 | |
| | | $W = 9.72\ 10^{-3}\ TL^{2.886}$ if $OL>15$ | 742 | 0.96 | |
| *Stromateus brasiliensis* | "pampanito" | $TL = 3.042\ LO^{1.159}$ | 51 | 0.98 | This study |
| | | $W = 6.418\ 10^{-4}\ TL^{3.917}$ | 63 | 0.98 | |
| *Notothenia angustifrons* | Southern cod | $TL = 4.142\ LO^{0.768}$ | 22 | 0.91 | Hecht, 1987 |
| | | $W = 3.73\ 10^{-6}\ (10\ TL)^{3.16}$ | 24 | 0.98 | |
| *Illex argentinus* | Argentine shortfin squid | $DML = -3.178 + 5.617\ LHL$ | 27 | 0.93 | This study |
| | | $DML = 8.257\ 10^{-2} + 6.009\ LRL$ | 63 | 0.87 | |
| | | $W = 9.82\ 10^{-3}\ LDM^{3.238}$ | 66 | 0.98 | |
| *Loligo gahi* | Patagonian squid | $DML = -0.712 + 4.622\ LHL$ | 98 | 0.76 | This study |
| | | $W = 2.6\ 10^{-2}\ LDM^{2.753}$ | 102 | 0.93 | |
| *Octopus vulgaris* | octopus | $W = e^{1.82 + 3.03\ \mathrm{Ln}(LHL)}$ | 108 | [1] | Clarke, 1986 |

[1] The determination coefficient of this regression was not available in the original source.

chovy average individual weight was used to estimate the W of these unidentified fishes. This last estimation was made to evaluate the relative contribution by weight of these unidentified fishes.

The "percent frequency of occurrence" (%FO), the "percent total number" (%N), and the "percent total wet weight" (%W) were calculated (Hyslop, 1980; Castley et al., 1991; McKinnon, 1994). The relative importance of each prey species was evaluated with the index of relative importance (IRI) (Pinkas et al., 1971), where the volumetric percentage was replaced by the %W ($IRI=(\%N+\%W)\%FO$) (Castley et al., 1991).

## Results

Dolphins used in this study (Table 2) were caught mostly at night in midwater hauls for the shrimp *Pleoticus muelleri*, with the exception of LO10 and LO23 dolphins that were caught in diurnal bottom hauls for shrimp, LO22 dolphin that was captured in a diurnal bottom haul for hake, and LO26 dolphin that was caught by an unknown fishing vessel. The locations of the catches were principally in the Golfo San Jorge (approximately between 45 and 46°30'S), except LO22 dolphin that was captured in the vicinity of Isla Escondida (43°S). There is no information

**Table 2**

Biological information (sex, size, age, and reproductive status), number of prey species eaten, and most important prey species by weight in the stomach of each dusky dolphin considered in this study. The biological information of females (F) were taken from Dans et al. (1997) and those of males (M) were provided by S.L. Dans.[1] The date of death is approximate and indicates which dolphins were caught in the same fishing trip.

| Field number | Date of death | Sex | Length (cm) | Age (years) | Reproductive status | No. of prey eaten | Important prey species in the stomach |
|---|---|---|---|---|---|---|---|
| LO01 | 19 Nov 89 | F | 158 | 5 | immature | 3 | Argentine anchovy and Argentine shortfin squid |
| LO02 | 19 Nov 89 | F | 157 | 4 | immature | 4 | Argentine shortfin squid and Argentine anchovy |
| LO04 | 27 Apr 90 | F | 159 | 6 | immature | 3 | Argentine shortfin squid and Argentine anchovy |
| LO05 | 01 Jun 90 | F | 166.5 | 6 | mature (lactating) | 1 | Argentine anchovy |
| LO06 | 01 Jun 90 | F | 174 | 8 | mature (resting) | 4 | Argentine anchovy |
| LO07 | Jul 90 | M | 169 | 6 | immature | 5 | Argentine anchovy |
| LO08 | Apr 92 | F | 161 | 7 | mature (pregnant) | 2 | Argentine anchovy |
| LO09 | Apr 92 | F | 174 | 11 | mature (pregnant) | 4 | Argentine anchovy |
| LO10 | 08 Sep 92 | F | 172 | 3+ | immature | 4 | Argentine shortfin squid and Argentine hake |
| LO11 | Sep 92 | F | 172 | 7+ | mature (resting) | 4 | Argentine anchovy |
| LO12 | Sep 92 | F | 162 | 7+ | mature (pregnant) | 6 | Argentine hake |
| LO13 | Sep 92 | F | 170 | 8+ | mature (resting) | 5 | Argentine anchovy and hake |
| LO14 | Sep 92 | F | 167 | 7+ | immature | 3 | Argentine hake |
| LO15 | 11 Mar 93 | F | 166 | 5 | immature | 2 | Argentine anchovy |
| LO16 | 11 Mar 93 | F | 174 | 6 | mature (pregnant) | 3 | Argentine anchovy |
| LO17 | 16 Mar 93 | F | 164 | 4 | immature | 2 | Argentine anchovy |
| LO18 | 06 Apr 94 | F | 171 | 5 | immature | 4 | Argentine anchovy |
| LO19 | 11 May 93 | M | 164 | 8 | mature | 3 | Argentine anchovy |
| LO20 | Sep 93 | M | 161 | 9 | mature | 2 | Argentine hake |
| LO21 | 02 Sep 93 | F | 158 | 3 | immature | 4 | Argentine hake |
| LO22 | 30 Oct 93 | F | 164 | 3 | immature | 2 | Unidentified fishes |
| LO23 | 15 Oct 93 | M | 169 | 9 | mature | 3 | Argentine shortfin squid |
| LO24 | Mar 94 | M | 173 | 10 | mature | 4 | Argentine anchovy |
| LO25 | Mar 94 | M | 162 | 8+ | unknown | 3 | Argentine anchovy |
| LO26 | 94 | F | 161 | 8 | mature | 5 | Argentine anchovy and hake |

[1] Dans, S. L. Laboratorio de Mamíferos Marinos, CENPAT (CONICET), Boulevard 3600, (9120) Puerto Madryn, Chubut, Argentina

about the location of collection of two dolphins (LO07 and LO26). The entire sample was biased toward females and it was composed of immature and mature dolphins (Table 2) (Dans et al., 1997).

Some dolphins in the sample may have been caught in the same haul because fishermen reported that occasionally more than one dolphin are caught. However, when fishermen capture several dolphins in a fishing trip (between 30 and 60 days), they may discard some of them. In these cases it is uncertain whether those dolphins caught during the same fishing trip (same date of death, see Table 2) were caught together in the same haul.

With the exception of one stomach (LO22) which contained fish eye lenses and a few beaks, all others were half full or full. On average (± standard deviation), 3.40 ±1.19 prey species per stomach were found, but only one or two of them were important by weight in the stomach (Table 2). The mean number of prey items per stomach was 148.08 ±137.91, and the mean regression-estimated ingested biomass was 2,675.63 ±1,848.44 g per stomach.

A total of 3,702 prey items belonging to eight species were found in the 25 stomach contents analyzed, including four fish and four cephalopod species. The fish species were Argentine anchovy, *Engraulis anchoita;* Argentine hake, *Merluccius hubbsi;* "pampanito," *Stromateus brasiliensis*, and the southern cod *Notothenia* sp. The cephalopods were Argentine shortfin squid, *Illex argentinus;* Patagonian squid, *Loligo gahi*, the sepiolid *Semirossia tenera;* and common octopus, *Octopus tehuelchus*.

Argentine anchovy was the most important prey species, representing 39% of prey by number, 46% by weight (Table 3). However, the most frequent prey was the Patagonian squid which was present in 84% of stomachs (Table 3). According to the IRI, the second species in importance was the Argentine shortfin squid, followed by the Patagonian squid and the Argentine hake, whereas by weight the second species was hake, followed by Argentine shortfin and Patagonian squid (Table 3). The "pampanito," octopus, and southern cod were of little importance in dusky dolphin diet (Table 3).

The Argentine anchovy had a unimodal length-frequency distribution with a mode at 16 cm (Fig. 1). Individual anchovies eaten by dusky dolphins were mostly of mature sizes (Hansen, 1994).

Both Argentine shortfin and Patagonian squids were consumed at small sizes. Patagonian squids had a modal DML of 3 cm (Fig. 2), and most of them were smaller than 8 cm, a size that corresponded to that of immature squid (Hatfield et al., 1990). The DML frequency distribution of shortfin squid showed two important peaks at 1–2 cm, and 7–8 cm of DML (Fig. 3) which corresponded to juvenile sizes (Brunetti and Ivanovic, 1992).

Argentine hake showed the widest size range (Fig. 4). Its TL frequency distribution showed three peaks at 8 cm, 22–24 cm, and 36 cm in order of importance (Fig. 4). These sizes corresponded to age-0 group, age 1–2 group, and age 2–5 group, respectively (Gaggiotti and Renzi, 1990).

Average individual length of fish eaten by dusky dolphins ranged from 7.54 cm (southern cod) to 19.81 cm (Argentine hake). The DML range for cephalopod preys was estimated to be between 2 cm (observed DML of *S. tenera*) and 6.35 cm (shortfin squid).

**Table 3**

Relative importance of prey species of dusky dolphins in the Patagonian continental shelf.

| | Percent total number (%N) | Percent total wet weight (%W) | Percent frequency of occurrence (%FO) | Index of relative importance (IRI) |
|---|---|---|---|---|
| Cephalopods | | | | |
| *Illex argentinus* | 30.71 | 21.05 | 68.00 | 3,520.11 |
| *Loligo gahi* | 20.64 | 4.58 | 84.00 | 2,118.09 |
| *Semirossia tenera* | 3.40 | 0.57 | 36.00 | 142.87 |
| *Octopus tehuelchus* | 0.05 | 0.00 | 4.00 | 0.22 |
| Fishes | | | | |
| *Engraulis anchoita* | 39.25 | 46.36 | 80.00 | 6,848.60 |
| *Merluccius hubbsi* | 5.19 | 26.46 | 48.00 | 1,518.82 |
| *Stromateus brasiliensis* | 0.14 | 0.29 | 12.00 | 5.05 |
| *Notothenia* sp. | 0.03 | 0.00 | 4.00 | 0.11 |
| Unidentified fishes | 0.59 | 0.70 | 4.00 | 5.18 |
| Total | 100.00 | 100.01 | | |

For all prey species, average individual length was smaller than 20 cm.

Average individual wet weights of Argentine shortfin squid, Patagonian squid, Argentine hake, and Argentine anchovy ranged from 4 to 92 g. The Argentine anchovy, Argentine hake, and Argentine shortfin squid had an average individual wet weight (± standard deviation) of 21.34 ±7.49, 92.17 ±121.62, and 12.39 ±33.62 g, respectively.

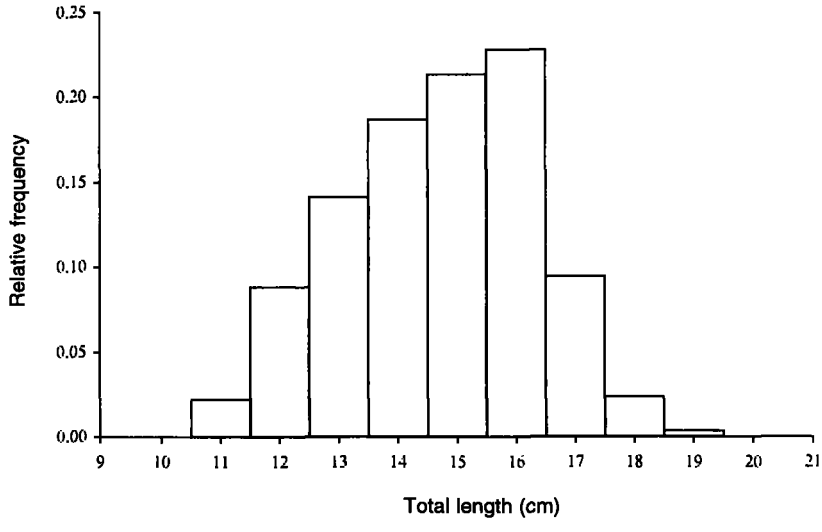


**Figure 1**

Length-frequency distribution of Argentine anchovy, *Engraulis anchoita*, eaten by dusky dolphins in Patagonia.

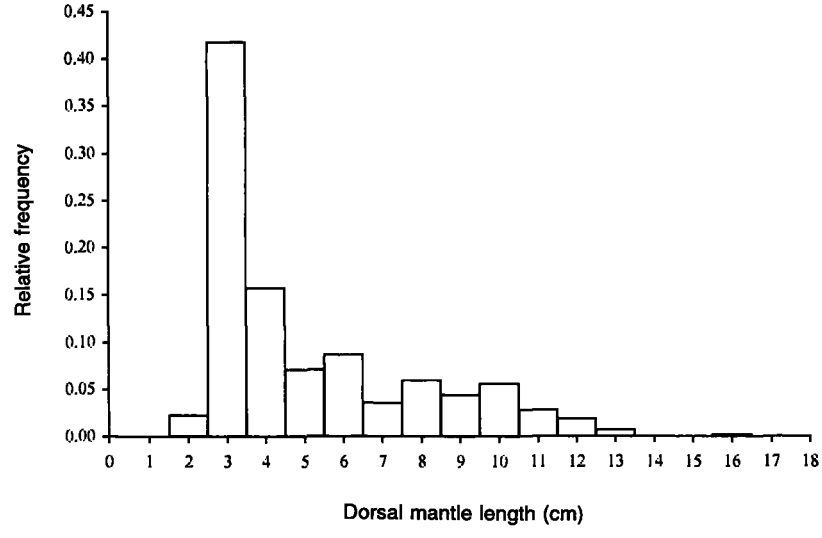


**Figure 2**

Length-frequency distribution of Patagonian squid, *Loligo gahi*, eaten by dusky dolphins in Patagonia.

## Discussion

Patagonian dusky dolphins fed mostly on pelagic species or pelagic stages of demersal species. Argentine anchovy is typically a pelagic species (Brandhorst et al., 1974; Angelescu, 1982; Angelescu and Anganuzzi, 1986; UNESCO, 1990), and Argentine shortfin squid, Patagonian squid, Argentine hake, and "pampanito" are demersal-pelagic species (FAO, 1983; Angelescu and Prenski, 1987; Nigmatullin, 1989; Hatfield et al., 1990; Rodhouse and Hatfield, 1990; Brunetti and Ivanovic, 1992). The sepiolid and southern cod are demersal-benthic species, whereas common octopus is benthic (Roper et al., 1984; Angelescu and Prenski, 1987).

Anchovies are the main food item for dusky dolphins in Argentine and Peruvian waters. *Engraulis ringens* was found to be the principal prey species for dusky dolphins in waters off Peru (McKinnon, 1994), and this study shows that *E. anchoita* is the most important prey species in Argentine waters. Furthermore, squids were the second prey by numbers (*I. argentinus* and *L. gahi* in Argentine waters, and *L. gahi* and *Dosidicas gigas* in Peruvian waters) and hakes were rated second by weight (*M. hubbsi* and *Merluccius gayi* in Argentine and Peruvian waters respectively) (McKinnon, 1994). Moreover, the number of commonly eaten and important prey species (by weight) was quite similar between Argentine and Peruvian dusky dolphins (4 and 6 prey species respectively), considering the difference in the sample size in this work ($n$=25) and that in McKinnon's (1994) study ($n$=136). Both populations of the dusky

dolphin feed on ecologically similar species, mostly schooling fishes. However, whereas anchoveta represented 80% in weight of the diet of Peruvian dolphins, Argentine anchovy represented between 40% and 50% in weight of the diet of Argentine dolphins.

Sample size in this study is relatively small and possibly biased by age and sex (Dans et al., 1997; in press). However, our sample included mature and immature dolphins of both sexes, and all the stomach contents were very similar in composition (Table 2). Moreover, dusky dolphins had never been reported to be feeding around fishing vessels on discards and disturbed fish, even when the dolphins in this sample were caught by shrimp trawlers. Furthermore, the diet composition of Peruvian dusky dolphins did not show any difference between sexes or reproductive status (McKinnon, 1994). At Península Valdés, dusky dolphin feeding groups consisted of individuals of both sexes and of almost all age classes (calves and small young could be excluded from the feeding group) (Würsig and Würsig, 1980). Therefore, considering the general similarities in diet composition between Argentine and Peruvian populations, the absence of differences in the diet between sexes and reproductive status in the Peruvian population, the lack of evidence to suggest that dolphins feed on discards and disturbed fishes, and the gregarious feeding behavior of patagonian dusky dolphins described by Würsig and Würsig (1980), we conclude that the sample analyzed in this study is a reasonable indicator of diet composition of dusky dolphins in Argentine waters.

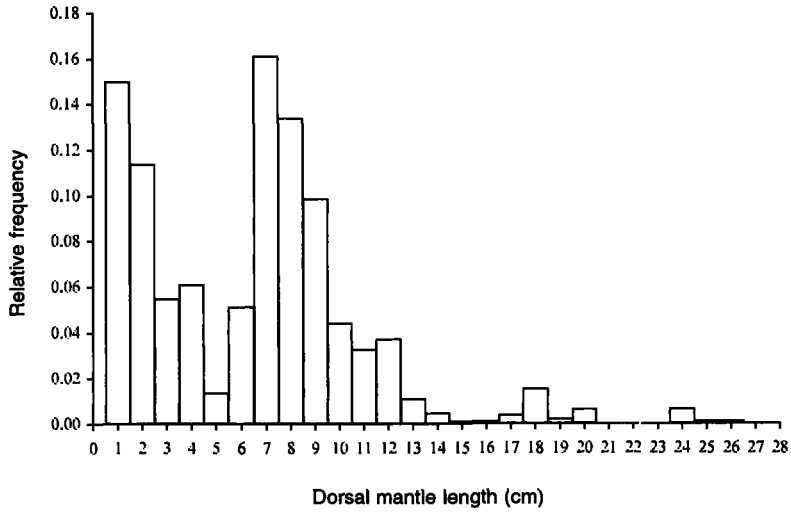


**Figure 3**

Length-frequency distribution of Argentine shortfin squid, *Illex argentinus*, eaten by dusky dolphins in Patagonia.

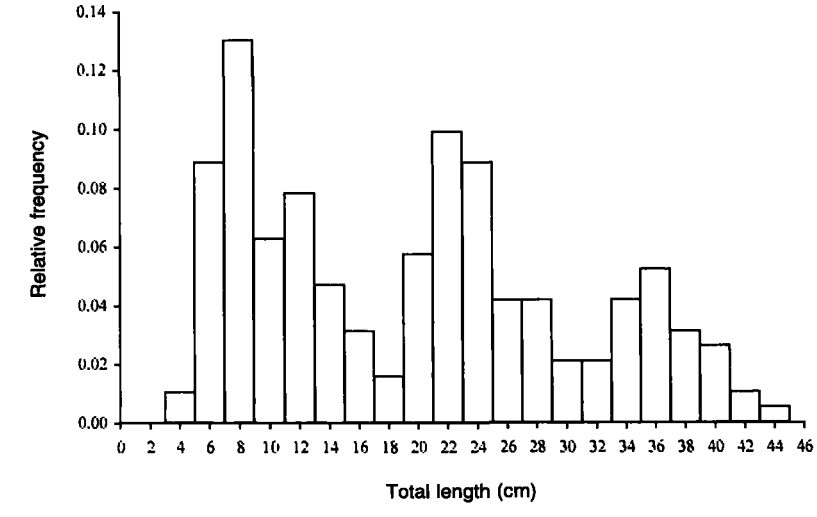


**Figure 4**

Length-frequency distribution of Argentine hake, *Merluccius hubbsi*, eaten by dusky dolphins in Patagonia.

At least two populations of Argentine anchovy have been reported over the Argentine Continental Shelf: the bonaerensis (northern) and the Patagonian (southern) stocks (Brandhorst et al., 1974; Angelescu, 1982; Angelescu and Anganuzzi, 1986; UNESCO, 1990; Hansen, 1994). Preadults and adults of the bonaerensis stock migrate northwest from coastal spawning areas to offshore feeding grounds; available information indicates that the Patagonian stock, however, does not show a seasonal migration (Brandhorst et al., 1974; Angelescu, 1982; Angelescu and Anganuzzi, 1986; UNESCO, 1990; Hansen,

1994). Dolphins in this study were caught off central Patagonia throughout the year between 43°S and 46°30'S; thus dusky dolphins appear to feed on Argentine anchovies from the Patagonian stock. The absence of a well-defined seasonal migration pattern in Argentine dusky dolphins (Würsig and Würsig, 1980) could be related to predation on the Patagonian stock of Argentine anchovy. However, long-distance movements of two dusky dolphins have been recorded after several years in Argentine waters (Würsig and Bastida, 1986).

The Argentine shortfin squid is a neritic-oceanic species, distributed from 30°S to 54°S (Rodhouse and Hatfield, 1990). At least three spawning stocks, 1) the bonaerensis to north Patagonian (early winter), 2) the south Patagonian (winter), and 3) the summer spawning stock (Nigmatullin, 1989; Brunetti et al., 1991; Brunetti and Ivanovic, 1992) have been described over the Argentine Continental Shelf. The latter spends its entire life cycle over the continental shelf, the former two have their spawning grounds on the shelf break and in oceanic waters. Their larvae and juveniles grow and mature over the continental shelf (Nigmatullin, 1989; Rodhouse and Hatfield, 1990; Brunetti and Ivanovic, 1992). The shortfin squids captured by dolphins could belong to any of the spawning stocks because their distributions overlap in the area where dolphins were caught. In addition, the size of squids eaten by dolphins corresponds with that for juvenile squids from all spawning stocks. These juvenile squids are pelagic (Brunetti and Ivanovic, 1992; Ivanovic and Brunetti,1994) and can be found mostly between the 50- and 100-m isobaths (Brunetti and Ivanovic, 1992).

The Patagonian squid is a neritic species and its life cycle is associated with the Malvinas Current over the continental shelf and slope (Hatfield et al., 1990). Its spawning grounds are in shallow and coastal waters, and it migrates to deeper waters to grow, reaching maturity at sizes larger than 10 cm of DML (Hatfield et al., 1990). Patagonian squids eaten by dusky dolphins were mostly of small size; thus feeding on this species could occur as juveniles migrate from the coastal area to deeper feeding grounds beyond the shelf break.

The main TL peak for Argentine hake eaten by dolphins corresponds to the age-0 group. This group exhibits pelagic schooling behavior (Angelescu and Prenski, 1987). Moreover, juveniles do not follow the adult hake migration pattern but remain in their nursery grounds (south of the Golfo San Jorge and Isla Escondida area) (Angelescu and Prenski, 1987).

In sum, these results indicate that dusky dolphins of Patagonia feed mostly on species whose stages exhibit pelagic and schooling behavior.

Finally, Argentine hake, Argentive anchovy, and squids are key species in the trophic web of the Patagonian Continental Shelf ecosystem and seem to present some degree of association (Angelescu and Prenski, 1987). Peneid crustaceans, like the shrimp, appear to be associated with these species in the study area even when their abundance is comparatively less (Angelescu and Prenski, 1987). Shrimp were not found in dolphins stomachs, even when they were caught incidentally in shrimp hauls. There are no data about the behavior of the dolphins at the moment of the catch, but the absence of shrimp in the diet suggests that dolphins avoid shrimp as a prey.

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# Preliminary estimate of spawning frequency and batch fecundity of striped weakfish, *Cynoscion striatus*, in coastal waters off Buenos Aires province*

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The striped weakfish, *Cynoscion striatus*, is a demersal species inhabiting coastal waters of the Southwest Atlantic. It ranges from Brazil (22°35'S) to the south of Buenos Aires province (Argentina) (42°S) (Cordo, 1986). The commercial catch takes place mainly off Buenos Aires province, between 35° and 40°S, to 50 m depths. The annual catch of this species is about 20,000 metric tons,[1] corresponding to 20% of the total commercial catch of coastal species in Argentina.

Despite a variety of studies describing *C. striatus* life history, such as feeding (Ciechomski and Ehrlich, 1977; Cordo, 1986), growth (Ciechomski and Cassia, 1978), embryonic and larval development (Ciechomski and Cassia, 1982), length distributions, and sex ratios (Cousseau et al., 1986), studies on reproductive biology are rare and largely incomplete. Only one previous report has included histological analysis of the ovaries and fecundity estimates (Cassia, 1986), providing evidence that striped weakfish is a multiple spawner.

In the present study, ovaries of *C. striatus* from the coastal area of the Buenos Aires province (Argentina, Southwest Atlantic) were examined histologically, and particular attention was paid to evidence for multiple spawning and to estimates of spawning frequency and batch fecundity.

## Material and methods

*Cynoscion striatus* was collt\ted in the zone known as "El Rincón" (Buenos Aires province, Argentina, 38°50'–40°30'S) during two research trawl cruises carried out in early November 1994 ($n$=179) and September 1995 ($n$=224) (Fig. 1). Mature females caught near "Punta del Este" (Uruguayan coast, 35°10'S–55°W) in November 1994 were also used to estimate fecundity ($n$=26).

Individuals were measured to the nearest centimeter (total length, TL) and weighed (total weight, TW). Length range of sampled females was 31–58 cm TL, which corresponds to 3–15 yr old individuals (Cioffi, 1992). The decision to sample only females of *C. striatus* greater than about 30 cm was based on the fact that this length is the size at maturity (Macchi and Acha[2]). Immature ovaries therefore were underrepresented in the samples.

The ovaries of individuals sampled were removed immediately after capture and fixed in 10% neutral-buffered formalin or in Davidson's fluid for two weeks. Later, fixed gonads were weighed (GW), and a portion of tissue (about 2.0 g) was removed from the center of each ovary, dehydrated in methanol, cleared in benzol, and embedded in paraffin. Tissues were sectioned at approximately 5 μm thickness, stained with Harris's hematoxylin followed by eosin counterstain. Histological classification of ovaries was based on the occurrence and relative abundance of five stages of oocyte development (Table 1) as well as on the occurrence and intensity of atresia. The terminology used in the description of oocyte stages was adapted from Forberg (1982), and the classification of atresia followed that given by Hunter and Macewicz (1985). Ovaries were classified into eight stages: 1) immature, 2) developing early, 3) developing late, 4) fully developed, 5) gravid, 6) partially spent, 7) spent, and 8) resting. This classification is a modification of that given by Mayer et al. (1988). Oocyte measurements were taken of the ovaries in different maturity stages (3 ovaries for each stage). Oocytes with visible nuclei showing were measured along the longest axes with an ocular micrometer. About 10 fields of view per histological section were chosen at random (Fig. 2).

To estimate the spawning fraction, only the samples collected during November 1994 were used. The percentage of spawning fe-

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[1] Secretaría de Agricultura, Pesca y Alimentación. 1996. Flota pesquera Argentina (capturas marítimas totales). [Available from SAPyA., Paseo Colón 982, Buenos Aires, Argentina.]

[2] Macchi, G. J., and M. E. Acha. In press. Chapter 4: Aspectos reproductivos de las principales especies de peces. *In* Lasta (ed.), Resultados de la campaña H-13/94, Serie Informes Técnicos INIDEP.

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males was determined by estimating the incidence of fish with postovulatory follicles (POF) (Hunter and Goldberg, 1980). These structures were classified as day-0, day-1, or day-2 postovulatory follicles, following the description by Goldberg et al. (1984) for *Sardinops sagax* and by Melo (1994) for *Engraulis capensis*.

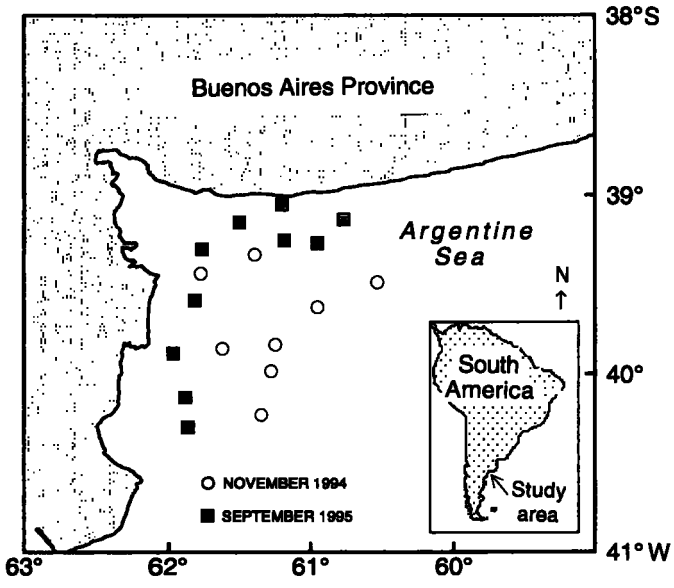


**Figure 1**

Location where samples of female striped weakfish were collected off "El Rincón" area.

The proportion of spawning females was estimated from the different stages of POF, but the spawning frequency was determinated by taking the average of the percentages of day-0 and day-1 spawning females (Fitzhugh et al., 1993).

Batch fecundity (BF) (number of oocytes released per spawning) was estimated gravimetrically with the hydrated oocyte method (Hunter et al., 1985) on fixed ovarian samples. Hydrated ovaries that contained new postovulatory follicles were not used for this estimation. Batch fecundity was determined for 41 females (17 from "El Rincón" and 24 from the Uruguayan coast). Three 0.1-g tissue subsamples were collected from the anterior, middle, and posterior sections of one ovary of each pair. These subsamples were weighed to the nearest 0.00001 g. All hydrated oocytes in each subsample were counted under stereoscopic microscope (magnification of 6×). Batch fecundity for each female was the product of the mean number of hydrated oocytes per unit weight and the total weight of the ovaries. Relative fecundity (RF) (hydrated oocytes per gram of body weight) was calculated as the batch fecundity divided by female weight (without ovary). To compare the "El Rincón" data with those from the Uruguayan coast, the length ranges coincident with the two zones were truncated between 40 and 50 cm TL ("El Rincón," $n$=15; Uruguayan coast, $n$=17). The fecundity values and the coefficients of the batch fecundity to

**Table 1**

Morphological changes observed in the different oocyte growth phases. Adapted from Forberg (1982).

| Oocyte growth stages | Description |
|---|---|
| First growth phase<br>Cromatin nucleolus stage<br>Early nucleolus stage<br>Late nucleolus stage | Previtellogenic oocytes with diameters smaller than 100 µm. Cytoplasm is basophilic and the nucleus shows a number of nucleoli situated peripherally. Follicular cells are flattened and become visible on the outer surface of oocyte. |
| Second growth phase<br>Yolk vesicle stage | Diameter ranged between 100–250 µm. Cytoplasm is basophilic and shows small uncolored vacuoles (yolk vesicles). Granulosa and follicular thecae are distinguished and the zona radiata becomes visible around the periphery of oocyte. |
| Primary yolk stage | Diameter ranged between 250 and 350 µm. Numerous eosinophilic yolk globules appear between the yolk vesicles. These yolk globules are composed mainly of proteins. The zona radiata and the follicle epithelium are more prominent. |
| Secondary yolk stage | Diameter between 400 and 600 µm. The yolk globules have multiplied and increased in size, occupying all the cytoplasm. The nucleus exhibits an irregular shape, and the zona radiata increases in thickness. |
| Tertiary yolk stage or final oocyte maturation | Oocyte diameter ranged between 600 and 700 µm. In the first instance, the nucleus is displaced to the animal pole (migratory nucleus stage). The nuclear membrane disintegrates and the yolk globules tend to coalesce. In the section, these oocytes appear with a cytoplasm weakly eosinophilic and an irregular shape. |

total length relationships obtained for both areas were compared with a test of equality of means and a test of equality of coefficients (Draper and Smith, 1981). The relations of batch fecundity to total length and total weight (without ovary) were assessed with regression analysis (Draper and Smith, 1981). Significance of these relations were evaluated by testing if the slope of the regression was significantly different from zero.

## Results

Oocyte diameter distributions of different maturity stages (immature to gravid) of *C. striatus* show that this species is a multiple spawner (Fig. 2). The gravid ovaries show four main groups of oocytes. The first group is composed mainly of primary growth oocytes (smaller than 100 µm). The second group is composed of partially yolked oocytes in several stages ranging approximately from 100 to 300 µm. The third group is formed by advanced yolked oocytes ranging between 400 to 600 µm. The fourth group corresponds to the hydrated oocytes between 600 to 700 µm.

During September, 95% of the females were found in the developing stages (early and late), with a small percentage (3%) in the fully developed phase (Fig. 3). The samples obtained during early November were composed mainly of females in the partially spent stage with postovulatory follicles; about 11% of the samples were gravid females. These results indicate that the beginning of spawning of *C. striatus* in "El Rincón" is in October.

Of the mature females taken in November, 12% had hydrated oocytes, 11% had new postovulatory follicles (phase 0), 13% had day-1 postovulatory follicles, and 11% had old postovulatory follicles (phase 2) (Table 2). Therefore, each female was calculated to spawn every 7–9 days. The average of the percentages of day-0 and day-1 spawning females was

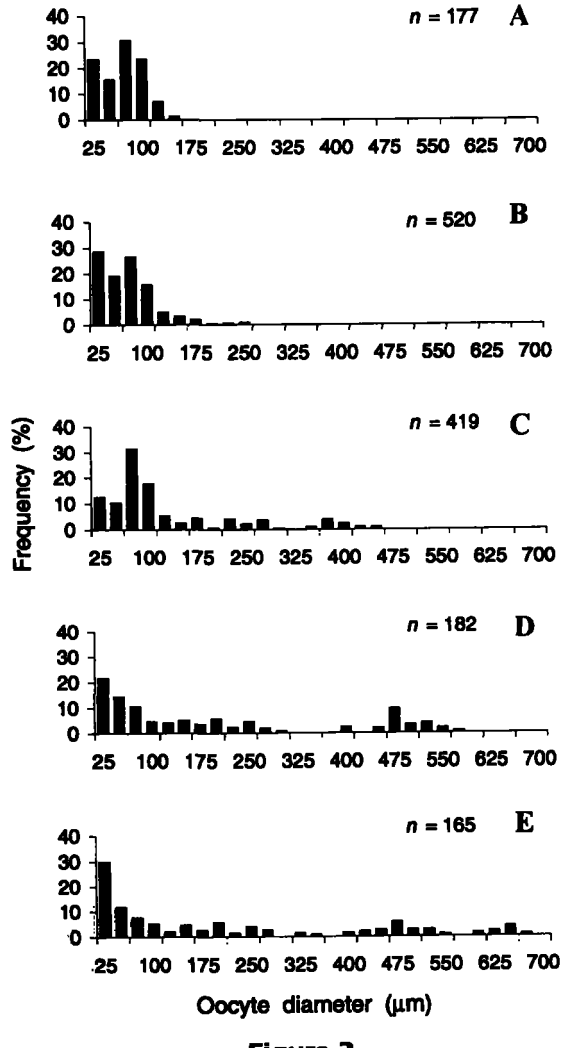


**Figure 2**

Oocyte diameter distributions for different maturity stages: A = immature; B = developing early; C = developing late; D = fully developed; and E = gravid.

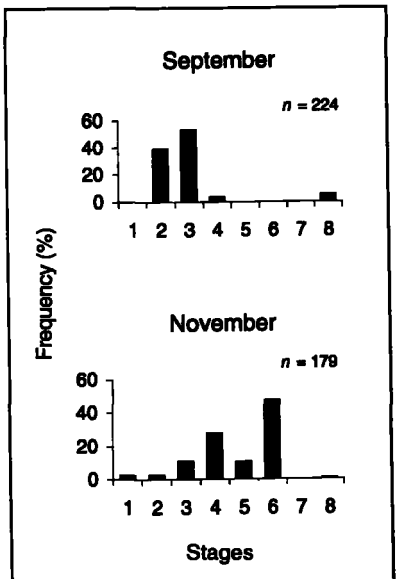


**Figure 3**

Maturity-stage frequency of striped weakfish during September 1995 and November 1994. Stages: 1 = immature; 2 = developing early; 3 = developing late; 4 = fully developed; 5 = gravid; 6 = partially spent; 7 = spent; and 8 = resting.

**Table 2**

Number of reproductively active females of *C. striatus* sampled in "El Rincón" area based on histological staging for determination of spawning frequency. POF = postovulatory follicles; CI = confidence interval.

| Day of month (November) | Hydrated oocytes | POF day-0 | POF day-1 | POF day-2 | Total mature |
|---|---|---|---|---|---|
| 2 | 1 | 2 | 2 | 4 | 23 |
| 3 | 3 | 2 | 2 | 5 | 28 |
| 3 | 1 | 3 | 4 | 1 | 13 |
| 3 | 5 | 1 | 0 | 1 | 13 |
| 4 | 0 | 1 | 8 | 5 | 27 |
| 5 | 4 | 7 | 1 | 2 | 22 |
| 5 | 1 | 0 | 0 | 2 | 17 |
| 6 | 2 | 3 | 4 | 1 | 17 |
| 8 | 1 | 0 | 2 | 0 | 12 |
| Total | 18 | 19 | 23 | 21 | 172 |
| % (average) | 11.71 | 11.09 | 13.44 | 10.65 | |
| 95% CI | 12 ±7 | 11 ±7 | 13 ±8 | 11 ±4 | |

12% (±6), which yielded an estimation that spawning occurred every 8 days.

The range in batch fecundity for females caught in "El Rincón" was 50,000 to 450,000 hydrated oocytes for fish between 40 and 53 cm TL. The samples collected from the Uruguayan coast ranged from 38,000 to 360,000 hydrated oocytes for females of 34 to 52 cm. A test of equality of means for the batch fecundity values of both zones showed no significant difference ($P>0.56$). A test of equality of coefficients indicated that no significant difference existed between the equations for BF vs. TL for the two areas ($P>0.05$). The general equations for the total length and total weight were determined by combining all data (Fig. 4, A and B). No statistical differences were observed between the mean values of relative fecundity obtained for both zones ($P>0.25$). This parameter ranged between 50 and 420 hydrated oocytes per gram of female (ovary free); an increase in the number of oocytes with size was observed (Fig. 4, C and D).

## Discussion

The results obtained indicate that striped weakfish is a multiple spawner with indeterminate annual fecundity. Hence, the potential annual fecundity is not fixed prior to the onset of spawning, and unyolked oocytes continue to mature and to be spawned during the reproductive season (Hunter et al., 1992). This assumption is based on two lines of evidence: 1) the presence of maturing ovaries with postovulatory follicles (partially spent stage), which indicates that after spawning one batch of eggs, a new batch develops and is released; and 2) oocyte size frequency, which shows a continuous distribution of growing vitellogenic oocytes.

Reproductive activity of striped weakfish in the coastal waters of Buenos Aires province ranges from October to March, with a main peak in November (Cassia, 1986). The histological examination of ovaries obtained during September did not show evidence of spawning, but those taken in early November indicated considerable reproductive activity, with a high proportion of postovulatory follicles and the appearance of hydrated oocytes. This corroborates the hypothesis that the spawning of *C. striatus* in "El Rincón" area generally begins in October. Unfortunately, it was not possible to sample this species during the rest of the spawning season, which lasts about 6 mo. according to Cassia (1986). The long reproductive season of this species has also been observed in other sciaenids inhabiting temperate waters, such as *Seriphus politus* (7 mo.) (De Martini and Fountain, 1981), *Cynoscion nebulosus* (7 mo.) (Brown-Peterson et al., 1988), *Micropogonias undulatus* (7 mo.) (White and Chittenden, 1977; Barbieri et al., 1994), *Genyonemus lineatus* (7 mo.) (Love et al., 1984), *Cynoscion nothus* (6 mo.) (De Vries and Chittenden, 1982) and *Cynoscion regalis* (5 mo.) (Merriner, 1976). In Argentinian coastal waters, the main sciaenid associated with *C. striatus* is the white croaker (*Micropogonias furnieri*), which has reproductive activity from November to March (Macchi and Christiansen, 1996).

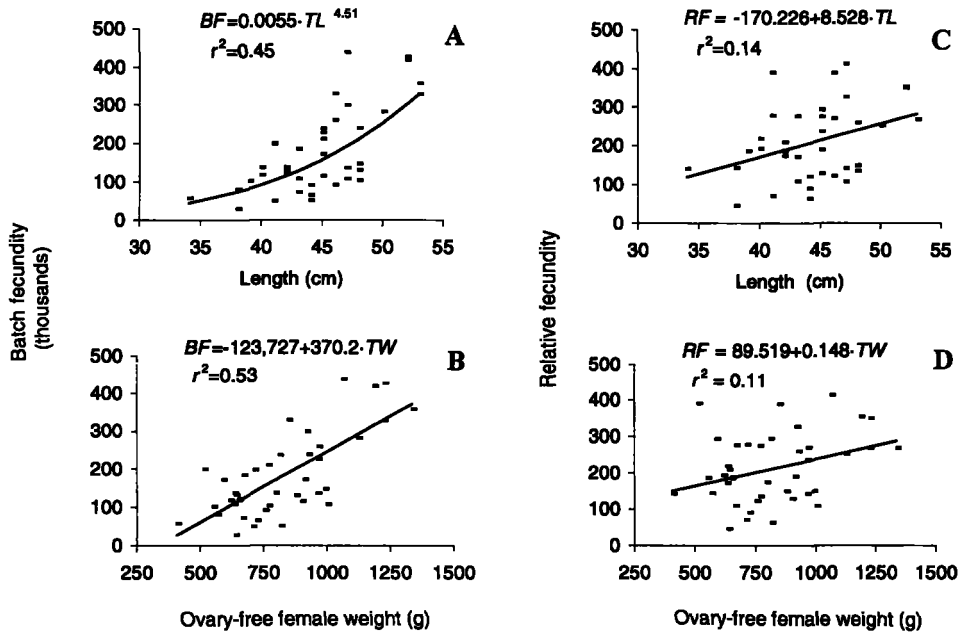


**Figure 4**

Batch fecundity as a function of total length (**A**) and total weight (without ovary) (**B**). Relative fecundity as a function of total length (**C**) and total weight (without ovary) (**D**).

Because vitellogenic oocytes are recruited continually during the reproductive season, it is necessary to determine the batch fecundity and the number of spawnings in the season in order to estimate total egg production (Hunter et al., 1985). Spawning frequency estimated from the percentage of hydrated ovaries (12%) was similar to those calculated with postovulatory follicles (11–13%). The average between day-0 and day-1 POF's (12 ±6%) indicates that spawning occurred once every 8 days during the main peak of the reproductive season (November). Daily spawning fraction of *C. striatus* was similar to that reported for three other scienids: *Seriphus politus* (De Martini and Fountain, 1981), *Genyonemus lineatus* (Love et al., 1984) and *Cynoscion nebulosus* (Brown-Peterson et al., 1988), but was lower than estimates for *Pogonias cromis* (31%) (Fitzhugh et al., 1993). Annual spawning frequency estimated for *Sciaenops ocellatus* (Wilson and Nieland, 1994) and *Cynoscion regalis* (Lowere-Barbieri et al., 1996) varied widely, 3 to 80 days and 2 to 13 days, respectively. Daily spawning percentage of white croaker (*Micropogonias furnieri*) in the Southwest Atlantic was 8.83% (Macchi et al., in press), indicating that the average interval between spawnings for this sciaenid is about 12 days .

Cassia (1986) estimated total fecundity for *C. striatus* by counting the number of growing oocytes, which is inappropriate for a multiple spawning species (Hunter and Goldberg, 1980). This author estimated a total fecundity of 600,000 oocytes for one 40-cm-TL female, when the batch fecundity for that length is about 100,000 hydrated oocytes. In the present study, analysis of variance applied to the fecundity data from "El Rincón" and the Uruguayan coast indicated no statistical differences between these areas. Batch fecundity was a power function of length and a linear function of ovary-free body weight and ranged between 50,000 (34 cm TL) and 450,000 (53 cm TL) hydrated oocytes. Batch fecundity values estimated for striped weakfish were higher than those obtained for smaller sciaenids, such as *Genyonemus lineatus* (800–37,200 oocytes) (Love et al., 1984) and *Seriphus politus* (5,000–90,000 oocytes) (De Martini and Fountain, 1981). Sciaenids with length ranges similar to *C. striatus,* such as *Cynoscion regalis* (Lowere-Barbieri et al., 1996) and *Cynoscion nebulosus* (Brown-Peterson et al., 1988), show slightly higher batch fecundity values. The relations between batch fecundity vs. length and batch fecundity vs. weight for these species had relatively low coefficients of determination, similar to those for striped weakfish. The mean relative fecundity for *C. striatus* (210 ±35 oocytes/g ovary-free body weight) was less than that obtained for *Cynoscion nebulosus* (451 ±43 oocytes) (Brown-Peterson et al., 1988) and

*Cynoscion regalis* (200–750 oocytes) (Lowere-Barbieri et al., 1996).

Accurate annual fecundity estimations are difficult to determine for multiple spawning fishes with an extended reproductive season (Brown-Peterson et al., 1988). During November–March, a female *C. striatus* would spawn 22 times with a spawning frequency of 8 days. Consequently, annual fecundity estimates for a 40.0-cm-TL female would be about 2.0 million eggs. However, annual egg production depends on spawning frequency, and it is possible that this parameter varies during the reproductive season and between years (Lowerre-Barbieri et al., 1996). The annual fecundity estimate for *C. striatus* was similar to that obtained for white croaker of the Rio de la Plata estuary (*Micropogonias furnieri*) (1.8 million eggs for a 40.0 cm TL female) (Macchi et al., in press). Both species are among the most heavily exploited coastal resources in Argentina and Uruguay.

## Acknowledgments

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# Direct validation of ages determined for adult black drum, *Pogonias cromis*, in east-central Florida, with notes on black drum migration

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Findings from indirect age validation studies, in which marginal increments in black drum, *Pogonias cromis*, otolith sections were examined, indicate that the number of opaque bands observed in otoliths is a measure of the true age in years of black drum (Murphy and Taylor, 1989; Beckman et al., 1990; Beckman et al.[1]). However, validation studies of scale-determined ages have indicated that more than one mark is deposited on black drum scales each year after they reach about age four (Richards, 1973; Cornelius, 1984). In addition, evidence from an analysis of the marginal increments for a related sciaenid, the croaker *Micropogonias operc ularis*, has indicated that more than one opaque band was deposited on its otoliths each year (Haimovici, 1977).

Unlike indirect validation studies which provide estimates of the periodicity of annulus formation for a sample of fish, mark-recapture studies provide proof of the accuracy of an age determination technique for an individual fish during the period of time between marking and recapture (Beamish and McFarlane, 1983). This direct technique has been used to validate ages for a variety of species, including red drum, *Sciaenops ocellatus* (Murphy and Taylor, 1991; Ross et al., 1995); snapper, *Pagrus auratus* (Francis et al., 1992); sablefish, *Anoplopoma fimbria* (McFarlane and Beamish, 1995); and the tropical parrotfish *Scarus schlegeli* (Lou, 1992). Because mark-recapture studies provide information on the validity of age marks formed since the mark was applied, they cannot be extrapolated to imply the validity of younger ages (Francis, 1995).

In assessing the status of black drum stocks, accurate age determination is especially critical. These fish are suspected to live to about 60 years old, and the large fisheries that they have supported apparently exploited infrequent, large year classes (Jones et al., in press; Beckman et al.[1]). The purpose of this study was to validate directly the ages of adult black drum by using mark-recapture methods. The sample of recaptured fish also provided insight into the population dynamics of black drum in east-central Florida.

## Materials and methods

We used a 549-m nylon trammel net (124- and 356-mm mesh, inside and outside stretch, respectively) to capture adult black drum in the southern Mosquito Lagoon and northern Banana River areas of the Indian River Lagoon system along Florida's Atlantic coast (Fig. 1). Black drum were captured for tagging in February, June, and September 1992, and in February, June, and August 1993. Each fish was measured for total length (mm), tagged with a 100-mm Hallprint plastic dart tag, injected intramuscularly with approximately 25 mg of oxytetracycline (OTC) per kilogram of body weight, and released to the capture area. The dart tag was placed in the side of the fish about 25 mm ventral to the anterior insertion of the second dorsal fin. This placement allowed the barb to lodge behind a pterygiophore while leaving the external message (streamer) visible. This external streamer bore an identification number and a message in-

[1] Beckman, D. W., C. A. Wilson, D. L. Nieland, and A. L. Stanley. 1990. Age structure, growth rates, and reproductive biology of black drum in the northern Gulf of Mexico. Final report, U.S. Dep. Commerce Cooperative Agreement NA89WC-H-MF017, Marine Fisheries Initiative (MARFIN) Program, 77 p.

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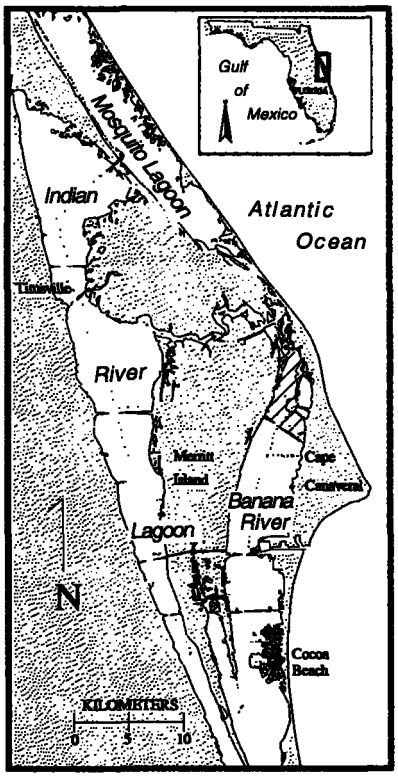


**Figure 1**

Sampling area for black drum along the Atlantic coast of Florida. Most sampling was done in the area shown by diagonal lines just west of Cape Canaveral. Some sampling was also done in the southern portion of Mosquito Lagoon.

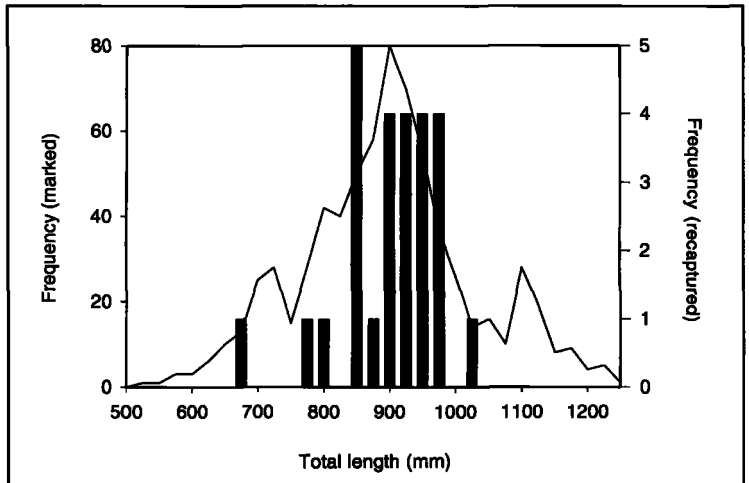


**Figure 2**

Total length-frequency distribution (mm) for black drum that were tagged and released (line, $n$=707) and for those that were recaptured (bars, $n$=26).

structing anglers to contact us. The OTC provided a reference mark defining the otolith margin at the time of initial capture; all recaptures of fish whose otoliths were recovered were made by biologists during sampling trips conducted in August 1993 and January, October, and December 1995.

Recaptured fish were sacrificed and returned to the laboratory, where they were measured for total, fork, and standard lengths; weighed to the nearest tenth of a kilogram; and sexed macroscopically. Sagittal otoliths were excised and stored dry. An Isomet low-speed saw was used to make transverse cuts near the core of the whole otolith. Otolith sections were about 0.5-mm thick and were mounted on glass slides with coverbond mounting media. Opaque bands and OTC marks were examined with a compound dissecting microscope (4× magnification) equipped with an ultraviolet light source. Distances from the otolith core to the proximal edge of the OTC mark and to each opaque band distal to the OTC mark were measured along the axis from the core to the ventral edge of the sulcus acousticus with the aid of an Optimus digital-image processing system.

## Results and discussion

A total of 707 adult black drum, from 515 to 1,237 mm TL, were captured, injected, and tagged during this study. Twenty-six of these fish were recaptured, and their otoliths were excised. Lengths of recaptured black drum ranged from 656 to 1,011 mm TL (Fig. 2). Most of the large (>1,050 mm TL) adult black drum found in our sample came from a school of very large fish caught in southern Mosquito Lagoon; according to two tag returns (see below), this school had apparently left the area shortly after tagging and release.

Ages of recaptured black drum ranged from 3 to 13 years (Table 1); 16 were age 8 and older and were likely to have been mature adults at time of recapture (Murphy and Taylor, 1989). Time-at-large for recaptured fish was from just over a month to just less than three years, i.e. 42–1,031 days.

Observations of the number of opaque bands deposited since the fish had been marked supported our hypothesis that one band formed each year from the late winter to early spring. We observed that five fish tagged during February or June 1993 and recaptured 42–176 days later in August 1993 had not deposited an opaque band since being marked (Table 1). One fish at large for 555 days between June 1993 and January 1995 had deposited one band since release. All other fish recaptured had been at large for 805 to 1,031 days, during which two late-winter to early-

**Table 1**

Tag, recapture, and otolith-measurement data for OTC-marked black drum. Otolith measurements were made from the core to the proximal edge of the OTC band and all subsequent opaque bands to the otolith edge along the ventral margin of the sulcus acousticus.

| Tagged | | Recaptured | | | | Distance from otolith core (mm) | | | |
|---|---|---|---|---|---|---|---|---|---|
| Date | Total length (mm) | Date | Total length (mm) | Days free | Age (yr) | OTC mark | Annulus | Annulus | Otolith edge |
| Jun 93 | 660 | Aug 93 | 656 | 42 | 3 | 2.33 | | | 2.35 |
| Feb 93 | 836 | Aug 93 | 838 | 176 | 5 | 2.75 | | | 2.86 |
| Feb 93 | 975 | Aug 93 | 945 | 176 | 11 | 3.99 | | | 4.08 |
| Feb 93 | 925 | Aug 93 | 921 | 176 | 11 | 3.85 | | | 3.90 |
| Feb 93 | 940 | Aug 93 | 926 | 176 | 11 | 3.79 | | | 3.86 |
| Jun 93 | 732 | Jan 95 | 790 | 555 | 4 | 2.39 | 2.65 | | 2.81 |
| Aug 93 | 832 | Oct 95 | 887 | 805 | 13 | 3.56 | 3.62 | 3.74 | 3.93 |
| Aug 93 | 899 | Oct 95 | 968 | 805 | 9 | 3.44 | 3.50 | 3.68 | 3.87 |
| Aug 93 | 922 | Oct 95 | 961 | 805 | 13 | 3.75 | 3.81 | 3.95 | 4.11 |
| Jun 93 | 711 | Oct 95 | 826 | 847 | 5 | 1.74 | 1.83 | 2.04 | 2.31 |
| Feb 93 | 975 | Oct 95 | 1,011 | 991 | 13 | 3.61 | 3.75 | 3.94 | 4.13 |
| Aug 93 | 821 | Oct 95 | 859 | 805 | 13 | 3.73 | 3.77 | 3.93 | 4.09 |
| Feb 93 | 873 | Oct 95 | 886 | 981 | 9 | 3.00 | 3.16 | 3.29 | 3.51 |
| Aug 93 | 925 | Oct 95 | 952 | 805 | 13 | 4.03 | 4.08 | 4.23 | 4.40 |
| Feb 93 | 673 | Oct 95 | 842 | 981 | 6 | 2.50 | 2.63 | 2.86 | 3.10 |
| Jun 93 | | Oct 95 | 903 | 847 | 5 | 2.44 | 2.55 | 2.81 | 3.03 |
| Aug 93 | 832 | Oct 95 | 843 | 805 | 13 | 3.77 | 3.80 | 3.96 | 4.11 |
| Aug 93 | 941 | Oct 95 | 943 | 805 | 13 | 3.95 | 4.00 | 4.17 | 4.33 |
| Aug 93 | 852 | Oct 95 | 886 | 805 | 13 | 3.98 | 4.02 | 4.15 | 4.29 |
| Jun 93 | 620 | Oct 95 | 771 | 847 | 5 | 2.37 | 2.55 | 2.83 | 3.06 |
| Feb 93 | 880 | Dec 95 | 965 | 1,031 | 9 | 3.30 | 3.45 | 3.67 | 3.92 |
| Feb 93 | 892 | Dec 95 | 936 | 1,031 | 13 | 3.78 | 3.90 | 4.03 | 4.20 |
| Aug 93 | 782 | Dec 95 | 899 | 855 | 6 | 2.99 | 3.08 | 3.40 | 3.67 |
| Feb 93 | 790 | Dec 95 | 911 | 1,031 | 7 | 2.79 | 2.96 | 3.18 | 3.44 |
| Aug 93 | 789 | Dec 95 | 917 | 855 | 8 | 3.24 | 3.28 | 3.53 | 3.76 |
| Aug 93 | 690 | Oct 95 | 830 | 806 | 5 | 2.55 | 2.64 | 2.91 | 3.24 |

spring periods of opaque band formation had occurred. All of the latter had deposited two bands on their otoliths (Fig. 3).

Our direct validation for most ages from 3 years to 13 years indicates that for young adult black drum, at least, age can be determined accurately by counting saggital otolith annuli. Our results extend the findings of an indirect validation study that had used the periodicity of marginal increments as evidence for validation of ages for black drum up to age four in northeast Florida (Murphy and Taylor, 1989). In addition, the seasonal appearance of opaque margins on the otolith sections in older black drum between 20 and 37 years old in the northern Gulf of Mexico (Beckman et al., 1990) is evidence for the validity of this aging technique in older fish. In contrast, the formation of two growth increments or marks per year on scales appears to begin at the time of maturity; formation of the second mark has been attributed to spawning (Richards, 1973). All black drum larger than 700 mm FL (717 mm TL) and more than four years old that were sampled in the northern Gulf of Mexico (Nieland and Wilson, 1993), and all black drum larger than 650 mm TL and more than 5 years old sampled off northeast Florida (Murphy and Taylor, 1989) were mature. Because our samples included adult fish of these sizes and ages, they were likely mature. Therefore black drum in our sample had clearly deposited only one opaque band on the sagittae each year for a number of years after they first matured. It seems likely then that, unless black drum begin to deposit multiple annuli each year after they attain some age older than that found in our samples, their maximum age would be at least equal to the highest reported opaque band count, about 60 for black drum in U.S. Atlantic coastal waters (Murphy and Taylor, 1989; Jones et al., in press).

Our relatively small sample of validated ages for black drum lends support to previous findings of highly variable year-class strength for this species, and for the generally rapid growth of some fishes inhabiting the Indian River and Mosquito Lagoons. Eleven of the 26 black drum we recaptured were members of the 1982 year class, the oldest year class

in our sample. Beckman et al.[1] also noted the persistence of several large year classes (the 1979, 1974, 1970, and 1966 year classes) in the purse-seine fishery catch in the northern Gulf of Mexico, during 1986–89, and Jones et al. (in press) noted that the exceptionally large 1942 and 1934 year classes were still prominent in 1990–92 samples collected from Chesapeake Bay fisheries. Observed sizes at age of black drum in our sample, when released, were 620–732 mm TL for 3 year olds, 782–836 mm for 4 year olds, and 789–880 mm for 6 year olds. These sizes at age were much larger than those predicted for northeast Florida black drum: 477, 555, 625, and 687 mm TL for ages 3–6 (Murphy and Taylor, 1989). Young red drum, *Sciaenops ocellatus,* and spotted seatrout, *Cynoscion nebulosus*, are also larger at age in the Indian River Lagoon than in other areas of Florida (Murphy and Taylor, 1990, 1994).

Limited tag-recapture information gathered during this study indicates that some larger black drum make extensive migrations from the Indian River Lagoon system. Seven of the 9 angler-recaptured, tagged black drum (none of whose otoliths were recovered) were caught in the northern Indian River Lagoon within 10 km of their release site. Two fish (1,025 and 1,163 mm TL), however, tagged and released in February 1992 travelled about 1,370 km north to Chesapeake Bay, where they were captured by anglers in late May and early June. Although the reproductive states of these two tagged fish were not recorded at release, many of the males tagged along with them were running ripe. The fact that these fish moved to Chesapeake Bay during the time period when peak spawning progresses up the Atlantic coast may imply that black drum continue spawning as they move northward during the spring. This migration would enable them to broadcast their average annual fecundity of 32–45 million eggs (Fitzhugh et al., 1993; Nieland and Wilson, 1993) over a wide range of suitable egg and larval habitats.

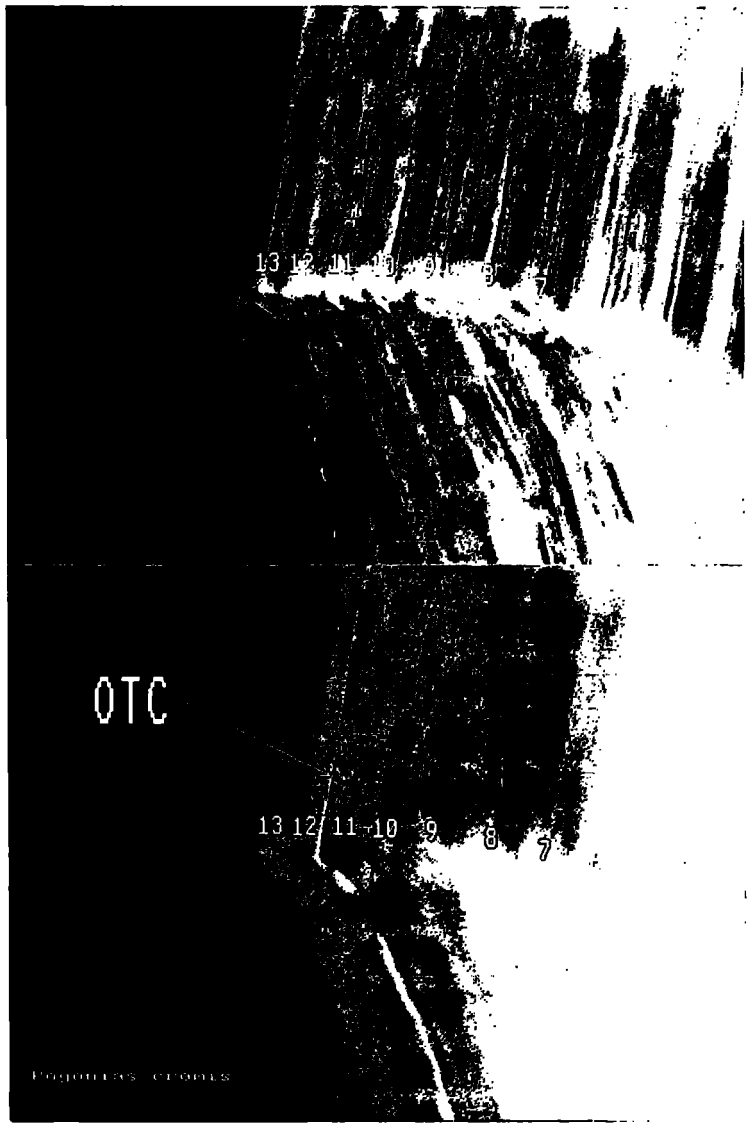


**Figure 3**

A black drum otolith section shown under reflected light only (top) and under reflected light and ultraviolet light (bottom). Opaque bands are numbered consecutively from the core, and the fluorescing oxytetracycline (OTC) band is indicated. This fish was tagged and injected in August 1993 and recaptured 941 days later in October 1995.

Extensive tagging studies in Florida during the early and mid-1960's showed that, except for some of those released on beaches, black drum hardly moved from a release site (Topp, 1963; Beaumariage, 1964, 1969; Beaumariage and Wittich, 1966); even the greatest movement of fish along the beaches was less than 145 km. The total lengths of fish tagged during these studies were generally less than 500 mm. In Texas, Osburn and Matlock (1984) found substantial intrabay movement of small immature black drum, but little movement between bays. Music and Pafford (1984) also found that most black drum tagged in Georgia did not move far from the area of release. However, in Georgia 13% of all returned fish

had moved more than 100 km, reaching as far south as West Palm Beach, Florida (619 km), and as far north as Murrells Inlet, North Carolina (437 km). Surprisingly, the two black drum that had travelled the farthest from their release sites in Georgia were less than 350 mm TL.

Because black drum are long-lived and capable of extensive movements, knowledge about the magnitude and frequency of their mixing during their potential 60-year life span is critical for understanding how fishing pressure within one geographic area affects fish populations in other areas. In Florida, strict regulations on the harvest of black drum were implemented in 1989 following unvalidated evidence that they were long-lived fish (Murphy and Taylor, 1989). Because many current stock assessment techniques often depend on an accurate estimate of maximum life span so that a natural mortality rate for a population can be determined, validation studies are especially critical in helping to prevent mismanagement of long-live species (Beamish and McFarlane, 1983).

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# The influence of spear fishing on species composition and size of groupers on patch reefs in the upper Florida Keys

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Groupers are an important fishery resource throughout tropical and subtropical regions of the world (Heemstra and Randall, 1993). Dependent and independent fishery surveys of grouper populations in south Florida and the Caribbean have shown drastic declines in populations, most likely due to intense fishing pressure (Sadovy, 1994; Bohnsack et al., 1994). Combined grouper species landings by weight have declined in the Florida Keys by more than half since the mid 1980's (Bohnsack et al., 1994).

Fishermen tend to target the larger fish in a population, with the result that a decrease in the density, average size, and relative abundance of exploited species is inevitable (Bohnsack, 1982; Russ, 1985; Plan Development Team (PDT), 1990; Roberts and Polunin, 1991). Grouper populations are especially sensitive to fishing pressure, exhibiting reductions in density and average size, as well as shifts in species composition between sites that are fished and those that are unfished (Russ, 1985). For example, the mean weight of three species of grouper was found to be significantly greater in unfished than in fished sites in the Red Sea (Roberts and Polunin, 1993). Similarly, the density and biomass of groupers was significantly greater in sites protected from fishing than in sites unprotected in the Philippines (Russ and Alcala, 1989). Craik (1981) found that a commercially important grouper (*Plectropomus leopardus*) on the Great Barrier Reef had a higher mean size at an unfished reef than at a fished reef. Russ (1985) and Craik (1981) observed that larger individuals of a grouper species were abundant only at unfished reefs. Sluka et al. (1997) showed that the biomass, average size, and reproduction (the total number of eggs produced per hectare) of Nassau grouper, *Epinephelus striatus*, was significantly greater inside a marine fishery reserve than outside. Many studies have attributed a change in the relative abundance of grouper species to fishing pressure (Goeden, 1982; Bohnsack, 1982; Russ, 1985; Watson and Ormond, 1994; Sluka, 1995).

In the Florida Keys there has been a history of management measures that have affected fishing pressure on groupers. In 1980, the state of Florida banned fish traps in its waters (<3 nautical miles), and in 1992 the United States government banned fish traps in federal waters of the Florida Keys (>3 nautical miles to the 150 fathom depth contour). During this study, there was a bag limit of five fish and a minimum size limit of 51 cm (20 in.) for six grouper species (red grouper, *Epinephelus morio*, black grouper, *Mycteroperca bonaci*, yellowmouth grouper, *M. interstitialis*, gag, *M. microlepis*, scamp, *M. phenax*, and yellowfin grouper, *M. venenosa*). Harvest of two species (jewfish, *E. itajara*, in 1990 and Nassau grouper, *E. striatus*, in 1991) has been prohibited in the south Atlantic waters of the United States. Reefs within Key Largo National Marine Sanctuary (KLNMS) and John Pennekamp Coral Reef State Park (JPCRSP) have been protected from spear fishing since 1960. Since the time of this study, the entire Florida Keys has come under the management of the Florida Keys National Marine Sanctuary.

One of the results of the previous management scheme is that the upper Florida Keys can be divided into two areas: one area protected from spear fishing and the other unprotected from spear fishing. It is assumed that the intensity of hook-and-line fishing is similar inside and outside of KLNMS and JPCRSP. Thus the goal of this study was to examine the influence of spear fishing on the size and species composition of groupers in the upper Florida Keys and to discuss potential implications for the management of these populations. These population parameters were

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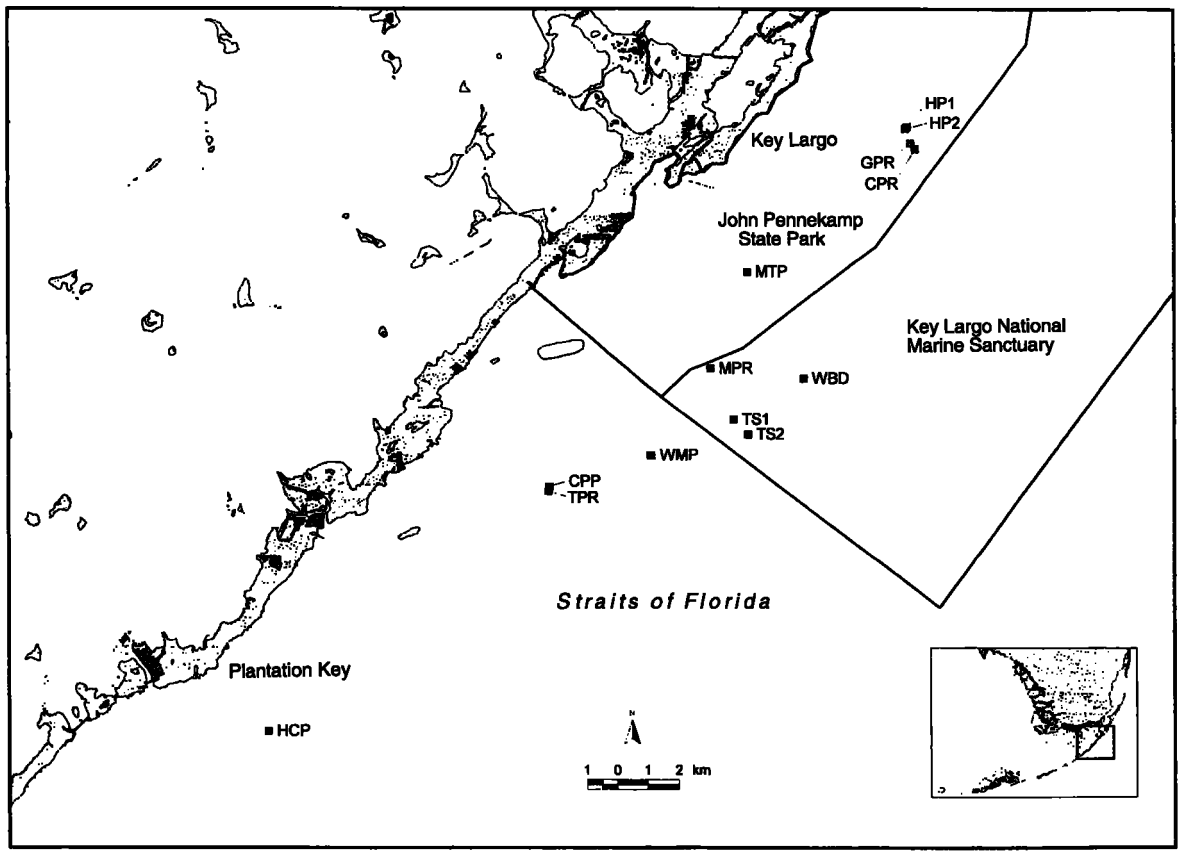


**Figure 1**
Map showing survey sites located in the upper Florida Keys.

expected to differ between sites under differing fishing intensities owing to the biology of the species, their site-attached nature, and the susceptibility of these species to fishing pressure.

## Materials and methods

Sampling on four patch (shallow-water, small) reefs occurred in February 1992, April 1993, September 1993, January 1994, April 1994, and September 1994. Nine additional patch reefs were sampled in September 1994. A total of 13 patch reef sites were sampled (Fig. 1). There were no significant seasonal differences in the size distribution of all grouper species combined at these sites (Sluka and Sullivan, 1996). Thus, data from all seasons were combined for analyses.

Researchers were trained to estimate lengths of fish consistently and accurately using methods outlined in Bell et al. (1985). Observers had approximately five minutes to estimate the length of a series of fish models of varying lengths. The length of each model was recorded in one of five categories: <5 cm, 5–15 cm, 16–25 cm, 26–35 cm, and >35 cm. The frequency distribution of estimated model lengths was compared to the known distribution by using a chi-square test. The bias of each observer was determined as either consistently underestimating or overestimating the size of the fish models. The information on biases was given to each observer. The observer then repeated the length estimation procedure until there was no significant difference between the observed and expected distributions ($P>0.05$). Observers were found to be competent for length estimation after 2–3 trials.

At four of the sites (MPR, TS1, TS2, and HCP), transect lines of 20 m or 25 m in length were used to sample the number, species, and length of groupers. The transect lines were laid in representative portions of each patch reef. The transect line was searched 6 m out from each side for a total width of 12 m (width by visual estimation). Within each transect all groupers were enumerated and their length category and species recorded on underwater paper. Observers using SCUBA searched throughout the width of the transect, examining all crevices, caves, and holes. At the other nine sites, observers sampled the entire patch reef. Patch reef size was not quantified at these sites; thus density could not

be compared between protected sites and those unprotected from spear fishing.

It was hypothesized that spear fishermen were targeting some species more than others owing to their larger size. Targeted species were assumed to be red grouper, black grouper, scamp, and gag. The latter two species were rare, constituting <14% of individuals observed by site. Nassau grouper were assumed to be a nontargeted species because of the ban on harvest. Differences in the relative abundance of targeted grouper were assessed with a $t$-test on the arcsine-transformed percentage of the total number of grouper observed at a site. Individual sites were the replicates for the analysis.

It was also hypothesized that the average size of targeted species would be significantly different between protected sites and those unprotected from spear fishing. A nested ANOVA was used to test this hypothesis, with the main factor being protection level (spear fished or protected) and sites nested within protection level. The mid points of size categories were used as an estimate of the individual sizes of sampled fish. Thus, for this analysis, individual fish sizes were the replicates. A value of 40 cm was used for individuals in the >35 cm category. This results in a conservative analysis because many of the fish in this category were much larger than 40 cm (R. Sluka, personal observation).

## Results

There was no significant influence of spear fishing on the relative abundance of targeted grouper species ($t$=0.658, $P$>0.55). Targeted species constituted an average of 65% ($n$=9) and 71% ($n$=4) on protected and unprotected sites, respectively. Nontargeted species (graysby, *Epinephelus cruentatus*, coney, *E. fulvus*, rock hind, *E. adscensionis*, red hind, *E. guttatus*, and Nassau grouper, *E. striatus*) constituted on average 35% and 29% of the total number of individuals on protected and unprotected sites, respectively. Nassau grouper constituted a greater proportion of the individuals observed at protected (15%) than at unprotected (2%) sites. These values were statistically different ($t$=2.46, $P$<0.05).

Patch reefs protected from spear fishing had a significantly greater size of targeted individuals than did unprotected patch reefs ($F_{1,211}$=3.874, $P$=0.05). The mean size (+/– 1 SE) of targeted grouper species on protected patch reefs was 29.3 (0.7) cm, whereas the mean size of targeted species on unprotected sites was 26.0 (0.8) cm. There was also a significant difference among sites nested within protection levels ($F_{11,211}$=5.151, $P$<0.001).

## Discussion

In this study, spear fishing appears to primarily influence the average size of groupers. Sites in which spear fishing was not allowed had grouper assemblages that were characterized by larger-size individuals. This result is similar to those found in studies examining the effects of hook-and-line fishing, where fishermen target the larger individuals in a population and thus decrease the average size of a fish species (Roberts and Polunin, 1991). Overall, grouper species composition was not significantly influenced by the presence or absence of spear fishing; targeted species were similarly abundant on protected and unprotected patch reefs. Sluka and Sullivan (1996) have shown that grouper species, such as black grouper, red grouper, and Nassau grouper, are more abundant, but smaller, on inshore patch reefs than on offshore bank reefs of the upper Florida Keys. It is likely that species such as these are recruiting inshore before they move offshore (Ross and Moser, 1995). Nassau grouper, however, were more abundant on patch reefs protected from spear fishing than on unprotected patch reefs. Although there is a ban on harvesting these species, spear fishermen may still collect individuals. It is important to examine how effective the ban on harvesting this species is in the Florida Keys.

Offshore bank reef sites in the upper Florida Keys protected from spear fishing had snappers (Lutjanidae) and grunts (Haemulidae) of larger size and greater abundance than did a lower Keys site subjected to spear fishing (Bohnsack, 1982). Clark et al. (1989) found similar results when sites inside Looe Key National Marine Sanctuary (lower Florida Keys) were compared before and after protection from spear fishing. The present study did not examine differences in abundance between protection levels. However, it is expected that there would be no significant differences in abundance between these sites; this result is due to the nature of both spear fishing and grouper growth and reproductive characteristics. Spear fishing targets the largest fish in an assemblage but only accounts for a small percentage of the total fishing effort (PDT, 1990). For example, spear fishing accounted for 10.5% of the total recreational fishing catch in Biscayne National Park.[1] Thus the magnitude of the selection pressure is likely much less than that from hook-and-line fishing because of

[1] Tilmant, J. T., and R. Stone. 1984. Reef fish harvest trends, Biscayne National Park, Dade County Florida. Unpublished report presented to the 1984 stock assessment workshop. Southeast Fisheries Center, National Marine Fisheries Service, Miami, Florida, 26 p.

the smaller number of spear fishermen. However, the lower number of spear fishermen may exert a more directed selectional effect on grouper species because they can be highly selective for the largest individuals.

The growth and reproductive characteristics of groupers render these species especially susceptible to overfishing (Bannerot et al., 1987; Shapiro, 1987; Huntsman and Schaaf, 1994). Groupers that are targeted by fishing grow slowly to a large maximum size (Manooch, 1987). The removal of larger individuals leaves behind smaller individuals to spawn. Over many generations, this can result in a decrease in the size and age at sexual maturity (Ricker, 1981) and also decrease the average size of the population (Roberts and Polunin, 1991). Many grouper species are protogynous hermaphrodites, changing sex from females to males later in life (Shapiro, 1987). Larger groupers are generally males, and at intensive fishing levels, the number of males in the population can be drastically reduced. If too many males are removed, sperm are reduced for reproduction (Bannerot et al., 1987). If sperm are reduced, protogynous stocks are more vulnerable to overfishing than are gonochoristic stocks (Huntsman and Schaaf, 1994). Species that are protogynous may experience a drastic reduction in reproductive capacity, even at moderate levels of fishing (Huntsman and Schaaf, 1994). However, there may be mechanisms by which the population can compensate for a changing sex ratio in the presence of overfishing (Claro et al., 1990; Huntsman and Schaaf, 1994). Huntsman and Schaaf (1994) showed that these types of compensation mechanisms can reduce the detrimental impacts of fishing pressure on protogynous species. In addition to protogyny, the reproductive behavior of groupers may increase their susceptibility to overfishing. Many species of grouper aggregate to spawn during one or two months of the year (Smith, 1972; Shapiro, 1987; Claro et al., 1990). These spawning aggregations are subject to intense fishing pressure (Olsen and LaPlace, 1978, Claro et al., 1990; Sadovy, 1994). In many parts of the Caribbean, aggregations have disappeared as a result of overfishing (Sadovy, 1994). Sluka et al. (1997) showed that reproduction (the total number of eggs produced per hectare) was six times greater in a marine fishery reserve in the central Bahamas than in the surrounding unprotected region.

It is concluded that the ban on spear fishing in the upper Florida Keys has significantly benefitted the size distribution of groupers. However, it appears that a ban on spear fishing alone has not resulted in recovering population levels of grouper in this region. Bohnsack et al. (1994) has clearly shown a decline in commercially and recreationally targeted grouper landings throughout the Florida Keys. Sluka and Sullivan (1996) have shown that the offshore grouper assemblage over shallow bank reefs of the upper Florida Keys is dominated numerically by graysby (88%), a small, nontargeted species. Densities of targeted species are low compared with regions where fishing was prohibited or had not yet taken place (Sluka and Reichenbach, 1996; Sluka et al., 1997).

It is recommended that marine fishery reserves be considered as a management measure because of their success in other regions and because of a strong theoretical basis (PDT, 1990). Grouper assemblages inside marine fishery reserves are more dense, of greater average size, and produce greater numbers of eggs per hectare than in similar, unfished sites (Bohnsack, 1982; Russ and Alcala, 1989, Roberts and Polunin, 1993; Watson and Ormond, 1994; Sluka et al.,1997). Although management measures, such as bans on spear fishing, have some beneficial effects, the available evidence suggests that the establishment of marine fishery reserves is the most successful method for restoring and conserving grouper assemblages.

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# A retrospective (1979–1996) multispecies assessment of coral reef fish stocks in the Florida Keys

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**Abstract.**—A baseline assessment of 35 economically and ecologically important Florida Keys reef fish stocks is provided by using a systems approach that integrates sampling, statistics, and mathematical modeling. Quantitative fishery-independent data from reef fish visual surveys conducted by SCUBA divers from 1979 to 1996 were used to develop estimates of population abundance, assemblage composition, and stock structures in relation to key physical and habitat factors. Exploitation effects were assessed with a new length-based algorithm that calculates total mortality rates from estimates of "average length of fish in the exploitable phase of the stock." These estimates were highly correlated for two statistically independent data sources on reef fish: fishery-independent diver observations and fishery-dependent head boat catches. We developed a reef fish equilibrium exploitation fishery simulation (REEFS) model and used estimates of fishing mortality to assess yield-per-recruit in relation to fishing intensity and gear selectivity and to assess spawning potential ratio (SPR) in relation to U.S. federal "overfishing" standards. Our analyses show that 13 of 16 groupers (Epinephelinae), 7 of 13 snappers (Lutjanidae), one wrasse (Labridae), and 2 of 5 grunts (Haemulidae) are below the 30% SPR overfishing minimum. Some stocks appear to have been chronically overfished since the late 1970s. The Florida Keys reef fishery exhibits classic "serial overfishing" in which the largest, most desirable, and vulnerable species are depleted by fishing. Rapid growth of the barracuda population (Sphyraenidae) during the same period suggests that fishing has contributed to substantial changes in community structure and dynamics.

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The Florida Keys support a rich tropical marine ecosystem, a productive multispecies coral reef fishery, and a billion dollar tourist economy. The Florida Keys are also considered an "ecosystem-at-risk" as one of the nation's most significant yet most stressed marine resources under management of the National Oceanic and Atmospheric Administration (NMFS, 1996). Concern about habitat degradation and escalating resource uses from a rapidly growing human population in southern Florida resulted in the establishment of the Florida Keys National Marine Sanctuary (FKNMS) in 1990. Because they are one of the most complex ecosystems on earth, coral reefs are a particular concern. The diverse fish community of these coral reefs is influenced by complicated biological and physical interactions (Sale, 1991; Lee et al., 1992; Polunin and Roberts, 1996). Reef fisheries can target a number of economically and ecologically important species (e.g. groupers, snappers, lobsters, conch, sponges, and corals). Over the past several decades, public use of and conflicts over fishery resources have increased sharply, while some fishery catches from historically productive snapper and grouper stocks have declined (Bohnsack et al., 1994). Concomitantly, the status and biological dynamics of these reef fishery resources are not well understood, and important stock assessment data are not available.

Another concern regarding reef fishery resources is the restoration of the Everglades north of the Florida Keys. Hydrological projects of historic proportions are expected to make a substantial change in the timing, volume, and location of freshwater outflows into the coastal marine environment (Harwell et al., 1996). These changes could affect the survivorship of juvenile reef fishes in critical shallow nursery areas of Florida Bay and Biscayne Bay and ultimately affect the productivity of the entire coral reef ecosystem.

The condition of most reef fish stocks is unknown because of the large number of species in the fishery, a lack of fishery-effort and landings data, and the quantity of population dynamics data needed to do traditional stock assessments. The goal of this paper is to develop a technically sound quantitative method for multispecies management assessments. For this purpose, we present an integrated baseline assessment to reference the status of the multispecies fishery so that the effects of management changes in the FKNMS may be accurately evaluated in the future (U.S. Dep. Commerce, 1996). Using fishery-independent data, we conducted an 18-year retrospective, analytical yield assessment of economically important Florida Keys reef fish stocks to elucidate the effects of fishing and to help define an effective fishery management strategy.

## Hypothesis

A key to our ability to assess reef fish stocks was the use of "average size" (in length) of fish in the exploitable phase of the population ( $\bar{L}$ ) as an indicator of stock status. Average size of fish was derived from visual survey data or headboat landings data. Headboats are party boats that carry more than 15 anglers per fishing trip (Dixon and Huntsman[1]). The use of $\bar{L}$ in stock assessment has deep roots in traditional fisheries management (Beverton and Holt, 1956, 1957; Ricker, 1975). The statistic provides a population level metric that integrates individual metabolic variables such as interdependent growth, mortality, and reproductive processes. The $\bar{L}$ statistic also is an important index of fishing effects because persistent heavy fishing reduces the average size of the population over time, making the stock younger through a process known as "juvenescence" which successively eliminates older, more fecund size classes (Ricker, 1963). This is extremely important in the context of stock and recruitment because the fecundity potential of individuals increases exponentially with size. In general, the average length of fish in the exploitable phase (i.e. between the size at first capture, $L'$, and the maximum size, $L_\lambda$) is highly correlated with average population size and thus reflects the rate of fishing mortality operating in the fishery.

Theoretically, the average size of fish landed for any given species should be equal to the average size in the exploited phase of the remaining population just after fishing. In other words, we hypothesize that fishery-independent survey estimates of average length derived from visual data reported by divers should equal fishery-dependent estimates derived from catch data reported by headboat anglers. The greater the correlation between the two independent estimates of $\bar{L}$, the more robust "average length" should be as an indicator of stock status subject to exploitation.

## Methods and materials

### Study area

The Florida Keys coral reef ecosystem is a unique tropical coastal marine environment stretching about 370 km from Key Biscayne southwest to the Dry Tortugas (Fig. 1). Situated parallel to the Florida current and Florida Bay, the coastal ecosystem encompasses many varied habitats comprising fresh- to saltwater marshes, estuaries, lagoons, mangrove stands, coral islands, sea grass beds, and coral reefs. Florida Bay and adjacent coastal estuaries serve as nursery areas for spiny lobster and many juvenile fishes that occupy reefs as adults. The clear water and high diversity of reef fish in the Florida Keys coral reef tract provide a unique environment to assess multispecies fisheries. Here we use a "systems approach" to facilitate effective decision making and to improve fishery management performance (Ault and Fox, 1989; Rothschild et al., 1996).

### Reef fish surveys

Fishery-independent visual estimates of the abundance and size distributions of multispecies reef fish populations were taken along the Florida Keys reef track continuously from 1979 to 1996 (Table 1) by 12 highly trained and experienced divers using the stationary visual survey method of Bohnsack and Bannerot (1986). This nondestructive method provides reliable quantitative estimates of species abundance, frequency-of-occurrence, and size structure for the reef fish community. Divers recorded the abundance as well as the minimum, mean, and maximum lengths of each species seen during 5 minutes within randomly selected 7.5-m radius circular quadrats. Underwater visual estimates of reef fish size and abundance have frequently been made (Bellwood and Alcala, 1988; Harvey and Shortis, 1996); however, accurate and precise visual estimates of fish length require well-trained and experienced observers because objects in water appear magnified and closer than their actual range (Bell et al., 1985; Harvey and

[1] Dixon, R. L., and G. R. Huntsman. 1992. Estimating catches and fishing effort of the southeast United States headboat fleet, 1972–1982. Beaufort Laboratory, Southeast Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, Beaufort, NC 28516. Draft report.

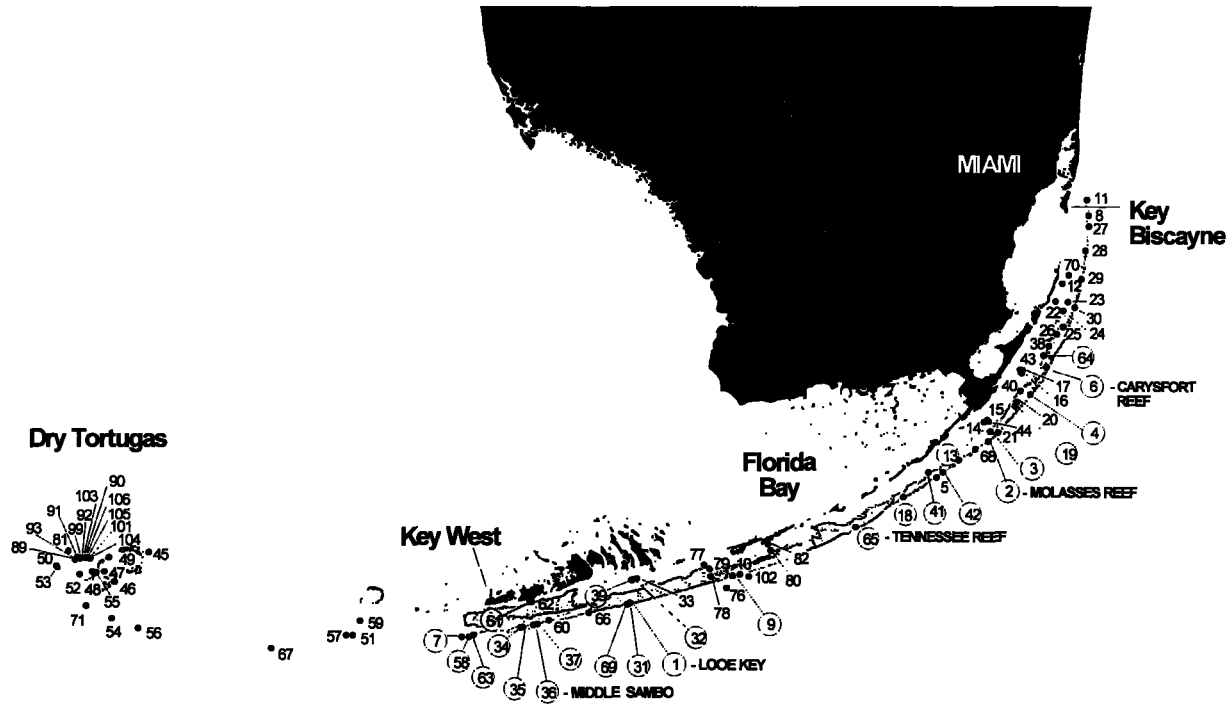


**Figure 1**

Map of the Florida Keys coastal marine ecosystem showing the coral reef tract (light gray) running offshore from Key Biscayne southwest to the Dry Tortugas, and the spatial relationships of Florida Bay, Key West, and the Miami urban center. Numbered darkened circles show the 89 reefs where 4,571 visual survey samples of the reef fish community were taken from 1979 to 1996. Open circles around numbers indicate sanctuary preservation areas (SPAs).

**Table 1**

Visual survey sampling effort (number of point samples) by habitat areas and depth intervals conducted from 1979 to 1996 in the Florida Keys reef tract. The offshore zone is exposed to the Florida Current.

| Depth | | Reef zone habitat type | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Artificial reef | Coral reef | | Hard bottom | | Sand bottom | Totals | |
| Feet | Meters | Inshore | Inshore | Offshore | Inshore | Offshore | Inshore | Total | Percent |
| 0–10 | 0–3.05 | 0 | 848 | 171 | 26 | 8 | 13 | 1,066 | 23.32 |
| 10–20 | 3.05–6.10 | 5 | 726 | 816 | 14 | 207 | 38 | 1,806 | 39.51 |
| 20–30 | 6.10–9.14 | 85 | 403 | 561 | 4 | 146 | 0 | 1,199 | 26.23 |
| 30–40 | 9.14–12.19 | 28 | 31 | 92 | 0 | 40 | 0 | 191 | 4.18 |
| 40–50 | 12.19–15.24 | 9 | 9 | 81 | 0 | 48 | 0 | 147 | 3.22 |
| 50–60 | 15.24–18.29 | 0 | 15 | 65 | 0 | 47 | 0 | 127 | 2.78 |
| 60–70 | 18.29–21.34 | 0 | 1 | 34 | 0 | 0 | 0 | 35 | 0.77 |
| Total | | 127 | 2,033 | 1,820 | 44 | 496 | 51 | 4,571 | |
| Percent | | 2.78 | 44.48 | 39.82 | 0.96 | 10.85 | 1.12 | | 100.00 |

Shortis, 1996). To improve accuracy, divers continuously calibrated their length estimates with a 30-cm ruler attached perpendicular to the far end of a meterstick. Divers without calibration sticks have been shown to obtain a mean accuracy of 86% for length estimates (St. John et al., 1990).

Maximum use of the visual survey data required statistical intercalibration of the sampling efficiency of each diver. We used multiple regression analysis (Neter et al., 1996) to estimate relative sampling efficiency by adapting the "fishing power" model of Robson (1966)

$$C(d,t) = F(d,t)N(t)\xi(d,t) = q(d)f(d,t)N(t)\xi(d,t)$$

$$\rightarrow \frac{C(d,t)}{f(d,t)} = q(d)\overline{N}(d,t), \quad (1)$$

where $C(d,t)$ = the fish count of diver $d$ at reef date $t$;
$N(t)$ = the average population size at reef date $t$;
$q(d)$ = the coefficient of sampling efficiency for diver $d$;
$f(d,t)$ = the nominal survey effort of diver $d$ at reef date $t$, and
$\xi(d,t)$ = a log normally distributed error variable.

To account for any sampling bias that may have been introduced by differences among divers, a simple log-linear transformation of Equation 1 makes it possible to obtain minimum variance estimates of relative sampling efficiency, given fish counts by species, by diver, and by reef date. Data used for model development were derived from a series of controlled experiments conducted during a 9-day sampling expedition to the Dry Tortugas during June 1994. A matrix of estimated efficiency coefficients for divers by species was used to adjust an individual diver's results in relation to a standard-normal diver, here the most experienced diver in the group. After standardization, all the individual visual "catch-per-unit-of-effort" measurements were comparable over time and space (Ault et al.[2]). Spatial and temporal patterns in abundance and correlative linkages to habitat types were qualitatively analyzed with 3-D visualization software (IDL, 1995) by reef site throughout the Florida Keys for various survey years. Multivariate statistical analysis (Johnson and Wichern, 1992; Venables and Ripley, 1994) was used to assess variance-covariance and correlation structures between reef fish density and selected environmental and fish community auxiliary covariates.

We also used the 1981–95 NMFS headboat catch-and-effort data (Bohnsack et al., 1994; Dixon and Huntsman, 1992) to provide fishery-dependent population estimates comparable to those from the visual survey. Headboat data provide total numbers of individuals in the catch as well as total weight in the catch by species by year.

## Stock assessment indicator variable

A stock assessment indicator variable is a quantitative measure that reflects the status of a population subjected to fishing or other environmental changes. Because reef fishes integrate aspects of the coastal ocean environment over their lifetime, a robust measure of population "health" or status can provide a sensitive indicator of direct and indirect stress on the stock, and perhaps on the regional marine ecosystem (Fausch et al., 1990). Population health for reef fish communities can best be described with the metabolic-based pool variable "average length in the exploitable phase of the stock." Therefore, to assess the health of each of the $s$ stocks in the reef fish community over the past two decades, the statistic "average length in the exploitable phase of the stock," $\overline{L}(t)$, was found for each stock by integrating between the population age limits from $t'$ (minimum age at first capture) to $t_\lambda$ (oldest age in the stock), written as

$$\overline{L}(t) = \frac{F(t)\int_{t'}^{t_\lambda} N(a,t)L(a,t)da}{F(t)\int_{t'}^{t_\lambda} N(a,t)da}, \quad (2)$$

where $N(a,t)$ = abundance for age class $a$ at time $t$;
$L(a,t)$ = length for class $a$ at time $t$; and
$F(t)$ = the instantaneous fishing mortality rate at time $t$.

Estimates of the mean, variance, and 95% confidence interval of the mean were computed by the methods of Sokal and Rohlf (1969).

To estimate the annual total instantaneous mortality rate $Z(t)$ for each fish stock in each year $t$ from population size structure and abundance statistics, we used a length-based method (Ault and Ehrhardt, 1991; Ehrhardt and Ault, 1992) particularly applicable to reef fish population dynamics

$$\left[\frac{L_\infty - L_\lambda}{L_\infty - L'}\right]^{\frac{Z(t)}{K}} = \frac{Z(t)\left(L' - \overline{L}(t)\right) + K\left(L_\infty - \overline{L}(t)\right)}{Z(t)\left(L_\lambda - \overline{L}(t)\right) + K\left(L_\infty - \overline{L}(t)\right)}, \quad (3)$$

where, $L_\lambda$ = maximum size;
$L'$ = the length at first capture;
$\overline{L}(t)$ = the average size in the exploitable phase in year t; and

[2] Ault, J. S., J. A. Bohnsack, and G. Meester. 1998. The relative fishing power of divers in tropical reef fish visual surveys. Unpubl. manuscript.

$K$ and $L_\infty$ = parameters of the von Bertalanffy equation.

Thus, the only unknown variable in Equation 3 is the total mortality rate in year $t$, $Z(t)$, which can be estimated fairly easily with an iterative algorithm called LBAR (Ault et al., 1996). Finally, by assuming that $M$, the annual instantaneous rate of natural mortality, is known and constant for the interval $\Delta t$, we can estimate the fishing mortality rate as $\hat{F}(t) = \hat{Z}(t) - M$.

## Reef fish exploited-population simulation model

To achieve a better understanding of the dynamics of multispecies tropical coral reef fish stocks, their response to exploitation, and the accuracy and precision of statistical estimates from the sampling surveys, we developed an object-oriented computer simulation model for exploited reef fish populations in the Florida Keys fishery (REEFS [reef fish equilibrium exploitation fishery simulator (Ault[3])]). The fundamental population-dynamic processes of growth, mortality, and recruitment are relatively similar for fishes of the temperate, boreal, and tropical seas; however, some distinct differences in rates exist for tropical marine fishes as reflected by quasicontinuous growth, protracted spawning and recruitment, and competition-based population dynamics (Ault and Fox, 1990; Sparre and Venema, 1992; DeMartini, 1993). To represent the continuous time dynamics of a tropical coral-reef fish population in the numerical model, following Ault and Olson (1996), we formalized the conservation law for population abundance as

$$dN(a,t) = \frac{\partial N(a,t)}{\partial a}da + \frac{\partial N(a,t)}{\partial t}dt = -Z(a,t)N(a,t)dt. \quad (4)$$

This partial differential equation expresses population age structure in terms of the average number of fish by age over time. The term $\partial N/\partial a$ is the contribution to the change in $N(a,t)$ resulting from individuals getting older. Because the variable $a$ is tied stepwise to chronological age, for each time step $t$, $a$ gets one unit older, so that $da/dt = 1$. This condition holds for $t > 0$ and $a > 0$. Equation 4 requires two conditions on $N(a,t)$: one initial condition for $N(0,t)$; and a boundary condition in age 0 tied to reproduction for $N(0,t)$. Integration of Equation 4 with a growth function allows efficient estimation of population biomass and average size in the stock over time. In the numerical model REEFS, we modified Equation 4 to a stochastic age-independent length-based population dynamics model to simulate efficiently the average or ensemble number at a given length for the entire population age structure as

$$\bar{N}(L) = \int_{t_r}^{t_\lambda} R(\tau - a)S(a)\Theta(a)P(L|a)da, \quad (5)$$

where $R(\tau-a)$ = recruitment lagged back to cohort birth date;
$S(a)$ = survivorship to age $a$;
$\Theta(a)$ = sex ratio at age $a$; and
$P(L|a)$ = the conditional probability of a fish being length $L$ given that it is age $a$.

The ensemble average length $L$ at age $a$ is represented by the von Bertalanffy growth function. The conditional probability distribution for length and age was assumed to be bivariate normal.

The reported maximum age of fish in the stock $t_\lambda$ (equal to a generation), usually obtained from age and growth studies by using either scales or otoliths, allows application of a convenient and consistent method to normalize the annual instantaneous natural mortality rate $M$ to life span. First, we assume that $S(t_\lambda)$, the fraction of the initial cohort numbers surviving from recruitment $t_r$ to the maximum age, can be expressed as

$$\frac{N(t_\lambda)}{N(t_r)} = S(t_\lambda) = e^{-M(t_\lambda - t_r)}. \quad (6)$$

Then, assuming an unexploited equilibrium, by setting the probability of survivorship of recruits to the maximum age to be 5% (i.e. $S(t_\lambda)=0.05$), and letting $t_r$ be equal to 0, we rearranged Equation 6 in order to provide an estimate of the natural mortality rate

$$\hat{M} = \frac{-\ln[S(t_\lambda)]}{t_\lambda}. \quad (7)$$

Mortality and growth estimation in tropical fishery populations are normally approached from a size-based perspective because of difficulties in ageing fish. Average size can be converted to mean age by making two assumptions: 1) that age $a$ maps directly into, or is a function of, size $L(a)$; and 2) that mean length-at-age from the von Bertalanffy equation can be inverted as

$$a = \frac{-\ln\left[\frac{L_\infty - L(a)}{L_\infty}\right]}{K} + t_0. \quad (8)$$

[3] Ault, J. S. 1998. Tropical coral reef fishery resource decision dynamics. Unpubl. manuscript.

Numbers-at-length were converted to numbers-at-weight for each species by means of simple allometric relationships.

## Assessment of exploitation effects

The REEFS model was configured to assess two fishery management decision-making endpoints, yield-per-recruit (YPR) and spawning potential ratio (SPR). Fishery management endpoints are relatively robust measures of potential yields and recruitment. As such, they help to focus on biological (size) and fishing (intensity) controls for managing current and future fishery production. Because biomass $B(a,t)$ is the product of numbers-at-age multiplied by weight-at-age, yield in weight $Y_w$ from a given species $s$ was calculated as

$$Y_w(F,L',t) = F(t)\int_{L'}^{L_\lambda} B(L|a,t)dL = F(t)\int_{L'}^{L_\lambda} N(L|a,t)W(L|a,t)dL . \quad (9)$$

Yield-per-recruit (YPR) is then calculated by scaling yield to average recruitment from the right-hand side of the above equation. Spawning stock biomass (SSB, in metric tons [t]) is a measure of the stock's reproductive potential or capacity to produce newborn, ultimately realized at the population level as successful cohorts or year classes. Spawning stock biomass is obtained by integrating over individuals between the minimum size of first maturity, $L_m$, and maximum reproductive size (here assumed to be the maximum size $L_\lambda$) in the stock

$$SSB(t) = \int_{L_m}^{L_\lambda} B(L|a,t)dL. \quad (10)$$

The size of first capture, $L'$, is that regulated by regional fishery management. The modeled fishing mortality rate of headboats (and "viewing power" of divers) was assumed to remove (and sight) fish with a "knife-edged selectivity pattern" (see Gulland, 1983) over the range of exploitable sizes

$$F(t) = \begin{cases} 0 & \text{if } L|a < L' \\ \hat{F}(t) & \text{if } L|a \geq L' \end{cases}. \quad (11)$$

Spawning potential ratio (SPR) is a contemporaneous management endpoint that measures the stock's potential capacity to produce optimum yields on a sustainable basis. SPR is a fraction expressed as the ratio of exploited spawning stock biomass in relation to the equilibrium unexploited SSB

$$SPR = \frac{SSB_{exploited}}{SSB_{unexploited}}. \quad (12)$$

Resultant estimated SPRs are then compared to the U.S. Federal standards which define 30% SPR as the "overfishing" threshold (Rosenberg et al., 1996). Linear regressions of estimated SPRs for snapper and grouper were made on 1996 average exvessel prices obtained from voluntary Monroe County dealer reports (NMFS[4]). Because sale of jewfish was prohibited, a theoretical 1996 jewfish price was estimated as 0.438 of the price of gag grouper on the basis of historical average annual price ratios (1987–90).

## Management analyses

This assessment focuses on 35 reef fish species in 5 families: groupers, Epinephelinae; snappers, Lutjanidae; grunts, Haemulidae; the hogfish, *Lachnolaimus maximus*, Labridae; and the great barracuda, *Sphyraena barracuda*, Sphyraenidae. These are the primary targets of the recreational, commercial, and headboat fleets. Population dynamics parameters for each of these fish used in the analyses were gleaned from summaries in Claro (1994) and taxa-specific literature (Tables 2 and 3). The hogfish was grouped with snappers for analytical purposes.

The assessment used the following 7 steps (Fig. 2):

**Step 1:** Conduct visual survey for the reef fish community in year $t$ and intercalibrate diver sampling efficiency by species, site, and year.

**Step 2:** Begin management analysis for species $s$ using intercalibrated visual survey data to compute within-year estimates of $\bar{L}$ and associated 95% confidence intervals from the size and abundance data, by species, integrated over the range of exploitable sizes.

**Step 3:** Compute a statistically independent set of annual mean estimates of $\bar{L}$ using fishery-dependent headboat data and compare these with visual survey estimates.

[4] NMFS. 1996. Fishery Statistics Div., Southeast Fisheries Sci. Center, Natl. Mar. Fish. Serv., NOAA, 75 Virginia Beach Dr., Miami FL 33149-1003.

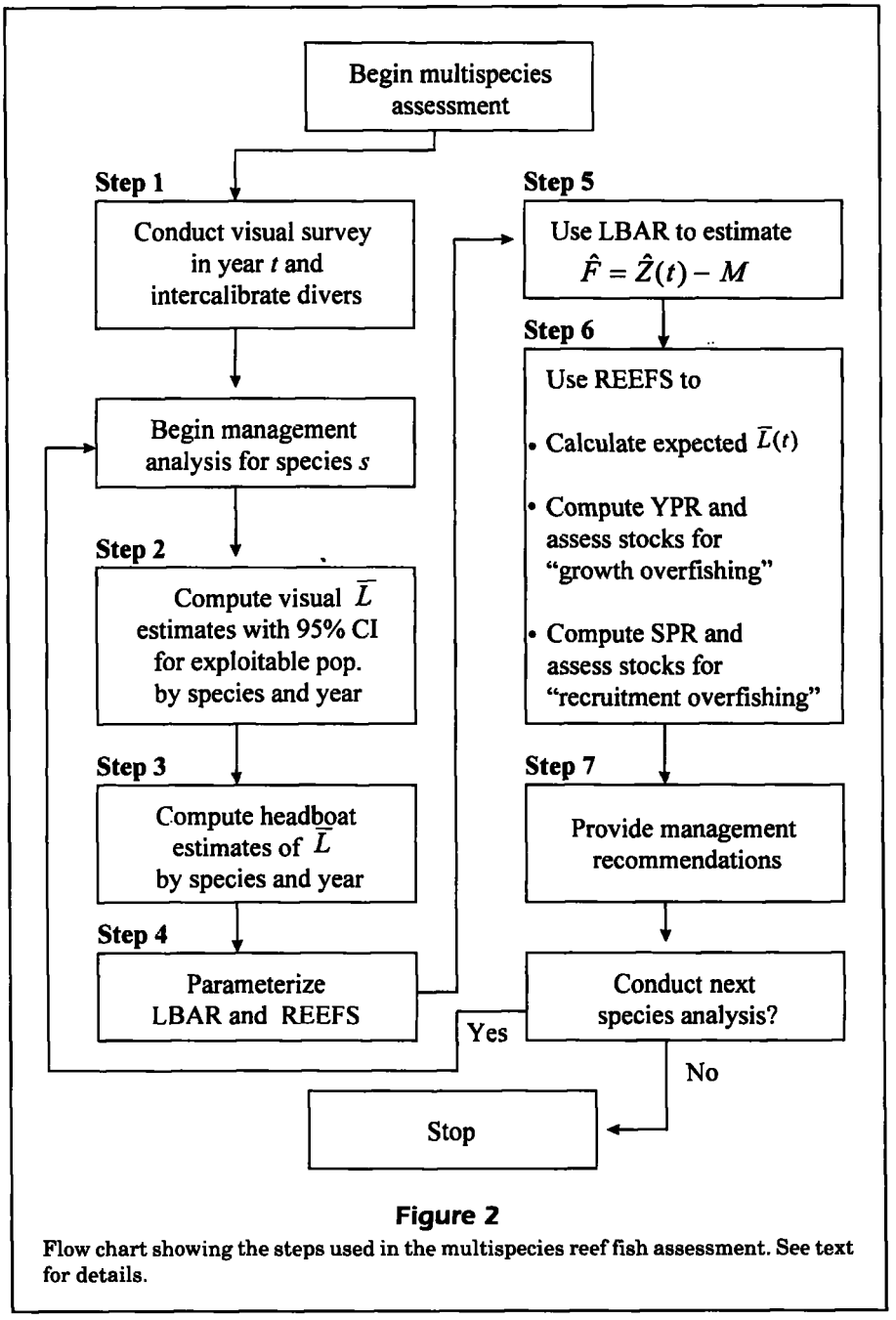


**Figure 2**

Flow chart showing the steps used in the multispecies reef fish assessment. See text for details.

**Step 4:** Use the population dynamics parameters of Table 3 to determine parameters of the LBAR (Ault et al., 1996) and the REEFS computer algorithms.

**Step 5:** Use $\bar{L}(t)$ estimate in LBAR to estimate by year fishing mortality rates for the two data sources; i.e. time series of visual and headboat data.

**Step 6:** Use the REEFS model to estimate: 1) expected $\bar{L}(t)$ given the reported population dynamics and $\hat{F}$ parameter values; 2) YPR and assess growth overfishing; and 3) spawning stock biomass (SSB) for the fishery in both exploited and unexploited states (i.e. $F = \hat{F}$, and $F$=0, respectively) and evaluate SPR to assess for recruitment overfishing.

**Step 7:** From these results, make specific fishery management recommendations on control strategies of $F$ and $L'$ consistent with eumetric fishing principles that minimize the potential for overfishing.

## Results

### Fishing effort and sampling intensity

Trends in nominal fishing effort, measured as the numbers of licensed recreational, commercial, and headboats vessels in Monroe County, show that recreational fishing effort has increased sharply since 1965 (Fig. 3). Since 1981, the largest increase has clearly come from the recreational sector and continues to increase whereas commercial and headboat sectors have been relatively stable.

In the 18-year (1979–96) visual survey, 4,571 point samples were collected over a variety of bottom types from 72 reefs located throughout the Florida Keys at depths to 21 m (Table 1; Fig. 1). The complete database contains information on 226 reef fish species in 55 families with 42 biological, habitat, and physical covariates.

**Table 2**

Parameters, definitions, and units for population dynamics variables common to the LBAR and REEFS numerical models used in simulation analysis of Florida Keys reef fish population dynamics. See Table 3 for parameter values.

| Parameter | Definition | Units |
|---|---|---|
| $s$ | Reef fish species ($s$=1, . . . ,$n$) | |
| $a$ | Cohort age class ($a$=1, . . . , $t_\lambda$) | |
| $t_r$ | Age of recruitment | months |
| $L_r$ | Size at recruitment | mm |
| $t_m$ | Minimum age of maturity | months |
| $L_m$ | Minimum size of maturity | mm |
| $t'$ | Minimum age of first capture | months |
| $L'$ | Minimum size of first capture | mm |
| $t_\lambda$ | Oldest (largest) age | years |
| $L_\lambda$ | Largest (oldest) size | mm |
| $W_\infty$ | Ultimate weight | kg |
| $L_\infty$ | Ultimate length | mm |
| $K$ | Brody growth coefficient | per year |
| $t_0$ | Age at which size equals 0 | years |
| $\alpha_{WL}$ | Scalar coefficient of weight-length function | dimensionless |
| $\beta_{WL}$ | Power coefficient of weight-length function | dimensionless |
| $W(a,t)$ | Weight at age $a$ at time $t$ | g |
| $L(a,t)$ | Length at age $a$ at time $t$ | mm |
| $N(a,t)$ | Numbers at age $a$ at time $t$ | number of fish |
| $M(a,t)$ | Natural mortality rate at age $a$ at time $t$ | per year |
| $F(a,t)$ | Fishing mortality rate at age $a$ at time $t$ | per year |
| $S(a)$ | Survivorship to age $a$ | dimensionless |
| $Z(t)$ | Total mortality rate in year $t$ | dimensionless |
| $\Theta(a)$ | Sex ratio at age $a$ | dimensionless |
| $B(a,t)$ | Biomass at age $a$ in year $t$ | kg |
| $Y_w(t)$ | Yield in weight in year t | metric tons |
| $SSB(t)$ | Spawning stock biomass in year $t$ | metric tons |
| $SPR(t)$ | Spawning potential ratio in year $t$ | percent |

### Average size and mortality

Average annual length was estimated for headboat catch statistics (1981–95) and for visual survey data (1979–96). Headboat data were used in the comparative analysis with the visual survey data because they provide consistent catch statistics and effort data. Typical comparisons of average length in the exploitable phase of the stock for the two data sets are shown for eight representative, economically important reef fishes: black grouper, red grouper, gray snapper, yellowtail snapper, white grunt, bluestriped grunt, hogfish, and great barracuda (Fig. 4). The 95% confidence intervals were computed for the visual estimates but could not be determined for the headboat data at this time owing to the survey estimation procedures used to calculate total numbers and total weight for the entire Florida Keys. In a few instances (e.g. 1985 and 1986), the computed confidence bounds were large owing to low sample sizes, but these mean estimates still correlated well with the rest of the data.

The estimated average lengths in the exploitable phase from the two independent data sources were highly correlated for groupers, snappers, and grunts (Fig. 4). The trend in average size also was relatively flat over the last 18 years and close to $L'$ (Fig. 4).

Although the relation between $\bar{L}$ for visual and headboat data was similar for all groupers, snappers, and grunts, it differed somewhat for hogfish and barracuda (Fig. 4, G and H). Average length ($\bar{L}$) for hogfish was consistently smaller in visual samples than in headboat landings. In both data sets, however, $\bar{L}$ declined in the early 1980s but has steadily increased since the late-1980s ($F$=3.96, df=9, $P$<0.0001) (Fig. 4G). Average length for barracuda increased significantly ($F$=2.2, df=10, $P$<0.018) in visual surveys but declined in headboat landings beginning in the early 1980s (Fig. 4H). Increased mean barracuda size in visual samples indicates that there has been a corresponding increase in abundance because larger $\bar{L}$ requires increased survival. In visual samples, barracuda are now the top ranked species in biomass among all Florida Keys reef fishes.

## Table 3

Florida Keys reef fish population dynamics parameters for 46 species used in mortality estimations and fishery simulations. Population dynamics parameter definitions and units are given in Table 2. The symbol * indicates that the species is present in recreational catch but not headboat catches or the visual survey. The dash (—) indicates that insufficient population dynamic data were available to conduct a management analysis. Complete parameter sets were available for 35 species.

| | Population parameters | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species groups | $M$ | $t_\lambda$ | $L_\infty$ | $W_\infty$ | $K$ | $t_0$ | $t_m$ | $L'$ | $t'$ | $\alpha_{wl}$ | $\beta_{wl}$ | $L_\lambda$ |
| Groupers ($n$=18) | | | | | | | | | | | | |
| Black Grouper *Mycteroperca bonaci* | 0.150 | 20 | 1200.0 | 31.6 | 0.160 | –0.300 | 48 | 508.0 | 39 | 4.27E-06 | 3.2051 | 1153.1 |
| Coney *Epinephelus fulvus* | 0.180 | 17 | 698.9 | 1.5 | 0.145 | –1.080 | 13 | 203.2 | 19 | 7.29E-05 | 2.5700 | 332.5 |
| Gag Grouper *Mycteroperca microlepis* | 0.200 | 13 | 1187.2 | 25.1 | 0.149 | –0.802 | 60 | 508.0 | 36 | 1.21E-05 | 3.0305 | 1034.4 |
| Graysby *Epinephelus cruentatus* | 0.200 | 15 | 415.0 | 1.1 | 0.130 | –0.940 | 36 | 203.2 | 52 | 1.22E-05 | 3.0439 | 362.5 |
| Jewfish *Epinephelus itajara* | 0.081 | 37 | 2394.0 | 244.9 | 0.054 | –3.616 | 72 | 508.0 | 68 | 2.09E-05 | 2.9797 | 2328.0 |
| Marbled Grouper * *Epinephelus inermis* | — | — | — | — | — | — | — | — | — | — | — | — |
| Misty Grouper * *Epinephelus mystacinus* | — | — | — | — | — | — | — | — | — | — | — | — |
| Nassau *Epinephelus striatus* | 0.180 | 17 | 698.9 | 5.9 | 0.145 | –1.080 | 83 | 508.0 | 95 | 3.83E-06 | 3.2292 | 648.2 |
| Red Grouper *Epinephelus morio* | 0.180 | 17 | 938.0 | 11.9 | 0.153 | –0.099 | 48 | 508.0 | 61 | 1.13E-05 | 3.0350 | 869.0 |
| Red Hind *Epinephelus guttatus* | 0.180 | 17 | 392.7 | 1.1 | 0.207 | –0.831 | 49 | 203.2 | 33 | 1.80E-04 | 2.6140 | 382.9 |
| Rock Hind *Epinephelus adscensionis* | 0.250 | 12 | 486.1 | 2.3 | 0.191 | –2.160 | 48 | 203.2 | 9 | 6.00E-06 | 3.1930 | 453.3 |
| Scamp *Mycteroperca phenax* | 0.143 | 21 | 999.7 | 19.3 | 0.126 | –1.357 | 48 | 508.0 | 52 | 2.02E-05 | 2.9932 | 932.2 |
| Snowy Grouper *Epinephelus niveatus* | 0.130 | 15 | 1091.3 | 19.5 | 0.113 | –0.915 | 48 | 508.0 | 57 | 2.45E-05 | 2.9300 | 909.0 |
| Speckled Hind *Epinephelus drummondhayi* | 0.200 | 15 | 967.0 | 16.6 | 0.130 | –1.010 | 48 | 508.0 | 58 | 1.11E-05 | 3.0730 | 861.0 |
| Warsaw Grouper *Epinephelus nigritus* | 0.080 | 41 | 2394.0 | 244.9 | 0.054 | –3.616 | 48 | 508.0 | 68 | 2.09E-05 | 2.9797 | 2328.0 |
| Yellowedge Grouper *Epinephelus flavolimbatus* | 0.180 | 15 | 860.0 | 15.7 | 0.170 | 0.000 | 67 | 508.0 | 64 | 2.82E-05 | 2.9800 | 960.0 |
| Yellowfin Grouper *Mycteroperca venenosa* | 0.180 | 15 | 860.0 | 15.7 | 0.170 | 0.000 | 67 | 508.0 | 64 | 2.82E-05 | 2.9800 | 960.0 |
| Yellowmouth Grouper *Mycteroperca interstitialis* | 0.180 | 17 | 881.8 | 8.6 | 0.063 | –9.030 | 36 | 508.0 | 56 | 2.58E-05 | 2.8937 | 710.7 |
| Snappers ($n$=13) and hogfish ($n$=1) | | | | | | | | | | | | |
| Black Snapper *Apsilus dentatus* | 0.300 | 10 | 618.3 | 3.2 | 0.097 | –1.728 | 29 | 203.2 | 30 | 4.52E-05 | 2.8146 | 418.4 |
| Blackfin Snapper *Lutjanus buccanella* | 0.230 | 9 | 729.7 | 2.4 | 0.084 | –2.896 | 20 | 304.8 | 43 | 7.40E-06 | 2.9735 | 458.8 |
| Cubera Snapper *Lutjanus cyanopterus* | 0.150 | 20 | 1200.0 | 34.9 | 0.160 | –0.300 | 28 | 304.8 | 19 | 1.32E-05 | 3.0601 | 910.0 |
| Dog Snapper *Lutjanus jocu* | 0.333 | 9 | 854.0 | 10.2 | 0.100 | –2.000 | 28 | 304.8 | 30 | 4.28E-05 | 2.8574 | 790.0 |
| Gray Snapper *Lutjanus griseus* | 0.300 | 10 | 722.3 | 5.2 | 0.136 | –0.863 | 24 | 254.0 | 29 | 3.05E-05 | 2.8809 | 556.2 |
| Lane Snapper *Lutjanis synagris* | 0.300 | 10 | 618.3 | 3.2 | 0.097 | –1.728 | 29 | 203.2 | 30 | 4.52E-05 | 2.8146 | 418.4 |

*continued*

**Table 3 (continued)**

| Species groups | Population parameters | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | $M$ | $t_\lambda$ | $L_\infty$ | $W_\infty$ | $K$ | $t_0$ | $t_m$ | $L'$ | $t'$ | $\alpha_{wl}$ | $\beta_{wl}$ | $L_\lambda$ |
| Mahogony Snapper *Lutjanus mahogoni* | 0.300 | 10 | 618.3 | 3.2 | 0.097 | –1.728 | 29 | 304.8 | 64 | 8.18E-05 | 2.7190 | 418.4 |
| Mutton Snapper *Lutjanus analis* | 0.214 | 14 | 938.7 | 14.1 | 0.129 | –0.738 | 24 | 304.8 | 29 | 1.57E-05 | 3.0112 | 797.8 |
| Red Snapper *Lutjanus campechanus* | 0.190 | 16 | 975.0 | 13.7 | 0.162 | –0.010 | 28 | 508.0 | 55 | 2.04E-05 | 2.953 | 955.0 |
| Schoolmaster *Lutjanus apodus* | 0.250 | 12 | 570.0 | 3.3 | 0.180 | 0.000 | 20 | 254.0 | 40 | 2.04E-05 | 2.9779 | 503.8 |
| Silk Snapper *Lutjanus vivanus* | 0.230 | 9 | 781.1 | 9.3 | 0.092 | –2.309 | 37 | 304.8 | 38 | 1.00E-05 | 3.1000 | 512.0 |
| Vermillion Snapper *Rhomboplites aurorubens* | 0.230 | 10 | 613.6 | 2.8 | 0.206 | 0.111 | 43 | 254.0 | 33 | 1.72E-05 | 2.9456 | 541.6 |
| Yellowtail Snapper *Lutjanus chrysurus* | 0.214 | 14 | 454.7 | 1.3 | 0.209 | –0.712 | 24 | 304.8 | 56 | 7.75E-05 | 2.7180 | 433.4 |
| Hogfish *Lachnolaimus maximus* | 0.250 | 12 | 566.0 | 3.8 | 0.190 | –0.776 | 18 | 203.2 | 20 | 2.55E-05 | 2.9700 | 439.0 |
| Grunts ($n$=13) and barracuda ($n$=1) | | | | | | | | | | | | |
| Black Margate *Anisotremus surinamensis* | — | — | — | — | — | — | 33 | 203.2 | — | 2.39E-06 | 3.3916 | — |
| Bluestriped Grunt *Haemulon sciurus* | 0.500 | 6 | 289.6 | 0.47 | 0.484 | –0.011 | 12 | 203.2 | 31 | 1.94E-05 | 2.9996 | 273.5 |
| Caesar Grunt *Haemulon carbonarium* | — | — | — | — | — | — | 27 | 203.2 | — | 1.29E-05 | 3.0559 | — |
| Cottonwick *Haemulon melanurum* | — | — | — | — | — | — | 27 | 203.2 | — | 2.52E-05 | 2.9527 | — |
| French Grunt *Haemulon flavolineatum* | — | — | — | — | — | — | 18 | 203.2 | — | 9.06E-06 | 3.1581 | — |
| Margate *Haemulon album* | 0.374 | 8 | 752.6 | 8.57 | 0.174 | –0.450 | 34 | 203.2 | 17 | 1.52E-05 | 3.0423 | 578.4 |
| Porkfish *Anisotremus virginicus* | — | — | — | — | — | — | 25 | 203.2 | — | 1.01E-05 | 3.1674 | — |
| Sailors Choice *Haemulon parrai* | 0.428 | 7 | 400.2 | 1.24 | 0.220 | –0.355 | 12 | 203.2 | 35 | 2.02E-05 | 2.9932 | 320.1 |
| Smallmouth Grunt *Haemulon chrysargyreum* | — | — | — | — | — | — | 24 | 203.2 | — | 2.77E-03 | 2.1567 | — |
| Spanish Grunt *Haemulon macrostomum* | — | — | — | — | — | — | 39 | 203.2 | — | 2.28E-05 | 3.0295 | — |
| Striped Grunt *Haemulon striatum* | — | — | — | — | — | — | 21 | 203.2 | — | 1.39E-05 | 3.0988 | — |
| Tomtate *Haemulon aurolineatum* | 0.333 | 9 | 441.6 | 1.89 | 0.091 | –2.095 | 24 | 203.2 | 57 | 6.19E-06 | 3.2077 | 279.9 |
| White Grunt *Haemulon plumieri* | 0.375 | 8 | 511.9 | 3.06 | 0.186 | –0.776 | 18 | 203.2 | 24 | 8.35E-06 | 3.1612 | 410.3 |
| Great Barracuda *Sphyraena barracuda* | 0.200 | 15 | 1238.3 | 14.03 | 0.172 | –0.461 | 36 | 619.2 | 44 | 4.11E-06 | 3.0825 | 1151.5 |

## Management analyses

We also conducted a multispecies stock assessment and management analysis with the estimates of fishing mortality to examine if current exploitation levels are commensurate with sustainable fisheries. Although 46 exploited reef fish species had been seen or captured in the visual and headboat surveys, only 35 species had population dynamics parameter sets sufficient to conduct a management analysis (Table 3). We noted striking similarities in key relations within taxa as shown by the somewhat discrete clusters of taxa when maximum size dependent on maximum age for a variety of species was plotted (Fig. 5). Mean $F$ estimates for visual survey and headboat data were used to encompass conservatively the range of feasible fishing mortality rates experienced in the fishery over the last two decades. A comparison of methods and data sources also allowed us to consider risks associated with the overall uncertainty bounds for each stock assessment. Results of an example assessment analysis is shown for gray snapper in which

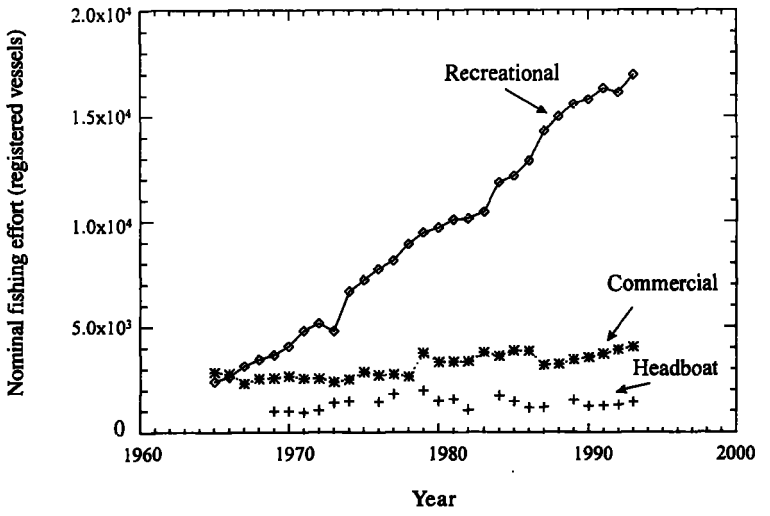


**Figure 3**

Time series of three types of nominal fishing effort directed at Florida Keys reef fish from 1965 to 1993 based on numbers of recreational ( $\square$ ) and commercial (*) vessels registered in Monroe County, Florida. Headboats (+) are considered to be a subset of the commercial fishing fleet.

management endpoints like yield-per-recruit (YPR) and spawning potential ratio (SPR) are provided (Fig. 6). These results are typical of the management information provided for each species.

Our analyses indicated that the average size in the exploitable phase for many economically important reef fish populations was marginally above the minimum size of capture regulated by fishery management agencies (i.e. South Atlantic Fishery Management Council and the Florida Marine Fisheries Commission). To assess the impact of these mortality rates on the stock production, we performed an analytical yield analysis to estimate the YPR for each stock, and evaluated the current YPR status in relation to "eumetric" (cf. Beverton and Holt, 1957) or well-balanced fishing in terms of the minimum size of fish captured and level of fishing effort (Fig. 6A). An issue of paramount concern in assessing analytical yield models are the settings of the two dynamic control variables, $F$ and $L'$ (Fig. 6A). From the perspective of optimal decision making, any transition of the fishery over the yield surface should minimize negative risks, while maximizing the economic, ecological, social, and aesthetic aspects. The YPR analysis for gray snapper suggests that the current size (or age) of first capture, $L'$ at 254 mm (=10 in), likely results in "growth overfishing." To maximize the YPR for the range of $F$ operating in the fishery for the last two decades, $L'$ should be increased to greater than 350 mm (Fig. 6B).

Figure 6C shows progressive reductions of gray snapper stock biomass when $F$ is increased to the estimate's lower bound shown in Figure 6B. The likelihood range of $\hat{F}$ (i.e. $\hat{F}$=[0.5,1.1]) is likely also contributing to a very low SPR for gray snapper. In fact, it is below the Federal minimum of 30% SPR (Fig. 6D). The minimum estimated $F$ still reduces SPR to about 29% of the unexploited state, whereas the upper bound estimate results in 15% SPR. The majority of the range of estimated $F$ suggest that the gray snapper stock is also "recruitment overfished" as reflected by reduced spawning potential.

The summary of the SPRs for Florida Keys reef fish (Fig. 7) shows that a total of 13 of 16 groupers, 7 of 13 snappers, and 2 of 5 grunts, for which there are data, are below the SPR that constitutes overfishing by Federal definitions. Overall, 63% of the 35 stocks that could be analyzed were overfished. Linear regressions of SPR on exvessel price showed a significantly negative ($F_{1,14}$=7.55, $P$=0.0157) slope for grouper and a marginally significant ($F_{1,11}$=4.77, $P$= 0.0514) negative slope for snapper (Fig. 8).

## Discussion

### Fishery dynamics

Our results indicate that Florida Keys reef fish populations have been heavily fished for at least the last

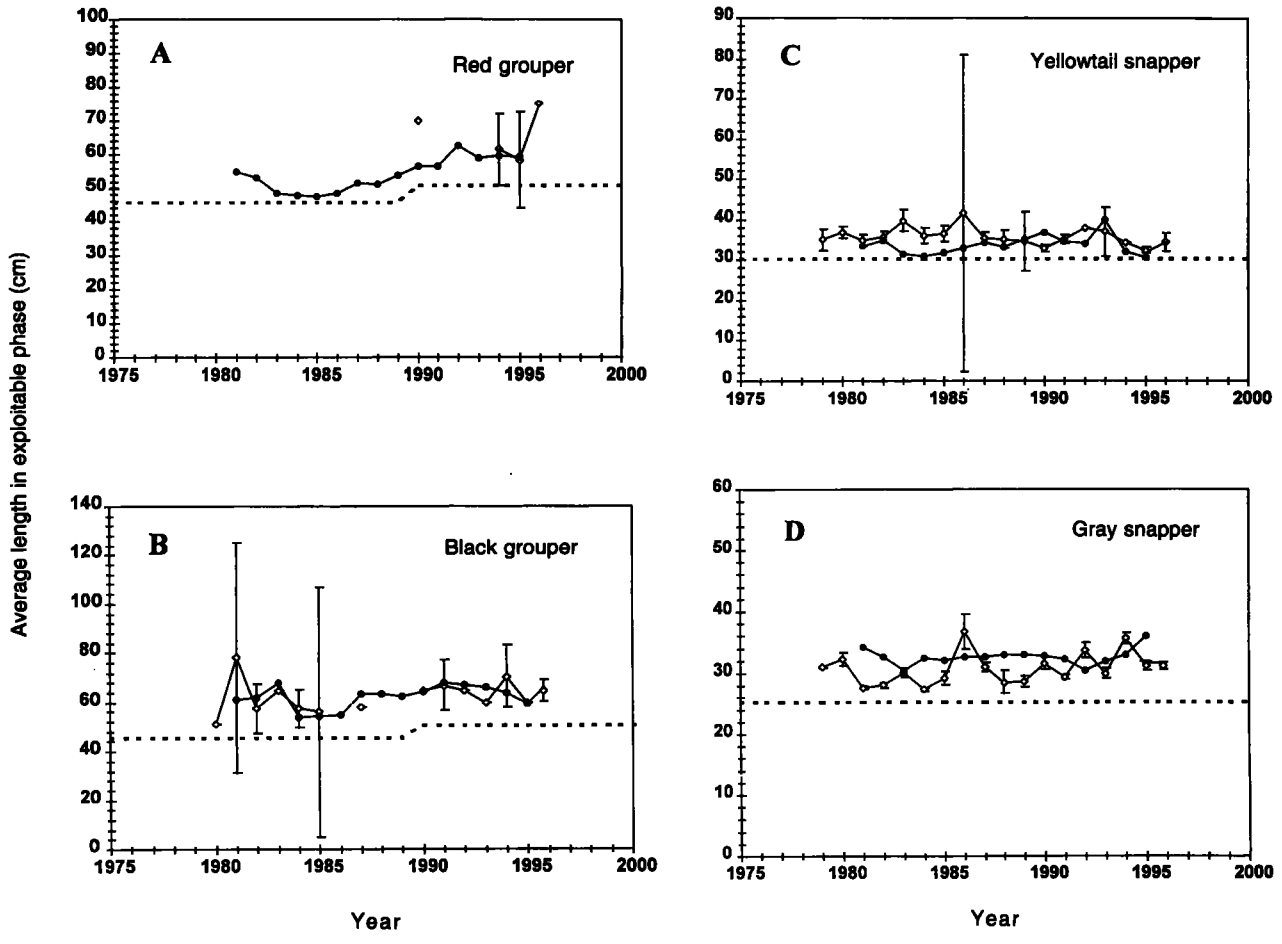


**Figure 4**

Average length (cm) in the exploitable phase of the stock estimated from headboat (●) and visual survey (◇) data for several reef fish stocks during the period 1979 to 1996: (**A**) red grouper, (**B**) black grouper, (**C**) yellowtail snapper, (**D**) gray snapper, (**E**) white grunt, (**F**) bluestriped grunt, (**G**) hogfish, and (**H**) great barracuda. Bars around visual survey estimates are 95% confidence intervals of the mean. Horizontal dotted lines show the minimum size at first capture $L'$ regulated by regional fishery management.

two decades. Total fishing effort has increased substantially because of greater average fishing power per vessel and a much larger recreational fishery. Mace (1997) estimated that the average "fishing power" per vessel (i.e. the average proportion of the stock removed per unit of fishing effort) has increased 4-fold over the previous 25 years mainly because of improved technology involving better vessel designs, hydroacoustics, hydraulics, and navigation (GPS, Loran C, charts). The arithmetic increase of recreational fishing vessels is an important factor also, although its absolute effect on reef fish stocks is unknown because the recreational fleet is distributed diffusely and heterogeneously and has not been well sampled to date.

## Stock assessment indicator variable

The estimated average lengths (size) of reef fish in the exploitable phase, determined from statistically independent visual and headboat data, were highly comparable for groupers, snappers, and grunts, supporting their use in the multispecies assessment. Average sizes of hogfish and barracuda, however, differed between the two data sets. The larger average hogfish size in headboat samples appears to be the result of life history patterns and different responses to fishing gears with depth. Hogfish tend to move from shallow to deeper water with age (Davis, 1976) and are more vulnerable to spearfishing than hook-and-line gear. Divers, however, are effectively

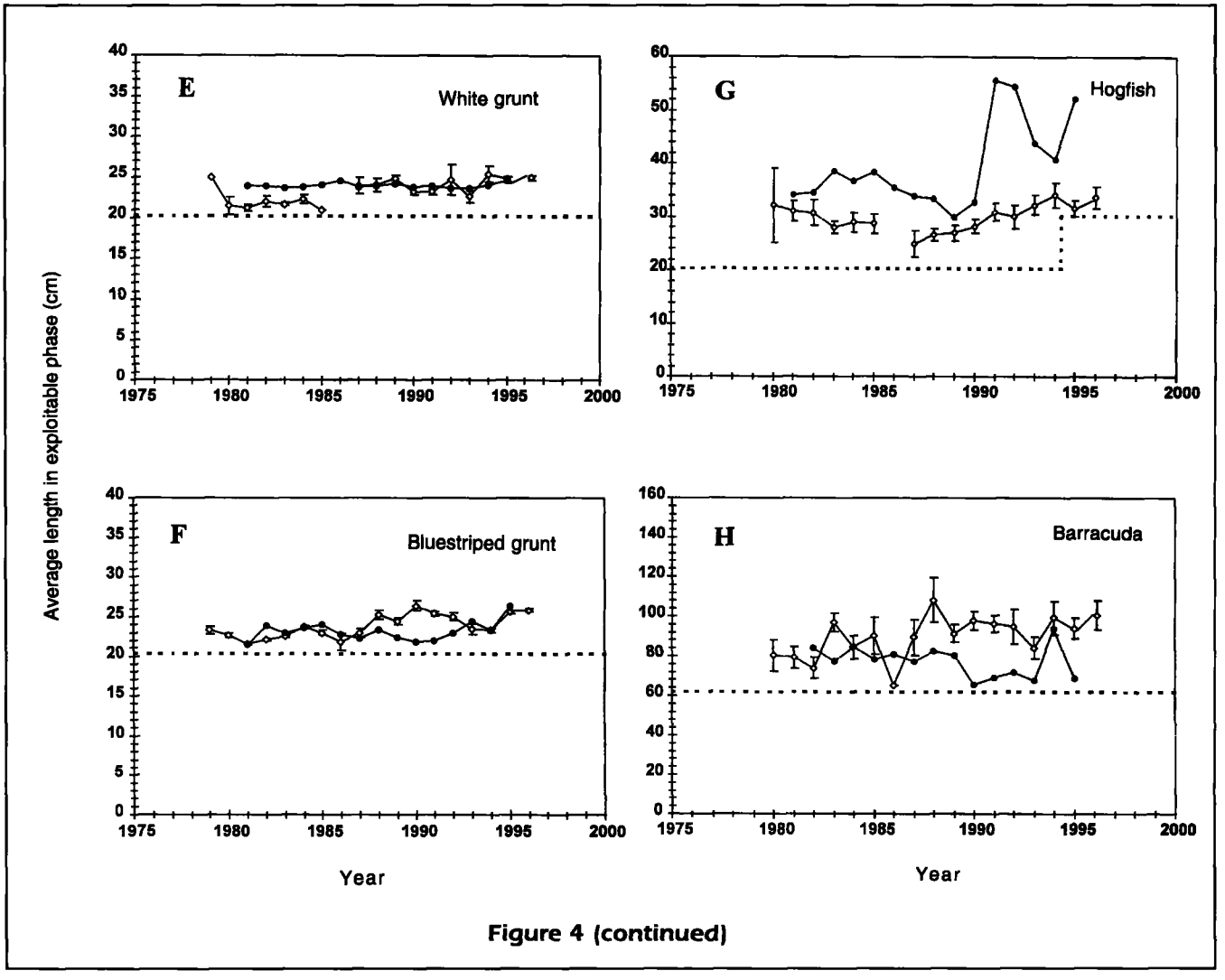


**Figure 4 (continued)**

restricted to shallower depths for safety reasons. Thus, large hogfish that inhabit depths below safe diving limits are available to only the headboat fleet. In shallow water, divers are more likely to see small hogfish because they are more abundant and because large hogfish are more likely to be selectively depleted by spearfishing. The increased average size in both data sets since the mid-1980s (Fig. 4G) is most likely the result of increased spearfishing regulation, imposed recreational bag limits, and initiation of minimum size limits.

The average size of barracuda diverged in visual samples and headboat landings since the early 1980s (Fig. 4H). This pattern is likely the result of the promotion and expansion of catch-and-release fishing for barracuda during that time period. Decreased fishing mortality resulting from more released barracuda would increase the average size of fish in the exploitable phase and be detected in visual samples. Headboat landings, however, could trend toward smaller fish because more large barracuda increase the frequency of angler "breakoffs" (i.e. fish biting through lines or leaders) and the proportion of releases because only small barracuda are normally retained for human consumption. Large barracuda are avoided because they carry greater risk of ciguatera poisoning, which can result in convulsions and death for humans (de Sylva, 1994).

The trend in average size for grouper, snapper, and grunt stocks was relatively flat over the past 18 years and close to the minimum exploitable length (Fig. 4). The flatness is explained by considering expected $\bar{L}$ from a modeled range of $F$ in an analytical model, given knowledge about current values of $\hat{F}$. The slope of $\bar{L}$ on $F$ was very shallow in the range of the analytical model (Fig. 9), corroborating the empirical estimates in Figure 4. Some stocks appear to have been chronically overfished since the late 1970s. We

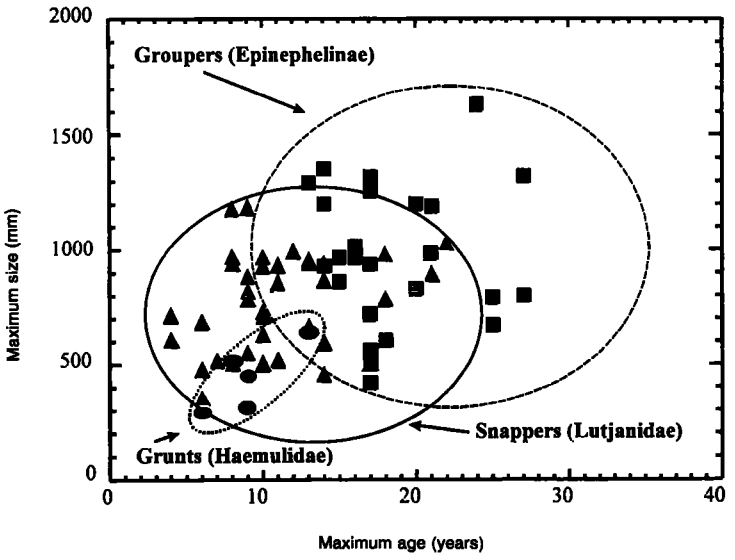


**Figure 5**

Relationship between the population dynamic parameters maximum size $L_\lambda$ and maximum age $t_\lambda$ for three economically important Florida Keys reef fish taxa: groupers, Epinephelinae (■); snappers, Lutjanidae (▲); and grunts, Haemulidae (●).

also noted similarities in key relations within various taxa that separated out into somewhat discrete clusters when maximum size versus maximum age by species is plotted (Fig. 5). This pattern of species clusters suggests that species within the various taxa groupings will likely respond to exploitation in a similar manner. The sensitivity to exploitation is highest for groupers, followed by snappers, and then grunts.

## Overfishing and community shifts

Despite conservative assumptions, the estimated fishery exploitation rates suggest that many Florida Keys reef fish stocks are overfished according to definitions for U.S. fisheries (Rosenberg et al., 1996) (Figs. 7 and 9). Many desirable grouper and snapper stocks have low spawning potential ratios (SPRs). Inverse relationships between increased fishing effort (particularly by the recreational sector) (Fig. 3) and the long-term decreased average size and stock biomass (e.g. Fig. 6C) of the most desirable species (e.g. groupers and snappers) are particular concerns.

The Florida Keys reef fishery shows the classic pattern of serial overfishing, in which the more vulnerable species are progressively depleted (Munro and Williams, 1985; Russ and Alcala, 1989). The longest-lived, latest-maturing, and lowest mortality ($M$) stocks [i.e. groupers] are those first to experience significant declines in population biomass, followed in sequence by intermediate-lived stocks [snappers], and finally by short-lived stocks [grunts] [Fig. 7]). Within families, the inverse relations between the spawning potential ratio and exvessel market price (Fig. 8) are consistent with serial overfishing. As expected, the most valuable snapper and grouper also tend to have the lowest spawning potentials. During the time frame of this study, numerous measures were taken to reduce fishing mortality in state and federal waters. Fish traps were progressively eliminated between 1980 and 1992, and numerous bag limits and minimum size limits were imposed. Fisheries were closed for queen conch (*Strombus gigas*), jewfish (*Epinephelus itajara*), and Nassau grouper (*E. striatus*). These actions are evidence of trends reported in this study.

Our data suggest that there may have been substantial changes in the composition of the biomass and abundance of the reef fish community over the past several decades. Although many groupers and snappers have declined, apparently in response to growing fishing effort, some grunts have increased in relative abundance. Claro (1991) noted a similar process in the Golfo de Batabano, Cuba, and hypothesized that chronic overharvesting of snappers resulted in shifts in community composition in favor

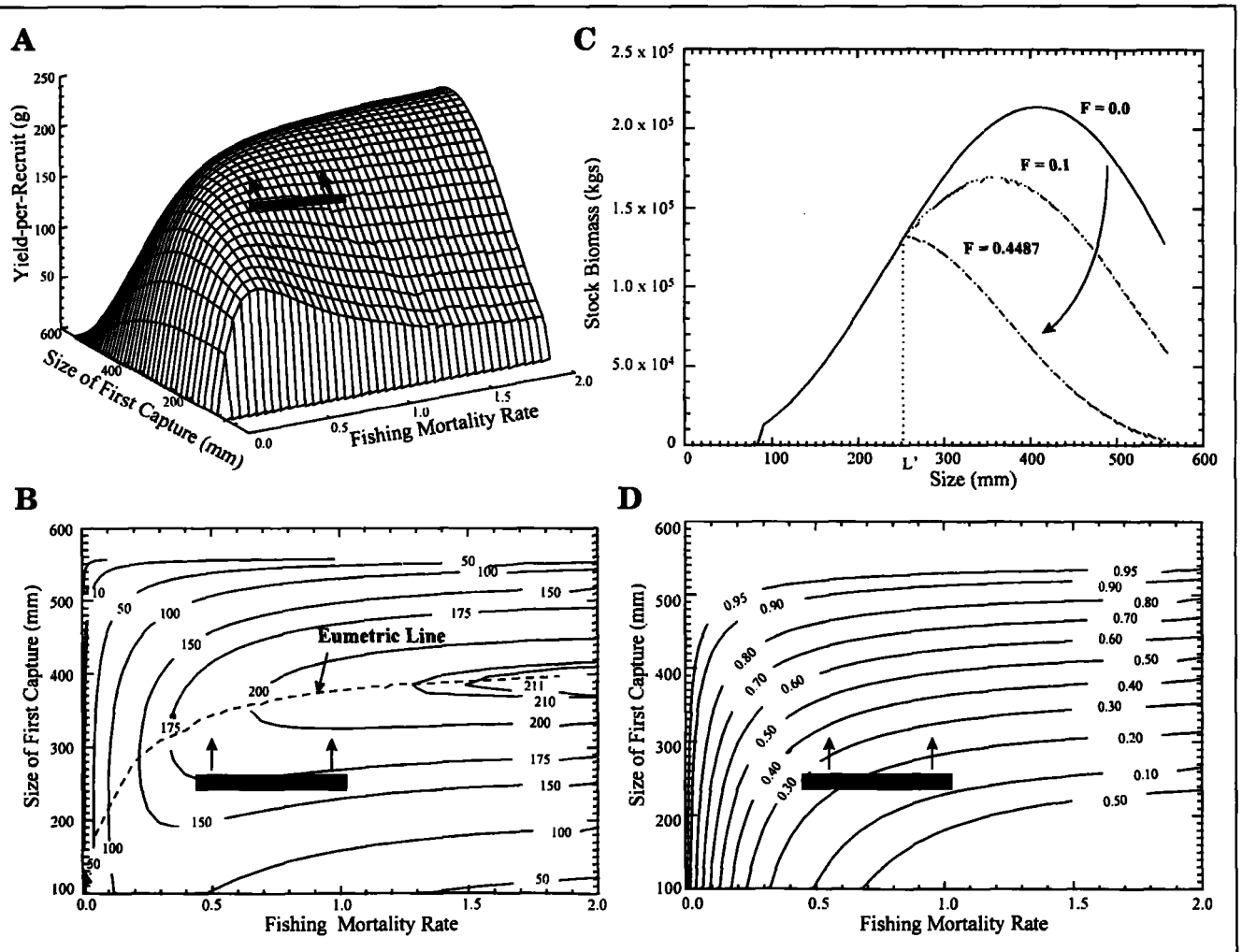


**Figure 6**

Example calculation of an analytical yield model management analysis for gray snapper: (**A**) 3-dimensional yield-per-recruit YPR surface (g) as a function of the fishing mortality rate $F$ (per yr) and size at first capture $L'$ (mm); (**B**) YPR isopleths in lifetime yield-per-recruit; (**C**) stock biomass dependent on size for several exploitation levels; and (**D**) spawning potential ratio (SPR) as a function of $F$ and $L'$. REEFS model input parameter values are from Table 3. Shaded rectangles in panels A, B, and D show estimated range of $F$ and $L'$. Darkened rectangle in panel D indicates the range of $F$ estimates that exceed the Federal 30% SPR overfishing definition following Rosenberg et al. (1996).

of grunts. Another indication of significant change was the explosive growth of barracuda (Fig. 4H) which may be explained by several factors. First, there is little directed commercial or recreational fishing for barracuda as food because of health concerns. Second, growth of catch-and-release fishing by sport anglers and reduced emphasis on spearfishing may have substantially lowered barracuda mortality. Third, other top predators, such as groupers, snappers, and sharks, have been intensively fished, therefore probably lowering competition for food, while, at the same time, barracuda still retain a large and possibly increasing prey base of grunts and other small fishes. Increased abundance and biomass of a top predator like barracuda could be a management concern if barracuda substantially impact reef fish community dynamics. For example, excessive predation on popular sport fishes like snappers could counteract potential reductions in fishing mortality sought by traditional management.

An adjustment of minimum sizes of first capture ($L'$) and fishing mortality rates ($F$) may mitigate the apparent growth and recruitment overfishing conditions in the fishery. This adjustment should be done in a multispecies context to optimize the biotic and fishery potential of the reef fish assemblage. However, traditional management actions alone are unlikely to be sufficient because they can be circum-

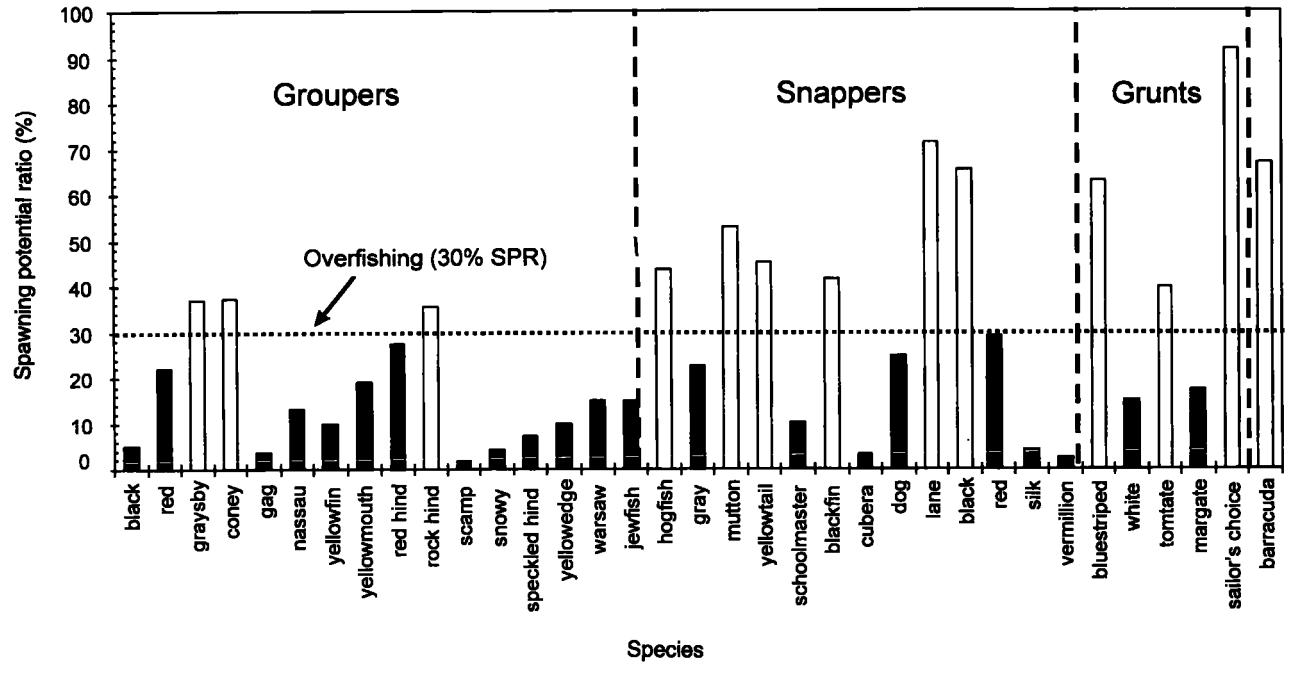


**Figure 7**

Estimates of percent spawning potential ratio (SPR%) for 35 species of Florida Keys reef fish comprise groupers, snappers, grunts, hogfish, and great barracuda. Darkened bars indicate stock "overfishing," and open bars indicate the stock is above the 30% SPR U.S. Federal standard.

vented and habitually fail to control fishing effort effectively, particularly in an open access fishery (Waters, 1991; Bohnsack and Ault, 1996). For example, bycatch mortality and high fishing effort from the expanding fleets can make size limits ineffective. In theory, every fish can be caught once it reaches minimum legal size with the result that insufficient mature adults survive to reproduce. The tradition of open-access management systems coupled with risk-prone management decisions remains a principal obstacle to achieving renewable resource sustainability (Rosenberg et al., 1993).

Reversing adverse trends in the Keys reef fishery are likely to require other innovative approaches for controlling exploitation rates. Rothschild et al. (1996) recommended that fishery management maintain a systems view of the resources, emphasizing strategy over tactics. With this in mind, we recommend coupling traditional management measures with a spatial network of areal closures called "no take" marine reserves. Marine reserves provide an ecosystem management strategy for achieving long-term goals of protecting biodiversity while maintaining sustainable fisheries. The establishment of a network of small (16 to 3,000 ha) no-take reserves in the FKNMS on 1 July 1997 (U.S. Dep. Commerce, 1996) is a first step. A key to the success of this effort is a conscientious, continuous assessment program for integrating fishery-independent and fishery-dependent data to evaluate the effectiveness of these reserves (Bohnsack and Ault, 1996). With adaptive management (Walters, 1986), improvements can be implemented over time.

## Multispecies assessment

Our overall goal was to improve the scientific basis for managing tropical multispecies fisheries by providing an efficient, quantitative framework to assess multispecies fisheries. New assessment methods are particularly needed for complex fisheries that have been poorly documented, are not well understood, and face increased exploitation. Traditional single-species stock assessment methods are at times inappropriate or inadequate to deal with the dynamics and structure of multispecies assemblages with large numbers of exploited species (Caddy, 1981; Ault and Fox, 1990; Appledorn, 1996). Owing to a lack of data and basic biological information, only a few reef species in the entire southeastern U.S. have had comprehensive stock assessments.

We emphasized a multispecies ecosystem approach because traditional fishery models have been ineffectual in creating sustainable fisheries (Ludwig et al., 1993; Sharp, 1995; Caddy, 1996; Russ, 1996).

Single-species fishery management models built to maximize fishery yield and economic rent ignore critical biological and physical interactions and cumulative stresses on habitats. Reef fish stocks are likely to be regulated by trophic interactions at the individual, population, and community levels. Also, application of "traditional" fishery management models developed for temperate species to tropical coral reef assemblages is tenuous. In response to these problems, the National Research Council Committee on Fisheries (1994) recommended developing multispecies ecosystem management programs for building sustainable fisheries. Successful implementation of such programs will require innovative research, new management strategies, less destructive and wasteful fishing methods, protection of critical and sensitive habitats, and more effective education.

Our retrospective analysis emphasized fishery-independent data. Although fishery-independent assessments can provide reliable measures of fish abundance, population dynamics, and community composition (Gunderson, 1993), their application in multispecies fishery assessments have been limited. We predict an increasing need to rely on such data for assessment purposes because fishery-dependent data will become less available and less useful as new regulations are imposed that will establish larger size limits, closed seasons, closed fishing areas, and species prohibited from being fished. Also, the shifting emphasis from commercial to recreational fishing makes collecting fishery-dependent data much more difficult and expensive.

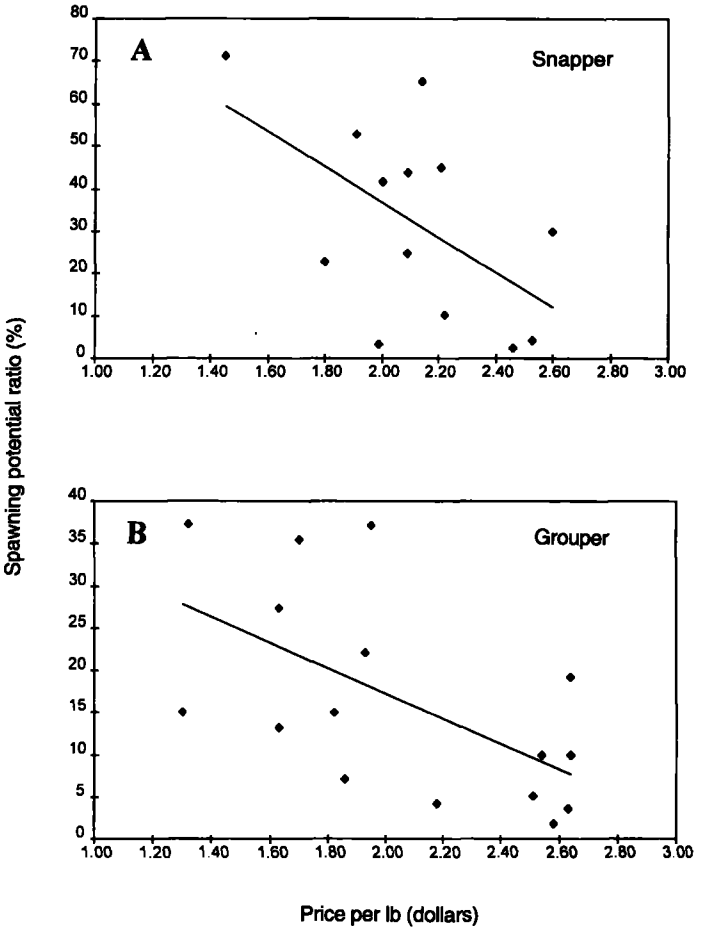


**Figure 8**

Linear regressions of estimated species spawning potential ratio ($y$) on average 1996 Monroe County exvessel price ($x$) for: (**A**) snapper: $y = 119.59 - 41.38x$; and, (**B**) grouper: $y = 47.35 - 15.03x$.

Results from this 18-year retrospective assessment are encouraging in providing estimates of stock status. However, several assumptions that simplify the population dynamics of the various species make it prudent to consider population estimates first-order approximations. The error intrinsic in population-rate estimates derived from surveys depends on the accuracy and precision of the basic survey. Errors ultimately propagate upwards during a series of calculations used to determine the average size, total mortality rates, fishing mortality rates, yield-per-recruit, and finally the spawning potential ratio, which is the current focus of management decisions. Also, although the Florida Keys fishery represents a major fishing area, it does not necessarily represent the entire stock range for an individual species. It is possible that mature stock components exist outside the fishing area.

Six actions could improve future assessments. First, develop suitably structured spatial models for linkages between habitat use and fish ontogeny to "fill-in" the map of population estimates for areas not sampled. Second, calibrate the relative statistical power of diver surveys and headboat fishing gear. Ideally, diver observations should relate to what fishermen catch. Because the fishing mortality rate of headboats (and viewing power of divers) are considered strictly proportional to average population abundance, we must understand the fraction of the stock assessed per unit of effort and the interrelationship of the efficiency of the two "gear" types. Third, increase temporal and spatial sampling coverage to increase survey precision and resolution. Fourth, tune fishery-independent surveys with other indices of stock abundance. In this retrospective analyses, no attempt had been made to have the two survey

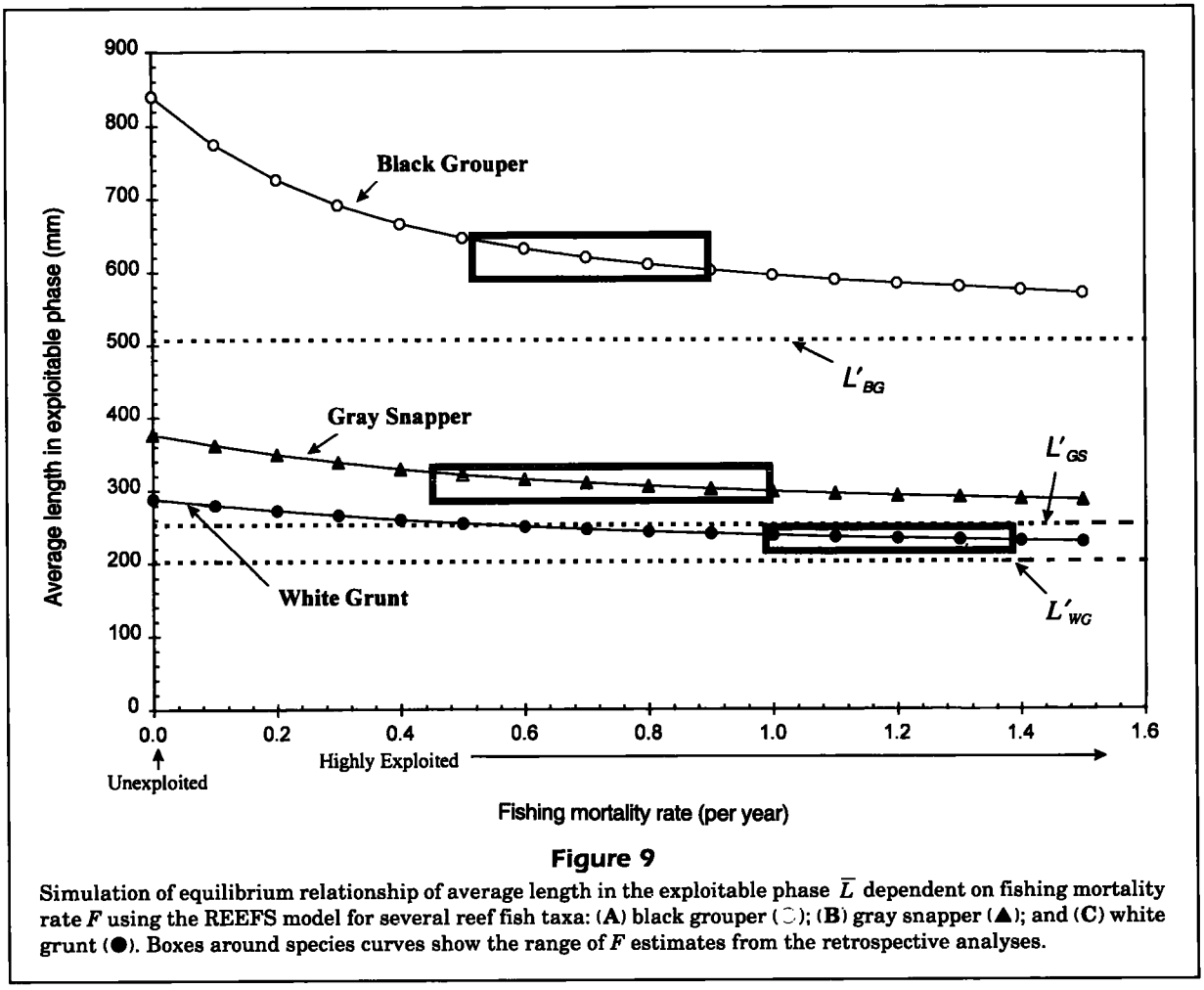


**Figure 9**

Simulation of equilibrium relationship of average length in the exploitable phase $\bar{L}$ dependent on fishing mortality rate $F$ using the REEFS model for several reef fish taxa: (**A**) black grouper (○); (**B**) gray snapper (▲); and (**C**) white grunt (●). Boxes around species curves show the range of $F$ estimates from the retrospective analyses.

types coincide with respect to sampling effort or locations within the Florida Keys. Fifth, employ new sampling technologies, such as hydroacoustics, green band lasers, and stereo video cameras to improve the accuracy and cost effectiveness of biomass and abundance estimates. Sixth, improve basic biological information on growth, reproduction, mortality, feeding, and recruitment, which are fundamental elements of stock assessment. The models and conclusions presented here are strongly influenced by the accuracy of the parameter estimates and the source for these estimates is not always reliable.

## Conclusions

We used a new approach involving fishery-independent data to conduct a quantitative retrospective multispecies assessment of changes in the Florida Keys multispecies reef fish community. Our results show that fishing effort and mortality levels are very intense, that many stocks are "overfished," and that exploitation has likely altered the structure and dynamics of the reef fish community. Inevitable increases in fishing effort, particularly by recreational anglers, combined with habitat degradation by rapid growth of human populations in the region, if unabated, will increase the potential for overfishing and ecosystem changes. Without effective intervention by regional fishery management to bring fishing effort under control, reef fish stocks will likely continue to decline. A spatial network of "no take" marine reserves, combined with traditional management measures, have the potential to reverse these trends for many species and to allow the long-term goals of building sustainable fisheries and protecting biodiversity to be achieved.

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# Reproductive patterns, sex ratio, and fecundity in gag, *Mycteroperca microlepis* (Serranidae), a protogynous grouper from the northeastern Gulf of Mexico

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**Abstract.**—We determined sex ratio, spawning season, batch fecundity, spawning frequency, and annual fecundity for gag (Serranidae: *Mycteroperca microlepis*), a protogynous hermaphrodite. Gag were randomly sampled from 1991 through 1993 ($n$=1398) and selectively sampled with a bias towards heavily pigmented fish in 1994 ($n$=648). All samples were taken from commercial and recreational fisheries in the northeastern Gulf of Mexico. Sex ratio was 49 females:1 male for the 1991–93 samples. Heavily pigmented gag ($n$=62), commonly thought to be males, were collected from waters >41.0 m during all months except January and March. Of these, 60 were histologically sexed and found to be 5.0% female, 3.3% possibly early transitional male, and 91.7% male. Indeterminate spawning generally occurred from February through April in water depths >30.5 m. Hydrated oocytes were homogeneously distributed in hydrated ovaries. Shortest length and youngest age at spawning were 577 mm total length (TL) and 3 years for females, and 981 mm TL and 8 years for males. The highest batch fecundity (865,295 hydrated oocytes) occurred in an 8-year-old, 1038-mm-TL gag. Batch fecundity had a significant ($\alpha$=0.01) positive correlation with TL, gutted body weight, and age but was most strongly correlated with TL. Average annual spawning frequency ranged from 8 to 27 for 2- to 9-year-old fish, varying significantly by year ($P$<0.05) and among years and age classes ($P$<0.02). Annual fecundity estimates ranged from 0.065 to 61.4 million and correlated well with age.

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Fishery Bulletin 96:415–427 (1998).

The spawning potential ratio (SPR), which is used to estimate the adult stock size as a percentage of the unfished stock, is an important assessment tool in the management of fish stocks (Goodyear, 1993). An accurate determination of SPR requires a basic understanding of reproduction (Huntsman and Schaaf, 1994), including information on sex ratio, spawning season duration, and size (and age) at first spawning, as well as estimates of batch fecundity, spawning frequency, and annual fecundity by fish size.

Gag (Serranidae: *Mycteroperca microlepis*), a large, economically important, shallow-water grouper found from Massachusetts to Rio de Janeiro, Brazil, (Briggs, 1958) is heavily fished in the Gulf of Mexico on Florida's western shelf, with 1986–92 annual commercial landings of about $6.80 \times 10^5$ kg (1.5 million lb) and recreational landings of 0.2–0.6 million fish (Gulf of Mexico Fishery Management Council[1]; Schirripa and Goodyear[2]). The gag is a winter-spring spawning, monandric protogynous hermaphrodite that matures sexually around 550 mm total length and 3 to 6 yr (McErlean and Smith, 1964; Collins et al., 1987; Bullock and Smith, 1991; Hood and Schlieder, 1992; Coleman et al., 1996; Koenig et al., 1996). Gilmore and Jones (1992), who described the reproductive behavior and color variation of gag off the east coast of Florida, assumed that large gag with heavy pigmentation ("black-belly" and "black-back") were males. Similarly, Bullock and Smith (1991) assumed that large gag "with dark pigmentation ventrally" from the Gulf of Mexico were male. More recently, Koenig et al. (1996) and Coleman et al. (1996) have described reproductive styles of gag and the apparent effects of fishing on gag spawning aggregations.

Although these studies (above) have examined some aspects of gag reproduction, few have addressed

[1] Gulf of Mexico Fishery Management Council. 1989. Amendment number 1 to the reef fish fishery management plan. GMFMC, Tampa, Florida, 356 p.

[2] Schirripa, M. J., and C. P. Goodyear. 1994. Status of the gag stocks of the Gulf of Mexico: assessment 1.0. Miami Laboratory, Natl. Mar. Fish. Serv., NOAA, 75 Virginia Beach Drive, Miami, FL 33149.

either fecundity or spawning frequency, and none have used the methods developed by Hunter et al. (1985) for multiple-spawning fishes. Hunter's methods have been used successfully to estimate batch fecundity, spawning frequency, and annual fecundity in other Gulf of Mexico fishes similar to gag in size and longevity (e.g. Fitzhugh et al., 1988; Taylor and Murphy, 1992; Render and Wilson, 1992; Fitzhugh et al., 1993; Nieland and Wilson, 1993; Wilson and Nieland, 1994; and Collins et al., 1996). Such estimates obtained with these newer methods are far more accurate than the previously used "ovarian egg number" methods for multiple spawning fishes (as described in Hunter et al., 1985).

In this study, we estimate sex ratio, spawning season duration, length and age at first spawning, depth of spawning, batch fecundity, spawning frequency by year, spawning frequency by size and age, and annual fecundity in gag from the Gulf of Mexico. We also test the assumption that heavily pigmented gag represent only males using histological examination of gonads of heavily pigmented fish.

## Methods

Gag were randomly sampled from commercial and recreational landings from Panama City to St. Petersburg, Florida, in 1991, 1992, and 1993. In 1994, we asked commercial fishermen to leave all heavily pigmented gag ungutted so that they could be examined for sex. Gag were considered heavily pigmented only if they retained the heavy-black pigment on the ventral portion of the abdomen after death (e.g. plate XVI, Fig. D., page 237, in Bullock and Smith, 1991). Total length (TL, in mm), fork length (FL, in mm), and total (ungutted) weight (TW, in g) were recorded before removing gonads, which were kept on ice prior to examination.

Gonads of reproductively active gag are so large that they require subsampling for determination of sex. To ensure that a single tissue sample per female would be adequate to estimate maximum oocyte diameter and hydrated oocyte counts, we first tested for tissue homogeneity. To test for homogeneity of oocyte diameter, three bilobed ovaries with hydrated oocytes were divided into six equal sections (three from each lobe) and subsampled to determine the frequency distributions of oocyte diameters; they were tested for homogeneity with a Kolmogorov-Smirnov two-sample test (Sokal and Rohlf, 1981). To test for homogeneity of density of hydrated oocytes, we used six hydrated ovaries divided in the same manner and determined the number of hydrated oocytes per gram; samples were tested for homogeneity with a two-way ANOVA (SAS, 1988).

We made a preliminary determination of sex in gag using fresh, unstained samples. A small sample was removed from each gonad, teased apart, and viewed microscopically (250×). Sex was assigned according to the following criteria: females had oocytes and no tissues that could be mistaken for spermatogenic tissue; males had no oocytes (or few small oocyte remnants); and transitional males had high numbers of oocytes and possible sperm (Shapiro et al., 1993).

Female gonads were then microscopically staged. Maximum oocyte diameter (MOD) was recorded; the most advanced oocyte type present was noted and used to assign individuals to one of five ovarian-maturation stages: 1) mature, resting (MOD<0.12 mm and clear); 2) early developing (MOD<0.20 mm and slightly opaque); 3) late developing (MOD=0.20 to 0.59 mm and opaque); 4) ripe (MOD>0.59 mm and mostly transparent); and 5) spent (much loose particulate matter in flaccid ovary) (West, 1990). After fat and mesentery were removed, gonads were blotted dry, weighed to the nearest 0.1 g., and placed in 10% buffered formaldehyde solution.

We then selected and prepared some of the gonad samples (above) to verify sex and stage using standard histological techniques. Five-µm-thick sections were prepared from tissues embedded in paraffin and stained with Harris's hematoxylin and eosin. Ovarian stages were assigned on the basis of the most advanced oocyte or follicle stage present: 1) primary growth; 2) cortical alveolar; 3) vitellogenic; 4) hydrated; and 5) spent (presence of postovulatory follicles [POFs]). Stages 1–4 followed Wallace and Selman (1981). Histological stages of possible early transitional males and functional males were as follows: 6) possible early transitional males had active female tissue with possible crypts containing primary spermatocytes (Moe, 1969; Johnson, 1995); 7) mature inactive males had a few secondary spermatocytes and remnant oocytes (primary growth and atretic only); 8) mature active males had many secondary spermatocytes and remnant oocytes; 9) ripening males had spermatids in ducts; and 10) ripe males had tailed spermatozoa in ducts. Sex and stage were compared by gonad-region for all heavily pigmented gag. Physical condition of the gonad (e.g. intactness, presence of parasites, possible preservation problems) was also noted.

We estimated duration of the spawning season by using two techniques: 1) plotting gonadosomatic index (GSI=gonad weight (100)/TW) by month for all gag with gonads in good condition (≥90% intact) and 2) determining when hydrated ovaries with nondegenerated POFs appeared. Proof of actual spawning (and not just the presence of "ripe" ovaries, as discussed in Sadovy et al., 1994) was provided by

POFs. Size and age at first spawning, and water depth of spawning, were determined with only histological stage-4 females and stage-10 males. Depth of spawning was indicated by depth of catch, as determined from interviews with fishermen.

Batch fecundity estimates involved counting whole, hydrated oocytes taken from cross sections of gonads and weighed (to the nearest 0.001 g) following Hunter et al. (1985). Samples were examined histologically for the presence of POFs and hydrated oocytes. The POFs in samples were noted as 0 (absent), 1 (degenerating), or 2 (nondegenerating) (Fitzhugh and Hettler, 1995). Ovaries with nondegenerating POFs were omitted from batch fecundity estimates to avoid biases in determining the number of hydrated oocytes per gram of tissue (Hunter et al., 1985). Batch fecundity estimates were calculated by dividing the product of gonad weight and number of hydrated oocytes by the sample weight. Any fish collected late in the spawning season were omitted from batch fecundity analyses because of apparent decreases in batch size (e.g. Fitzhugh et al., 1988).

Spawning frequency (the number of spawnings per year by a female) was estimated by dividing the duration of the spawning season by the average number of days between spawning for all females (Hunter and Macewicz, 1985; Hunter et al., 1986). Duration of the spawning season was the number of days between the first and last occurrence of hydrated oocytes or POFs each year. The average number of days between spawning for all females (> or = TL of the smallest hydrated fish) was 100% divided by the percentage frequency of hydrated females. For example, if the spawning season was 100 days long and females spawned every two days (with 50% hydrated), then spawning frequency would be 50.

We obtained annual fecundity estimates by multiplying batch fecundity by spawning frequency. Age-dependent spawning frequency was estimated with stage-4 females within each age group. Because spawning frequency varied by age and year, these variables were considered separately in calculating annual fecundity. We analyzed the following relationships using regression: batch fecundity (*BF*) × *TL*, *BF* × *age*, and *BF* × *gutted body weight* (*GBW=total weight – gonad weight = TW – GW*); *spawning frequency* × *age*; *annual fecundity* (*AF*) × *TL*, *AF* × *age*, and *AF* × *GBW*.

Most fish were aged by using whole or sectioned sagittal otoliths (Johnson et al., 1993). Whole otoliths were adequate for ageing smaller fish (<900 mm TL). We sectioned otoliths for larger gag (>899 mm TL) to facilitate reading outer rings.

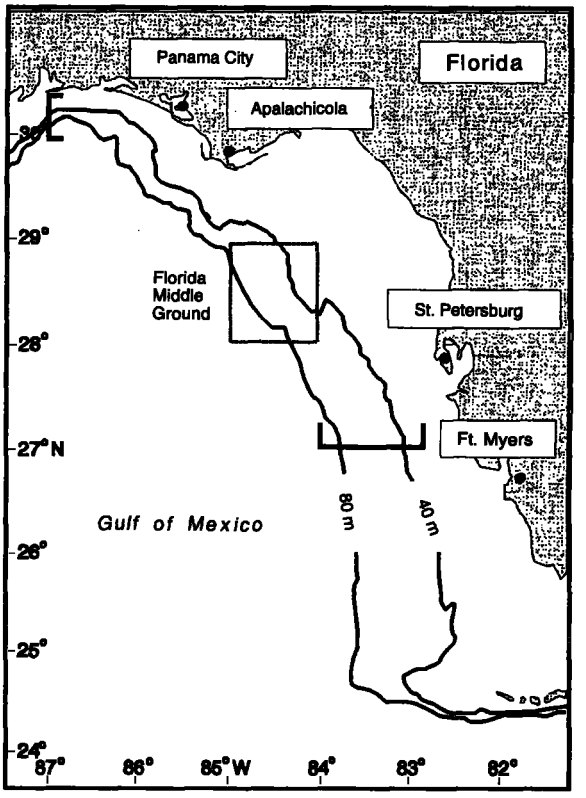


**Figure 1**

Area sampled for gag from commercial and recreational catches, 1991–94. Total area sampled, along the 40–80 m contour, is encompassed by brackets; most samples were collected from gag caught in the area south of Panama City to the Florida Middle Ground (the latter is indicated by the box).

## Results

Of all the gag collected from February 1991 through December 1994 ($n$=2,046), most (61.7%) were taken from February through May between Panama City and the Florida Middle Ground (Fig. 1). A few samples were collected from off Pensacola, St. Petersburg, and Ft. Myers, FL. The majority of commercial and recreational landings were <24 h old when sampled. Depth data recorded with samples were predominately from commercial catches (57.2%). Commercial catches were usually from greater water depths (mean=57.2 m, $n$=697) than those for recreational catches (mean=32.6 m, $n$=73). Most 1991 samples ($n$=463) were from the commercial fishery (78.1%). Most 1992 samples ($n$=318) were from the recreational fishery (85.5%). Samples in 1993 ($n$=617) came from each of the fisheries in approximately equal numbers (commercial =49%). Most 1994 samples ($n$=648) were from the commercial fishery (68.6%).

Because neither oocyte diameter-frequency distributions for oocytes >0.08 mm in diameter ($\alpha$=0.05; Kolmogorov-Smirnov two-sample test; $d_{0.05}$=0.1103;

**Table 1**

Effect of location of gag tissue samples on hydrated oocyte counts per unit of weight (g). Locations are anterior (1), mid (2), and posterior (3) of ovarian lobes. Analysis of variance indicates significance of location within a lobe for number of hydrated oocytes per gram of tissue. SS = sum of squares; MS = mean square.

| Positions of sample in ovary | Lobe 1 | | | Lobe 2 | | | Both lobes | | |
|---|---|---|---|---|---|---|---|---|---|
| | $\bar{x}$ | SD | $n$ | $\bar{x}$ | SD | $n$ | $\bar{x}$ | SD | $n$ |
| 1 | 918 | 92 | 6 | 951 | 107 | 6 | 934 | 97 | 12 |
| 2 | 914 | 81 | 6 | 932 | 180 | 6 | 923 | 133 | 12 |
| 3 | 875 | 140 | 6 | 931 | 144 | 6 | 903 | 138 | 12 |
| Total | 902 | 103 | 18 | 938 | 138 | 18 | 920 | 121 | (36) |

| Source | df | SS | MS | $F$ | $P>F$ |
|---|---|---|---|---|---|
| Lobe | 1 | 11,460.23 | 11,460.23 | 0.74 | 0.40 |
| Region | 1 | 6018.21 | 6018.21 | 0.39 | 0.54 |
| Interaction | 1 | 803.81 | 803.81 | 0.05 | 0.82 |
| Error | 32 | 496,556.28 | 15,517.38 | | |
| Total | 35 | 514,838.52 | | | |

$n$=5,450 oocytes; range=0.04 to 1.20 mm) nor hydrated oocyte counts per gram (Table 1) differed significantly among ovarian regions, we randomly sampled one region on each ovary to determine maturation stage, maximum oocyte diameter, and fecundity. Gag hydrated ovaries contained a mean of 920 hydrated oocytes per gram of ovarian tissue (range=875 to 951, SD=121, $n$=6 fish) (Table 1). The distinct clusters of oocytes of various diameters, including stage-1 and stage-2 oocytes, in gag ovaries throughout the spawning season indicated that gag is a multiple and indeterminate spawner.

Gag ovaries were usually much larger than testes (mean ovary weight=46.5 g, mean testes weight= 26.7 g). The largest ovary and testes weighed 1.60 kg and 120.0 g, respectively. Wormlike parasites were common in ovaries. Histological appearance of gag ovaries (nontransitional) was typical for marine teleosts (Wallace and Selman, 1981), except that some functional females appeared to contain crypts of spermatogonia.

An unusual condition observed in three females (stage 1 or 2) was the presence of a 5-mm thick lining (around the inside perimeter of the abdominal cavity) of compressed, hydrated oocytes apparently caused by rupture of the ovarian wall. These three fish were caught after the peak spawning season (May 1994, June 1993, and July 1994). We found no such lining in any of the other specimens examined.

We found that sex determinations and maturation-stage determinations were made with variable accuracy in fresh and histologically prepared samples. The two examinations gave the same results 89% of the time for sex determination but only 70% of the time for stage determination. The main reason for this poor comparison of the two staging techniques was that we could not accurately identify spent females (with POFs) or transitional males from fresh samples, because POFs and sperm could only be positively identified histologically.

## Sex ratio

Sex ratio from all random samples (pooling data for 1991–93) was approximately 49 females: 1 male. Our emphasis on collecting gag with dark ventral pigmentation in 1994 clearly increased the overall percentage of males: 52.5% of all males for 1991–94 ($n$=59) were collected in 1994. Percentage of males was 1.9% in 1991–93 and 4.7% in 1994. Females were collected year round and males were collected in all months but January. Possible early transitional male gag ($n$=3) were found only during February, April, and May.

## Ventral pigmentation

Gag with heavy ventral pigmentation ($n$=62) were collected in all months but January and March in waters >41 m (Table 2). Sex determination ($n$=60) showed that 5% were females (Fig. 2A), 3.3% were possible transitional males (Fig. 2, B and C), and 91.7% were males (Fig. 2D). Sex and stage were homogeneous among six gonad regions in all heavily pigmented fish.

## Spawning period

Winter-spring spawning, indicated by the presence of hydrated oocytes, was corroborated by GSI (Fig.

**Table 2**

Results of histology on gonads of gag observed with heavy ventral pigmentation, 1991–94 (M = male, F = female, T = possible early transitional male). Stage (see "Methods" section): 1 = primary growth; 3 = vitellogenic; 4 = hydrated; 6 = possible sperm crypts; 7 = inactive; 8 = active; 9 = ripening; and 10 = ripe. C = commercial and R = recreational. Numbers in parentheses indicate number aged.

| Year and month | *n* | Total length (mm) | Age (yr) | Gonad wt.(g) | Catch depth (m) | Fishery | Sex | Stage |
|---|---|---|---|---|---|---|---|---|
| 1991 | | | | | | | | |
| Feb | 1 | 985 | — | 31.2 | — | C | T | 6 |
| | 1 | 886 | — | 15.4 | 45.7–54.9 | C | M | 8 |
| May | 2 | 1140,1150 | 12,14 | 47.2,69.4 | — | C | M | 10 |
| Sep | 1 | 1140 | — | 33.1 | — | R | M | 10 |
| Dec | 1 | 1170 | — | 28.9 | — | C | M | 10 |
| Total | 6 | 886–1170 | 12,14 (2) | 15.4–69.4 | 45.7–54.9 | C,R | T,M | 6–10 |
| 1992 | | | | | | | | |
| Jun | 2 | 1100,1162 | 8,11 | 19.2,22.4 | — | R | M | 8–10 |
| Oct | 1 | 1276 | 20 | 8.9 | 39.6–[1] | R | M | 9 |
| Dec | 6 | 965–1143 | 11 (1) | 24.7–58.6 | 57.9–68.6 | C | M | 7–10 |
| Total | 9 | 965–1276 | 8–20 | 8.9–58.6 | 57.9–68.6 | C,R | M | 7–10 |
| 1993 | | | | | | | | |
| Feb | 1 | 1170 | 17 | 84.5 | 54.9–76.2 | C | M | 10 |
| | 1 | 858 | 7 | 54.6 | — | R | F | 3 |
| Jun | 1 | 1030 | 9 | 55.2 | — | R | F | 1 |
| Jul | 6 | 1070–1290 | 10–20 | 12.8–25.7 | 57.9–59.4 | C,R | M | 7–10 |
| Aug | 1 | 1105 | 11 | 13.9 | 54.9–67.1 | C | M | 9 |
| Oct | 2 | 1065,1095 | 13,– | 13.6,17.9 | 115.8 | C | M | 9 |
| Total | 12 | 858–1290 | 7–20 | 12.8–84.5 | 54.9–115.8 | C,R | M,F,T | 1–10 |
| 1994 | | | | | | | | |
| Apr | 8 | 980–1201 | 7–12 | 35.7–49.9 | 67.1–109.7 | C | M | 10 |
| | 1 | 1120 | 12 | 267.7 | 67.1 | C | T | 6 |
| | 1 | 1090 | 9 | 152.6 | 67.1 | C | F | 4 |
| May | 11 | 1055–1240 | 8–22 | 6.4–120.0 | 53.3–106.7 | C | M | 8–10 |
| Jul | 4 | 1130–1210 | 11–20 | 12.8–22.7 | 54.9–99.1 | C | M | 9–10 |
| Aug | 4 | 1085–1235 | — | 18.2–27.8 | 79.2 | C | M | 9–10 |
| Sep | 1 | 1175 | — | 40.9 | 50.3 | C | M | 10 |
| Oct | 1 | 1242 | — | 30.9 | 79.2 | R | M | 10 |
| Nov | 1 | 1230 | — | 21.8 | — | C | M | 10 |
| Dec | 1 | 981 | — | 5.4 | 41.1-44.2 | C | M | 10 |
| Total | 33 | 980–1240 | 7–22 | 5.4–267.7 | 41.1–109.7 | C | M,F,T | 4–10 |
| Grand total (1991–94) | 60 | 858–1290 | 7–22 | 5.4–267.7 | 41.1–115.8 | C,R | M,F,T | 1–10 |

[1] Questionable depth from spearfishing tournament.

3, A and B). Female GSIs ($n$=1,695) ranged from 0.01 to 8.29, with greatest mean GSI (0.21–2.60) occurring from February through March in all years (Fig. 3A). Male GSIs ($n$=59) ranged from 0.02 to 0.82, with greatest GSI occurring during February ($n$=1) in 1991 (Fig. 3B). Possible early transitional male GSI ($n$=1) was 1.65 in April 1994 (only one possible transitional male with an intact gonad and an accurate total weight was collected).

Histological staging of ovaries collected in 1993 ($n$=209) and 1994 ($n$=437) also confirmed winter–spring spawning (Fig. 4). All ovaries were stage 1 from June through September and stage 2 from October through January. Stage-3 ovaries first appeared in December and stage-4 in February. Stage-4 and stage-5 ovaries indicated that spawning occurred from February through April in 1993–94, corroborating GSI analysis. Stage-5 ovaries (containing nondegenerating POFs) were extremely rare ($n$=7), occurring only in January, March, and July 1993, and April 1994. Small numbers of hydrated oocytes appeared as remnants in the center of stage-1 ovaries after the spawning season.

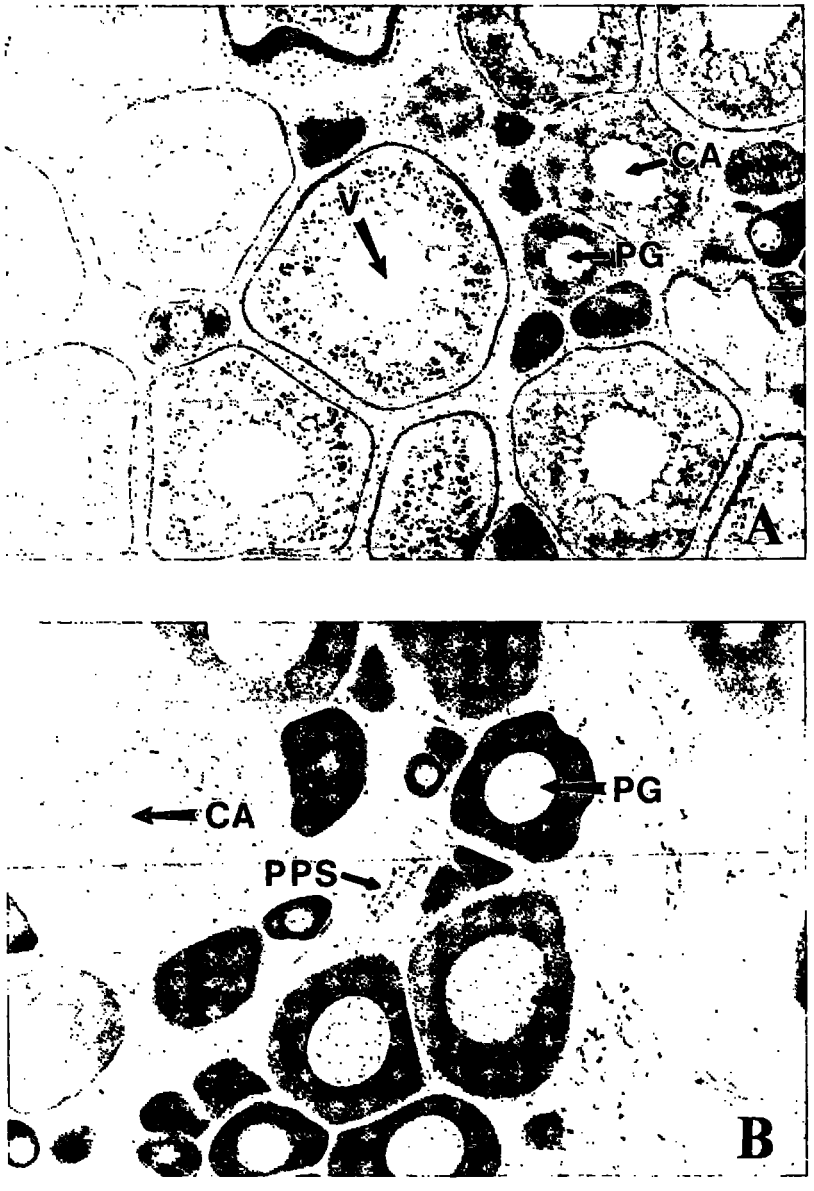


**Figure 2**

Photomicrographs of histological sections of gag with heavy ventral pigmentation: (**A**) ovarian tissue from an 858-mm-TL female caught in February 1993; (**B**) tissue from a 985-mm-TL possible early transitional male caught in February 1991; (**C**) tissue from a 1120-mm-TL possible early transitional male caught in April 1994; (**D**) testicular tissue with remnant oocytes from a 1143-mm-TL male caught in December 1992; PG = primary growth oocyte; CA = cortical alveolar oocyte; V = early vitellogenic oocyte, EHO = early hydrated oocyte (with coalescing yolk globules); PPS = possible primary spermatocytes; PS = primary spermatocytes; SS = secondary spermatocytes; MS = mature spermatids; and RO = remnant oocyte. Magnification was 132× for A and 264× for B–D.

Spawning mainly occurred from February through April 1991–94, but some evidence of spawning also occurred in December, January, May, June, and July. A total of 173 stage-4 and stage-5 ovaries were found during February, March, and April ($n$=895). No hydrated ovaries and only one ovary with POFs were found during December ($n$=58) and during January ($n$=77). Only one hydrated ovary, one ovary with hy-

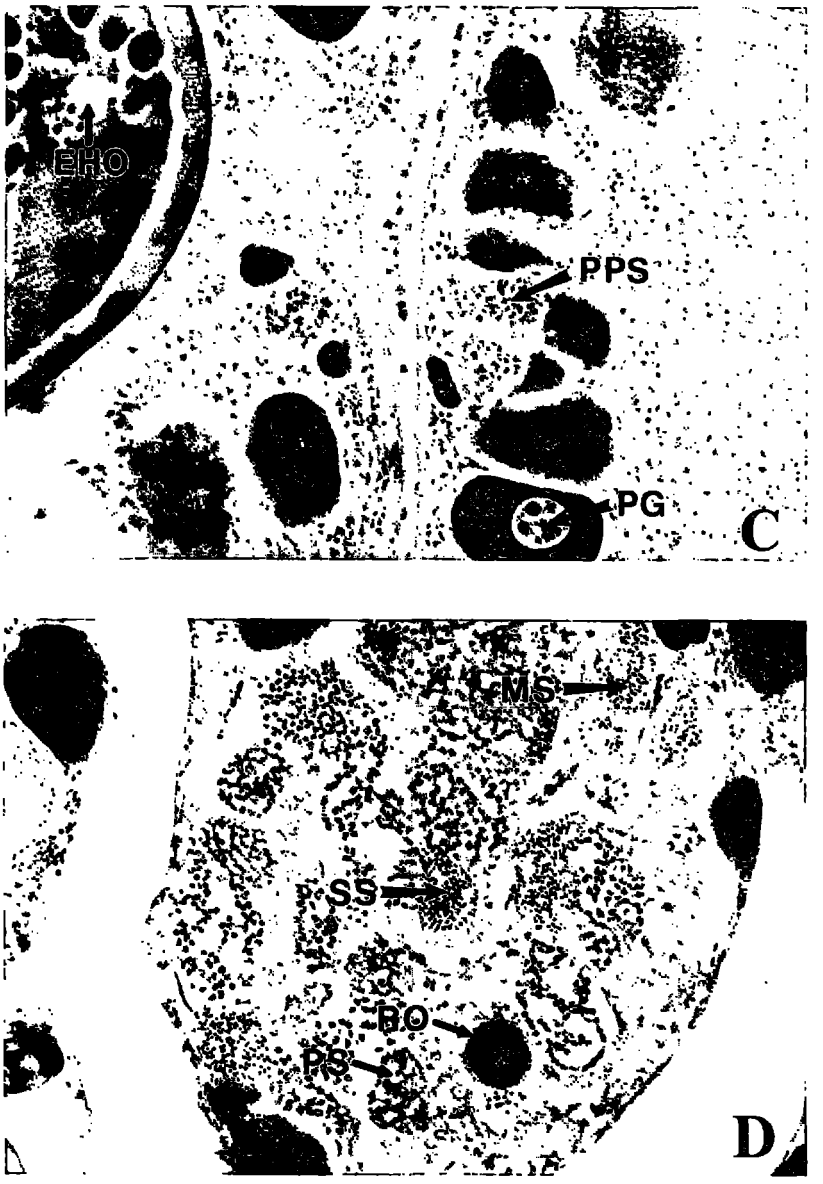


**Figure 2 (continued)**

drated oocyte remnants, and no ovaries with POFs were found during May ($n$=306). Hydrated oocyte remnants (in two ovaries) and POFs (in one ovary) were found in June ($n$=180) and July ($n$=159).

### Length and age at first spawning, and depth of spawning

Length at first spawning (see "Methods" section for definition) was 710 mm TL in 1991, 570 mm TL in 1993, and 670 mm TL in 1994 for females, and 980 mm TL for males in 1994. Age at first spawning was 3 years for females and 7 years for males. Stage-4 females were caught at depths of 30 m and greater. All males were caught at depths greater than 41 m.

### Batch fecundity

Batch fecundity estimates ($n$=39) ranged from 10,864 to 865,295 hydrated oocytes (Fig. 5). These estimates came from gag 690–1065 mm TL, 4.5–16.5 kg TW, 23.4–871.9 g ovary weight, and 3–9 years of age.

Regression analysis showed significant positive linear correlations between batch fecundity estimates

(BFE) and TL, gutted body weight (GBW), and age. Total length was the best predictor of batch fecundity (Fig. 5; $BFE = 1.773 \times 10^3(TL) - 1.119 \times 10^6$; $r^2$=0.600, $P$<0.0001, $n$=39); followed by $GBW$ ($BFE = 5.942 \times 10^4(GBW) - 9.517 \times 10^4$; $r^2$=0.576, $P$<0.0001, $n$=35); then age ($BFE = 9.476 \times 10^4(\text{age}) - 1.213 \times 10^5$; $r^2$=0.474, $P$<0.0001, $n$=38).

## Spawning frequency: by year, and age × year

Spawning frequency estimates were determined for females >709 mm TL in 1991, >576 mm TL in 1993, and >669 mm TL in 1994. Variations in spawning frequency were significantly different among years tested ($t$-test, $P$<0.02). Spawning frequency for females in 1991 was 27 times, with 29.3% (93/317) of individual females spawning at an average of every 3.4 d. Spawning frequency was not determined in 1992 owing to the absence of samples from January and February. Spawning frequency in 1993 was 14 with 16.1% (36/224) of individual females spawning at an average of every 6.2 d. Spawning frequency for 1994 was 8 with 14.0% (18/129) of individual females spawning at an average of every 7.2 d.

Spawning frequency also varied significantly among ages ($t$-test, $P$<0.01) and by age × year (ANOVA, $P$<0.05) for gag ($n$ >5 per age × year) (Table 3; Fig. 6). Age-2 females in 1993 had a spawning frequency = 0, although one spawning female of this age occurred in 1994. Age-3 females in 1991 also had a spawning frequency = 0; 1993 and 1994 spawning frequencies were also low (6 and 7, respectively). Spawning frequency varied the most (6–71) among years for 4- to 8-yr-old gag. Nine year old gag spawned 41 times in 1991. All sample sizes for 10- to 12-yr-old, 16-yr-old, and 26-yr-old gag were inadequate ($n$<6) for estimation of spawning frequency.

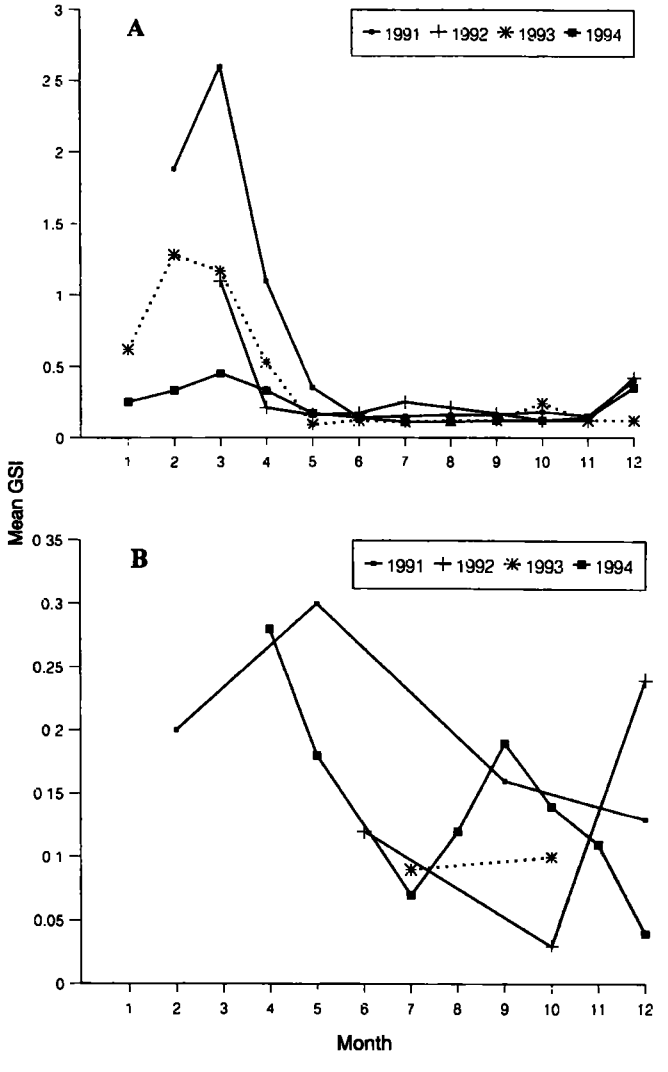


**Figure 3**

Mean gonadosomatic index (GSI) by month and year for gag. (**A**) females ($n$=1685) and (**B**) males ($n$=39) from the northeastern Gulf of Mexico, 1991–94. Note different scales for y axis in A and B.

## Annual fecundity

Annual fecundity estimated with spawning frequency estimates by age and year ranged from 0.065 to 61.4 million (Table 4; Fig. 7). Only spawning frequencies for aged fish ($n$>5 per age and year) were used. Age was an effective predictor of annual fecundity ($AFE$=9.276 × $10^3(age)^{3.94}$; $r^2$=0.76, $P$<0.0001; $n$=33).

# Discussion

We found both the peak and maximum length of the spawning period for gag to be slightly longer than previously determined (e.g. McErlean, 1963; Hood and Schlieder, 1992; Coleman et al., 1996; Koenig et al., 1996) in the Gulf of Mexico. Both GSI and percent frequency of hydrated oocytes and POFs were greatest in February through April, but a few POFs were present in December–January and May–July. Our sampling may not have included peak spawning from 1992 through 1994, as it had in 1991. McErlean (1963), through macroscopic examination of gonads, estimated that spawning occurred January through March. Hood and Schlieder (1992), through histological examination, showed that peak spawning occurred in

February and March and females were spent from December to May. Coleman et al. (1996) and Koenig et al. (1996) used GSIs, fresh "squashes," histological examinations, and juvenile otolith daily increments and found peak spawning to occur in February–March, but some gag were reproductively active from January through mid-May in 1991.

McErlean's (1963) estimates of (annual) fecundity in 7–8 yr-old gag ($n$=3, 930–946 mm TL) were somewhat similar to our batch fecundity estimates for the same age fish (his and our range of estimates were 0.526–1.457 million and 0.249–0.865 million, respectively) although the exact oocyte size and stage counted by McErlean are unknown. We can infer, however, from the "bright-yellow eggs" he counted (McErlean[3]) that they were vitellogenic (nonhydrated) oocytes because fresh hydrated oocytes are clear. We counted only hydrated oocytes ($n$=12 fish, 860–1065 mm TL). McErlean's ovary weights averaged 231.1 g, whereas ours averaged 656.7 g. This comparison of ovary weight of similar size and age fish strongly suggests that McErlean's gag were not ready to spawn. Gag population changes between 1961 (McErlean, 1963) and 1991–94 (present study) may also have affected length, age, ovary weight, and fecundity (Johnson et al., 1993).

Our estimates of gag batch fecundity (0.011–0.865 million), spawning frequency by age and year (6–71; see Tables 3 and 4), and annual fecundity (0.065–61.4 million) are similar to those of several multiple spawning, demersal marine species similar to gag in size and longevity. Fitzhugh et al. (1993) estimated mean batch fecundity (1.6 million) and spawning frequency (46, $n$=25) for black drum, *Pogonias cromis*, whereas Nieland and Wilson (1993) estimated ranges of batch fecundity (0.510–2.42 million), spawning frequency (25–28), and annual fecundity (13.0–67.0 million, $n$=41) for the same species. Wilson and Nieland (1994) estimated batch fecundity (0.160–3.27 million), and their data indicated a spawning frequency of 1–30 (calculated by the senior author (LAC) of this paper) for red drum, *Sciaenops ocellatus* ($n$=51). Recently, Collins et al. (1996) estimated batch fecundity (0.001–1.70 million), spawning frequency (21–35), and annual fecundity (0.012–59.7 million) for red snapper, *Lutjanus campechanus* ($n$=66).

Spawning frequencies and possibly GSIs may be useful in forecasting trends in fishery production. For instance, our estimates of GSI and spawning frequency were greatest during 1991 and 1993, suggesting that population reproductive efforts may have been greater and gag juveniles may have been more

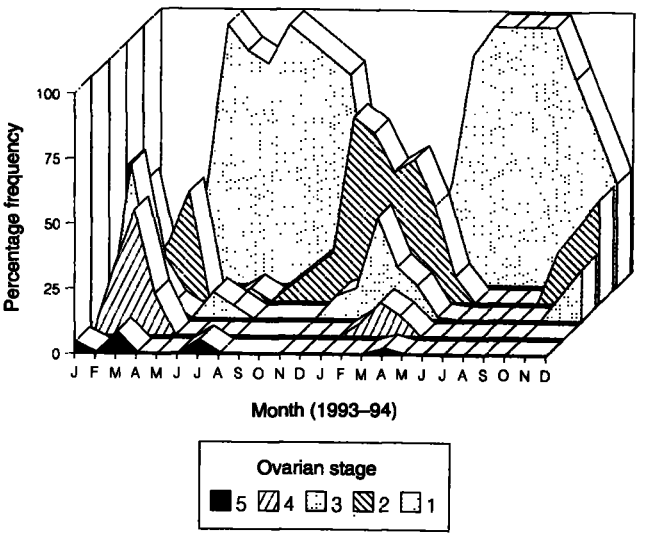


**Figure 4**

Percentage frequency of gag ovarian stages examined histologically by month and year, 1993–94 ($n$=636).

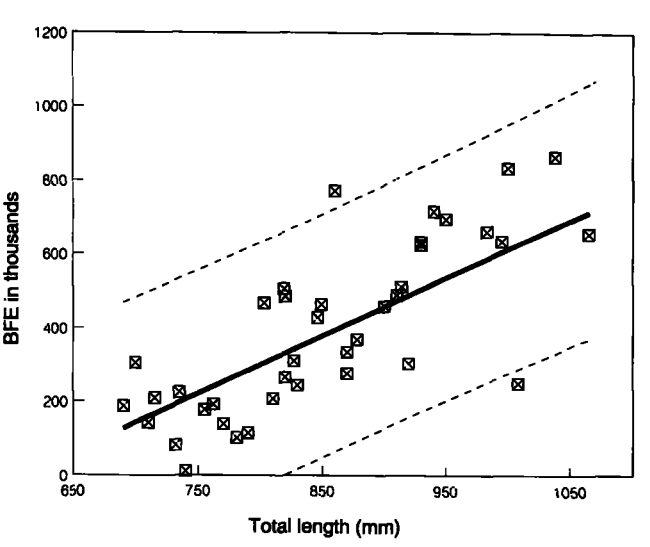


**Figure 5**

Gag batch fecundity estimates (BFE) plotted and regressed against total length (TL): $BFE = 1.773 \times 10^3 (TL) - 1.119 \times 10^6$ ($r^2$=0.60, $P$<0.0001, $n$=39), and 95% confidence limits (lighter line above and below bold regression line).

[3] McErlean, A. J. [retired]. 1997. 4364 Hickory Shores Blvd., Gulf Breeze, FL 32561. Personal commun.

abundant in these years. This finding is corroborated by studies of Johnson and Koenig (in press), wherein abundance of age-0 gag in north Florida seagrass beds was higher in 1991 and 1993 than it was in 1992 and 1994. Johnson and Koenig (in press) also found that an alternating pattern of abundance was evident in the age structure of the gag fishery from 1984 through 1989, with odd years producing dominant year classes, if the same number of females are assumed to spawn each year.

**Table 3**

Spawning frequency estimates (SFEs) by age and year for female gag (≥total length (TL) of smallest female with hydrated oocytes (HOs) or postovulatory follicles (POFs) during the spawning season).

| Age (yr) | Year | *n* | *n* with HOs/POFs | % with HOs/POFs | SFE |
|---|---|---|---|---|---|
| 2 | 91 | 0 | — | — | — |
| | 93 | 6 | 0 | 0 | 0 |
| | 94 | 1 | 1 | 100.0 | 57 |
| 3 | 91 | 9 | 0 | 0 | 0 |
| | 93 | 119 | 8 | 6.7 | 6 |
| | 94 | 8 | 1 | 12.5 | 7 |
| 4 | 91 | 20 | 6 | 30.0 | 28 |
| | 93 | 10 | 2 | 20.0 | 17 |
| | 94 | 78 | 8 | 10.3 | 6 |
| 5 | 91 | 105 | 28 | 26.7 | 25 |
| | 93 | 34 | 6 | 17.6 | 15 |
| | 94 | 8 | 1 | 12.5 | 7 |
| 6 | 91 | 8 | 2 | 25.0 | 23 |
| | 93 | 13 | 4 | 30.8 | 26 |
| | 94 | 12 | 3 | 25.0 | 14 |
| 7 | 91 | 13 | 1 | 7.7 | 7 |
| | 93 | 28 | 13 | 46.4 | 40 |
| | 94 | 2 | 0 | 0 | 0 |
| 8 | 91 | 6 | 1 | 16.7 | 16 |
| | 93 | 6 | 5 | 83.3 | 71 |
| | 94 | 8 | 2 | 25.0 | 14 |
| 9 | 91 | 9 | 4 | 44.4 | 41 |
| | 93 | 1 | 1 | 100.0 | 85 |
| | 94 | 2 | 0 | 0 | 0 |
| 10–12 | 91 | 2 | 1 | 50.0 | 47 |
| | 93 | 0 | — | — | — |
| | 94 | 3 | 1 | 33.0 | 19 |
| 16 | 91 | 1 | 0 | 0 | 0 |
| | 93 | 0 | — | — | — |
| | 94 | 0 | — | — | — |
| 26 | 91 | 1 | 0 | 0 | 0 |
| | 93 | 0 | — | — | — |
| | 94 | 0 | — | — | — |
| 3–26 | 91 | 174 | 43 | 24.7 | 23 |
| 2–9 | 93 | 217 | 39 | 18.0 | 15 |
| 2–12 | 94 | 122 | 17 | 13.9 | 8 |

The scarcity of nondegenerating POFs and the relatively low $r^2$ values of regression equations suggest that some of our annual fecundity estimates are low, a problem prevalent in some past studies on other species (Nieland and Wilson, 1993; Taylor and Murphy, 1992). The age of POFs is an important factor in judging whether POFs in a sample are from the same spawn as that for hydrated oocytes (Fitzhugh and Hettler, 1995). Delayed preservation in formalin may have caused some incompletely spawned ovaries to appear fully hydrated (if the fragile POFs were lost [Hunter et al., 1985], thus causing low estimates of batch fecundity, spawning fre-

**Table 4**

Data used for gag annual fecundity estimation, 1991–94. SFE=spawning frequency estimate by age and year.

| Catch date | Total length (mm) | Age (yr) | Batch fecundity estimate | SFE | Annual fecundity estimate |
|---|---|---|---|---|---|
| 1991 | | | | | |
| 21 Mar | 820 | 5 | 265,294 | 25 | 6,632,350 |
| 5 Apr | 732 | 4 | 82,183 | 28 | 2,301,124 |
| 5 Apr | 755 | 5 | 176,552 | 25 | 4,413,800 |
| 5 Apr | 810 | 5 | 208,438 | 25 | 5,210,950 |
| 8 Apr | 830 | 5 | 243,231 | 25 | 6,080,775 |
| 8 Apr | 870 | 5 | 276,416 | 25 | 6,910,400 |
| 8 Apr | 710 | 5 | 144,265 | 25 | 3,606,625 |
| 1993 | | | | | |
| 25 Feb | 870 | 7 | 335,275 | 40 | 13,411,000 |
| 25 Feb | 1065 | 7 | 657,268 | 40 | 26,290,720 |
| 25 Feb | 1038 | 8 | 865,295 | 71 | 61,435,945 |
| 25 Feb | 950 | 8 | 696,251 | 71 | 49,433,821 |
| 20 Mar | 860 | 7 | 772,158 | 40 | 30,886,320 |
| 21 Mar | 878 | 8 | 368,974 | 71 | 26,197,154 |
| 21 Mar | 914 | 8 | 510,637 | 71 | 36,255,227 |
| 22 Mar | 983 | 7 | 661,993 | 40 | 26,479,720 |
| 23 Mar | 1000 | 8 | 834,425 | 71 | 59,244,175 |
| 23 Mar | 930 | 6 | 625,159 | 26 | 16,254,134 |
| 28 Mar | 762 | 3 | 191,767 | 6 | 1,150,602 |
| 29 Mar | 920 | 5 | 302,604 | 15 | 4,539,060 |
| 29 Mar | 715 | 3 | 208,878 | 6 | 1,253,268 |
| 29 Mar | 740 | 3 | 10,864 | 6 | 65,184 |
| 29 Mar | 820 | 5 | 484,514 | 15 | 7,267,710 |
| 29 Mar | 900 | 5 | 458,392 | 15 | 6,875,880 |
| 29 Mar | 930 | 6 | 633,481 | 26 | 16,470,506 |
| 29 Mar | 995 | 7 | 635,329 | 40 | 25,413,160 |
| 29 Mar | 940 | 7 | 717,445 | 40 | 28,697,800 |
| 3 Apr | 700 | 3 | 304,997 | 6 | 1,829,982 |
| 3 Apr | 735 | 3 | 224,684 | 6 | 1,348,104 |
| 1994 | | | | | |
| 15 Mar | 846 | 4 | 428,371 | 6 | 2,570,226 |
| 15 Mar | 690 | 4 | 187,216 | 6 | 1,123,296 |
| 15 Mar | 827 | 5 | 310,357 | 7 | 2,172,499 |
| 15 Mar | 910 | 6 | 487,719 | 14 | 6,828,066 |
| 6 Apr | 1008 | 8 | 249,162 | 14 | 3,488,268 |

quency, and annual fecundity). Varying amounts of "missing" hydrated oocytes due to partial spawning would have then caused the low $r^2$s. An incomplete hydration process in some of the gag is another possible explanation for the low $r^2$ values; samples were taken from gag caught at different times of the day, causing variable hydration (Hunter et al., 1985). Relatively low $r^2$ values for the relation between batch fecundity and length and weight were also found for black drum ($r^2$<0.47, in Nieland and Wilson, 1993) and swordfish, *Ziphias gladius* ($r^2$<0.41, in Taylor and Murphy, 1992). Because dockside sampling was also used in these studies, delayed preservation may have caused some black drum and swordfish POFs to be missed, thereby causing low $r^2$ values.

In this study, we used histological sections to identify sex in gag with heavy abdominal pigmentation. Because male behaviors are associated with fish demonstrating this pigment pattern (Gilmore and Jones, 1992), the assumption is widespread that all these fish are males. Yet we found that 5% of such pigmented fish were females. It is possible that these fish were actually in the early stages of sex change, a phase undetectable even with histology.

Our observation of a lining of hydrated oocytes around the outside of the abdominal cavity in gag suggests that the ovary or the oviduct, or both, had ruptured at the time of hydration. This rupture probably did not occur during the fish's capture and handling because the lining of hydrated oocytes was dry and firm when we observed this phenomenon on the boat. A similar rupture may have occurred in a captive population of laboratory-matured female gag where two individuals spontaneously developed hydrated oocytes but did not ovulate; no oocytes were shed although no ovarian rupture was noted, possibly due to the absence of a male.[4] Although the proportion of males required for adequate fertilization is unknown for gag, the sharp decline of males observed by Coleman et al. (1996), Koenig et al. (1996), McGovern et al. (in press), and in this study suggests a restricted availability of males during the spawning period. Ovarian hydration in females in the absence of males could lead to ovarian rupture.

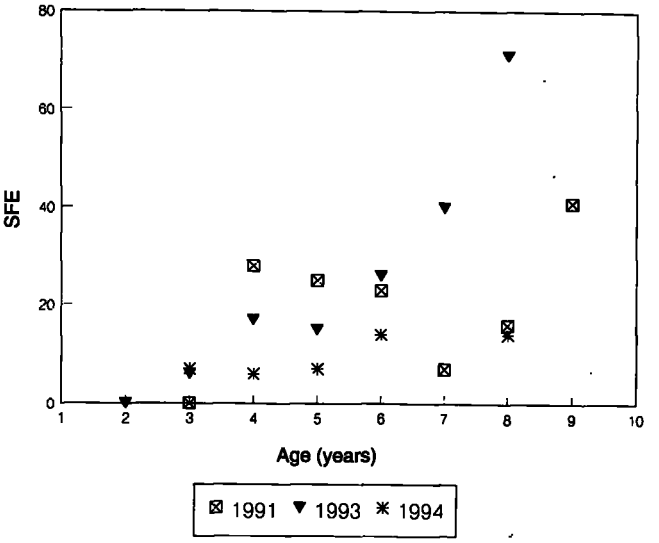


**Figure 6**

Gag spawning frequency estimates (SFE) by age and year, for ages with $n$>5 by year.

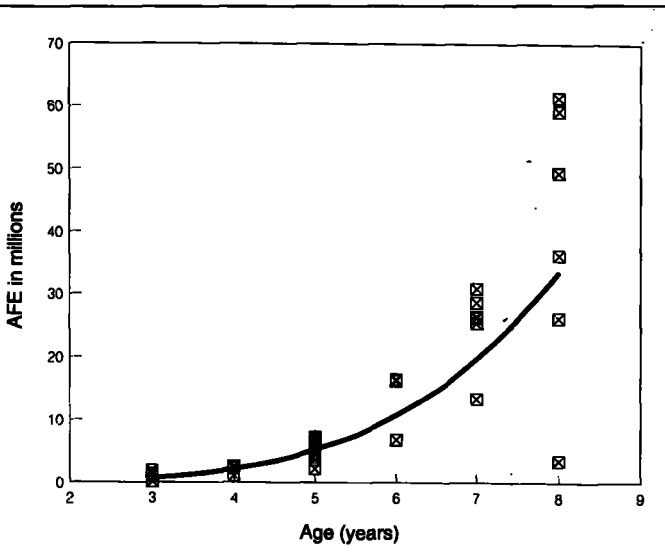


**Figure 7**

Gag annual fecundity estimates (AFE) plotted and regressed against age in years: $AFE = 9.280 \times 10^3 (age^{3.94})$ ($r^2$=0.76, $P$<0.0001, $n$=33).

Although recent studies have increased our knowledge of gag reproduction, several significant questions remain. Gag appear to spawn at a discrete depth; therefore should only those females from a known spawning area be used for spawning frequency and fecundity estimates? Do fewer males in proportion to females prevent some mature female gag from spawning every year (Coleman et al., 1996;

[4] Carr, W. 1992. Whitney Laboratory, University of Florida, St. Augustine, FL. Personal commun.

Koenig et al., 1996)? Would oocytes hydrate and then be resorbed if there was no male in close proximity? Can gag spawn as females early in the spawning season, change sex, and then spawn as males late in the same season, as suggested for red grouper, *Epinephelus morio*, by Moe (1969)? Would measurement of hormones be a better indicator of the state of transition than our histological examination? Does the possibility that sex change in serranids may occur quickly (captive *Anthias squamipinnis* changed from female to male in two weeks [Fishelson, 1970]) explain why our number of possible early transitional males was low? Questions such as these can only be answered with specifically designed laboratory and field studies.

## Acknowledgments

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**Abstract.**—This study describes the stomach contents of 95 harbor porpoises (*Phocoena phocoena*) killed in groundfish gill nets in the Gulf of Maine between September and December, 1989–94. The importance of prey was assessed by frequency of occurrence, numerical proportion, and proportion of ingested mass. Atlantic herring (*Clupea harengus*) was the most important prey, occurring in 78% of noncalf porpoise stomachs and contributing 44% of ingested mass. Pearlsides (*Maurolicus weitzmani*), silver hake (*Merluccius bilinearis*), and red and white hake (*Urophycis* spp.) were common prey items. There were no significant differences among diets of sex and maturity groups, but the calf diet differed significantly from adults in number of Atlantic herring eaten and the total mass of food consumed. At four to seven months of age, calves were eating pearlsides, small silver hake, and euphausiids (*Meganyctiphanes norvegica*) while still nursing.

# Autumn food habits of harbor porpoises, *Phocoena phocoena*, in the Gulf of Maine

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Harbor porpoises (*Phocoena phocoena*) from the Bay of Fundy and Gulf of Maine are believed to comprise a single population, hereafter referred to as the Gulf of Maine population (Palka et al., 1996; Wang et al., 1996). To date, studies of the food habits of this population have been restricted to samples collected in the Bay of Fundy during summer, where porpoises feed primarily on Atlantic herring (*Clupea harengus*; Smith and Gaskin, 1974; Recchia and Read, 1989; Smith and Read, 1992). Many porpoises leave the Bay of Fundy in fall, moving southward into the Gulf of Maine (Gaskin, 1977; Gaskin, 1984; Read and Westgate, 1997). During winter, a portion of the population disperses over the continental shelf from New England to North Carolina (Polacheck et al., 1995; Read et al., 1996).

Because of their small size and limited energy stores, harbor porpoises must remain close to food resources to avoid starvation (Koopman, 1994). Moreover, their unusual life history incurs high energetic costs; most females attain sexual maturity at three years of age and give birth to a calf each year (Read and Hohn, 1995). Lactation lasts for at least eight months; thus mature females spend most of their lives simultaneously pregnant and lactating. This intensive reproductive schedule requires calves to become nutritionally independent at a relatively early age, usually before the end of their first year (Smith and Read, 1992).

Large numbers of harbor porpoises are killed each year in gill nets in the Bay of Fundy, Gulf of Maine, and Mid-Atlantic Bight (Read and Gaskin, 1988; Read et al., 1993; Bravington and Bisack, 1996). For the Gulf of Maine, the estimated average annual harbor porpoise bycatch for 1990 to 1995 was 1800 (Bisack[1]). Little is known about the process by which porpoises become entangled in gill nets, and thus efforts are hampered in mitigating this conservation problem. Porpoises may become entangled because they feed on fish species targeted by the fish-

[1] Bisack, K. 1996. Harbor porpoise bycatch estimates in the U.S. Gulf of Maine sink gillnet fishery: 1994 and 1995. Paper presented to the International Whaling Commission Scientific Committee Meeting in Aberdeen, Scotland, June 1996 (in review).

Manuscript accepted 10 December 1997.
Fishery Bulletin 96:428–437 (1998).

ery or because they feed on the same prey as the target species.

In this paper, we examine the stomach contents of harbor porpoises in the Gulf of Maine during autumn and investigate dietary differences amongst various sex and maturity categories. Our main objectives were to elucidate seasonal changes in the harbor porpoise diet and expand our knowledge of the dynamics between porpoises and their prey that may be responsible for entanglement of porpoises in gill nets.

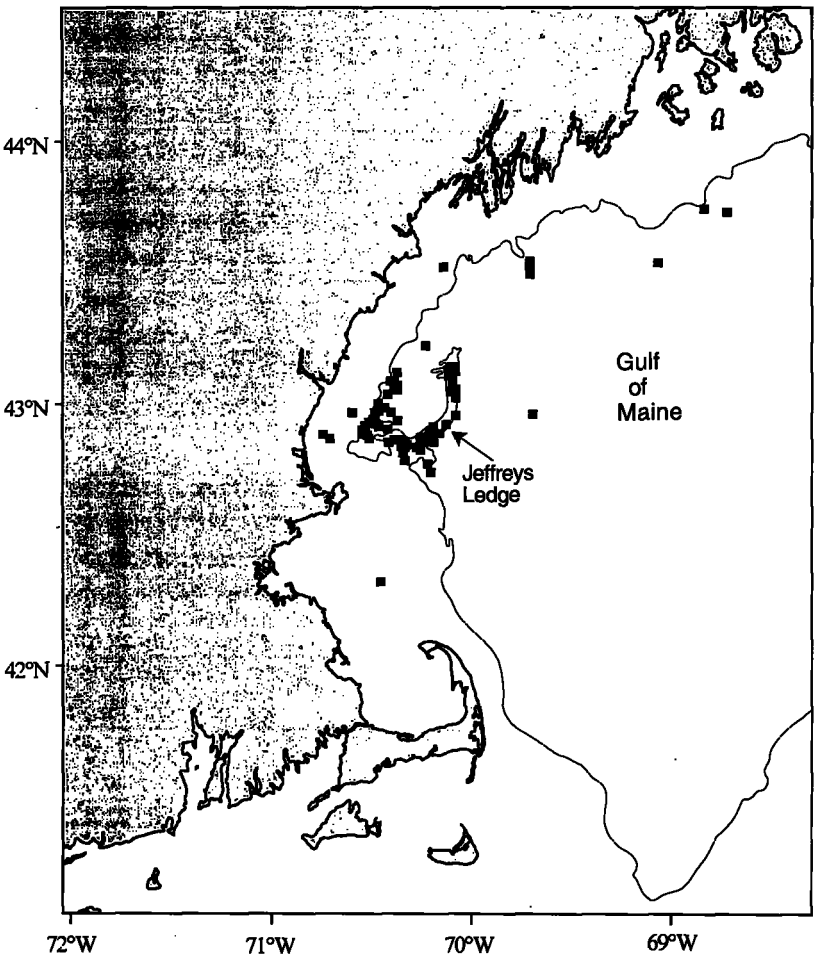


**Figure 1**

Capture locations of harbor porpoises taken during the autumn (1989–94) in the Gulf of Maine sink gillnet fishery and used in this analysis of food habits. The isobath shown is 91.4 m (50 fathoms).

## Methods

### Sample collection

The sample consisted of 95 porpoises killed in gill nets during autumn (1 September– 31 December) of 1989 and 1991–94. All porpoises were captured in bottom tending gill nets set for groundfish, principally cod (*Gadus morhua*), pollock (*Pollachius virens*), goosefish (*Lophius americanus*), and several species of flatfish. Most porpoises were taken in the vicinity of Jeffreys Ledge in the west central Gulf of Maine, at water depths between 35 and 185 m (Fig. 1). All samples were obtained by fisheries observers working onboard gillnet vessels. Observers were instructed to retain whole porpoise carcasses whenever possible, but when sea conditions or other factors prevented retention of carcasses, observers excised stomachs in the field. Carcasses and excised stomachs were frozen after the vessels returned to shore (usually 12–48 hours post mortem) for later examination.

On the basis of age (determined from dentinal growth layers and body length; see Read and Hohn, 1995) and reproductive condition (determined by examination of gonads and mammary glands; see Read and Hohn, 1995), porpoises were classified to the following sex, maturity, and reproductive categories: porpoises were considered calves (less than one year of age, not fully weaned), juveniles (older than one year but sexually immature), or sexually mature. The sex and maturity composition of the sample was as follows: (males and females combined) calves = 13; female juveniles = 12; male juveniles = 18; female mature adults = 10; male mature adults = 34; and unknown sex or maturity = 8. Because sample sizes were small, pregnant ($n$=4), simultaneously pregnant and lactating ($n$=5), and resting adult females ($n$=1) were pooled in the "mature female" group for statistical analyses. However, to facilitate comparisons with the findings of Recchia and Read (1989), data for lactating and nonlactating mature females are also presented separately.

### Prey identification

The contents of all three stomach chambers were examined in the laboratory. Intact prey were removed first, then loose flesh was decanted. The remaining stomach contents were poured through a 1-mm metal sieve to separate hard parts from liquefied digesta. Solid prey remains used for identification were separated from other skeletal remains by hand. Structures used to identify partially digested food items included sagittal otoliths, dentary bones, and skulls

of teleosts; lower mandibles ("beaks") from cephalopods; tooth cusp plates ("combs") from agnathans; and exoskeletons and eyes from crustaceans. Prey items were identified with the aid of a laboratory reference collection and published guides, including those of Bigelow and Schroeder (1953), Clarke (1986), Harkonen (1986), and Scott and Scott (1988).

## Prey importance

Relative food importance in the autumn diet of the harbor porpoise was determined by 1) frequency of occurrence, 2) proportion of numerical abundance, and 3) proportion of total ingested mass. Frequency of occurrence is the percentage of porpoise stomachs containing a particular food type. Proportion of numerical abundance is the number of individuals of a prey species recovered from all stomachs, divided by the total number of all prey from all stomachs. The number of individuals from each fish species in each stomach was determined by summing the number of intact fish and half the number of free otoliths. The number of either upper or lower beaks (whichever were more abundant) from each species was used to determine the number of squid present.

Proportion of prey mass is the percentage of total prey mass in the stomach at the time of death that was represented by a particular species. Reconstituted mass, or the mass of prey prior to ingestion, rather than the existing mass of partially digested prey, was used in this calculation. Reconstituted prey masses were estimated from body lengths of intact prey and the lengths of otoliths or cephalopod beaks (Table 1). If a stomach contained more than 25 otoliths from the same species, all otoliths from that species were counted, and a subsample of 25 was randomly selected and measured. Otoliths were scored on a scale from 0 (undamaged otoliths re-

**Table 1**

Equations used to estimate length and mass of harbor porpoise prey. ML = mantle length; H = hood length; M = mass; FL = fork length; OL = otolith length; LRL = lower rostral length; and SL = standard length. Length is in millimeters and mass is in grams.

| Prey species | Equations | Source |
|---|---|---|
| *Bathypolypus arcticus* (North Atlantic octopus) | $ML = 15.4 + 12.28\,H$ | Clarke, 1986 |
| | $\ln M = 1.06 + 2.55 \ln H$ | Clarke, 1986 |
| *Clupea harengus* (Atlantic herring) | $FL = 69.23\,OL - 27.48$ | Recchia and Read, 1989 |
| | $\log M = 3.12 \log FL - 5.41$ | Recchia and Read, 1989 |
| *Gadus morhua* (Atlantic cod) | $\ln(FL/10) = 3.3138 + 1.6235 \ln(OL/10)$ | Hunt, 1992 |
| | $M = 0.0124\,(FL/10)^{2.93}$ | Bowen and Harrison, 1994 |
| *Illex illecebrosus* (Northern short-fin squid) | $\ln M = 1.773 + 2.4 \ln LRL$ | Clarke, 1962 |
| *Loligo pealei* (Long-fin inshore squid) | $\log ML = 1.767 + 1.4 \log LRL$ | Gannon et al., 1997b |
| | $M = 0.25662\,(ML/10)^{2.1582}$ | Lange and Johnson, 1981 |
| *Maurolicus weitzmani*[1] (Weitzman's pearlsides) | $FL = 9.82 + 28.75\,OL$ | Harkonen, 1986 |
| | $M = 0.3737\,OL^{2.503}$ | Harkonen, 1986 |
| *Merluccius bilinearis* (Silver hake) | $FL = 20.9\,L - 0.41$ | Recchia and Read,1989 |
| | $\log M = -2.26 + 3.08 \log(FL/10)$ | Kohler et al., 1970 |
| *Peprilus triacanthus*[2] (Butterfish) | $SL = -9.15919 + 25.01871\,OL$ | Present study ($r^2$=0.983) |
| | $\log M = -0.67576 + 3.222 \log OL$ | Present study ($r^2$=0.924) |
| *Pollachius virens* (Pollock) | $\ln(FL/10) = 3.251 + 1.6251 \ln(OL/10)$ | Harkonen, 1986 |
| | $M = 0.0134\,(FL/10)^{2.94}$ | Bowen and Harrison, 1994 |
| *Scomber scombrus* (Atlantic mackerel) | $FL/10 = 7.33\,OL + 0.37$ | Recchia and Read, 1989 |
| | $M = 0.00756\,(FL/10)^{3.082}$ | Kulka and Stobo, 1981 |
| *Sebastes* spp.[3] (Rockfish) | $FL = 16.165\,L^{1.224}$ | Harkonen, 1986 |
| | $M = 0.0741\,OL^{3.295}$ | Harkonen, 1986 |
| *Urophycis* spp.[4] (Red and white hake) | $FL/10 = 1.525\,OL^{1.1456}$ | Clay and Clay, 1991 |
| | $M = 0.003998\,(FL/10)^{3.1718}$ | Clay and Clay, 1991 |

[1] Taxonomy of the genus *Maurolicus* has been revised recently (Parin and Kobylansky, 1996). The equations used to estimate *M. weitzmani* size are those given by Harkonen (1986) for *M. muelleri*.
[2] Standard length range: 49–153 mm; weight range: 3–104 g; $n$ = 44.
[3] Equations given by Harkonen (1986) for *S. marinus*.
[4] Equations given by Clay and Clay (1991) for *U. tenuis*.

trieved from skulls) to 5 (severely degraded, free otoliths) following the methods of Recchia and Read (1989). Otoliths categorized as 3 or higher were not used in size estimations, unless no undamaged otoliths were present. When only damaged otoliths from a particular prey species were present in a porpoise stomach, the available skeletal structures were measured; consequently the reconstituted prey mass for that stomach may have been underestimated (see Jobling and Breiby, 1986; Sekiguchi and Best, 1997)

These three measures of prey importance were applied to data from the 82 noncalf porpoises as a group and to each sex and maturity class. Food habit studies in which different methods are used can yield widely disparate results, making it difficult to draw comparisons between studies (Gannon et al., 1997a, 1997b). Because one of the primary objectives of this research was to obtain information on seasonal changes in the diet, it was important for these data to be treated in a manner similar to those of Recchia and Read (1989) and Smith and Read (1992).

## Results

### Overall sample

Table 2 lists the numbers and mean sizes of 15 prey taxa recovered from the 95 porpoise stomachs. Atlantic herring (78%), silver hake (*Merluccius bilinearis*, 68%), pearlsides (*Maurolicus weitzmani*, 38%), and red and white hake (*Urophycis* spp., 29%) occurred most frequently in the stomachs of the 74 noncalf porpoises (Table 3). Atlantic herring represented only 7% of the food by proportion of numerical abundance but accounted for 44% of ingested mass. Pearlsides accounted for 67% of food by proportion of numerical abundance but only 3% by ingested mass, owing to their small size. The unknown fish present in porpoise stomachs may have been alewives (*Alosa pseudoharengus*) but this could not be determined with certainty. Both red and white hake (*Urophycis chuss* and *U. tenuis*) were present; however it is difficult to differentiate between small, eroded otoliths from red and white hake, therefore all *Urophycis* otoliths were grouped together. Atlantic hagfish (*Myxine glutinosa*) and euphausiids (*Meganyctiphanes norvegica*) were included in analyses of frequency of occurrence only because the numerical abundance and mass of these two species were difficult to estimate. To allow comparisons to be drawn with the summer diet, data from Recchia and Read (1989) are also given in Table 3.

Figure 2 shows length-frequency distributions for the three most abundant prey: pearlsides, silver hake, and Atlantic herring. On average, Atlantic herring was the largest prey consumed by length (254 mm ±36 SD) with a range from 159 to 339 mm. The average fork length

**Table 2**

Number and mean sizes of food items present in the stomachs of harbor porpoises sampled in the Gulf of Maine during autumn. ML = mantle length, FL = fork length, and SL = standard length. Present = present in porpoise stomach contents but numerical abundance not determined.

| Food item | *n* | Length measurement | Mean length ± SD (mm) | Mean mass ± SD (g) |
|---|---|---|---|---|
| *Bathypolypus arcticus* | 1 | ML | 52 | 48 |
| *Clupea harengus* | 507 | FL | 254 ± 36 | 133 ± 56 |
| *Gadus morhua* | 5 | FL | 241 ± 133 | 137 ± 201 |
| *Illex illecebrosus* | 18 | ML | — | 55 ± 22 |
| *Loligo pealei* | 8 | ML | 129 ± 30 | 68 ± 29 |
| *Maurolicus weitzmani* | 5898 | FL | 50 ± 4 | 0.9 ± 0.2 |
| *Meganyctiphanes norvegica* | present | — | — | — |
| *Merluccius bilinearis* | 1605 | FL | 164 ± 96 | 65 ± 88 |
| *Myxine glutinosa* | present | — | — | — |
| *Peprilus triacanthus* | 38 | SL | 97 ± 12 | 24 ± 7 |
| *Pollachius virens* | 76 | FL | 195 ± 101 | 136 ± 130 |
| *Scomber scombrus* | 15 | FL | 224 ± 53 | 127 ± 91 |
| *Sebastes* spp. | 47 | FL | 37 ± 3 | 0.7 ± 0.2 |
| *Urophycis* spp. | 474 | FL | 159 ± 146 | 111 ± 172 |
| Unknown fish | 4 | — | — | — |
| Milk | present | — | — | — |

**Table 3**

Relative food importance, measured by frequency of occurrence (%FO), numerical proportion (%Num), and proportion of total mass (%Mass), in the diet of noncalf harbor porpoises during autumn in the Gulf of Maine (present study) and summer in the Bay of Fundy (Recchia and Read, 1989).

| | Gulf of Maine | | | Bay of Fundy | | |
|---|---|---|---|---|---|---|
| Prey | %FO | %Num | %Mass | %FO | %Num | %Mass |
| *Alosa pseudoharengus* | 0 | 0 | 0 | 3 | <1 | — |
| *Bathypolypus arcticus* | 1 | <1 | <1 | 3 | <1 | <1 |
| *Clupea harengus* | 78 | 7 | 44 | 88 | 44 | 64 |
| *Gadus morhua* | 4 | <1 | <1 | 14 | 14 | 14 |
| *Illex illecebrosus* | 10 | <1 | <1 | 6 | 1 | <1 |
| *Loligo pealei* | 4 | <1 | <1 | 1 | <1 | <1 |
| *Macrozoarces americanus* | 0 | 0 | 0 | 2 | <1 | — |
| *Maurolicus weitzmani* | 38 | 67 | 3 | 0 | 0 | 0 |
| *Meganyctiphanes norvegica* | 12 | — | — | — | — | — |
| *Merluccius bilinearis* | 68 | 16 | 22 | 41 | 33 | 19 |
| *Myxine glutinosa* | 7 | — | — | — | — | — |
| *Peprilus triacanthus* | 12 | 1 | 1 | 0 | 0 | 0 |
| *Pollachius virens* | 7 | 1 | 2 | 0 | 0 | 0 |
| *Pleuronectes americanus* | 0 | 0 | 0 | <1 | <1 | — |
| *Scomber scombrus* | 9 | <1 | 1 | 6 | 1 | 2 |
| *Sebastes* spp. | 11 | <1 | <1 | 0 | 0 | 0 |
| *Urophycis* spp. | 29 | 7 | 26 | 13 | 3 | 2 |
| Unknown fish | 1 | <1 | <1 | 26 | 4 | — |

for silver hake was 163 mm (±95 SD), with the length-frequency distribution showing a strong peak between 30 and 55 mm and another peak between 180 and 205 mm. The mean length of pearlsides was 50 mm (±4 SD), ranging from 40 to 62 mm.

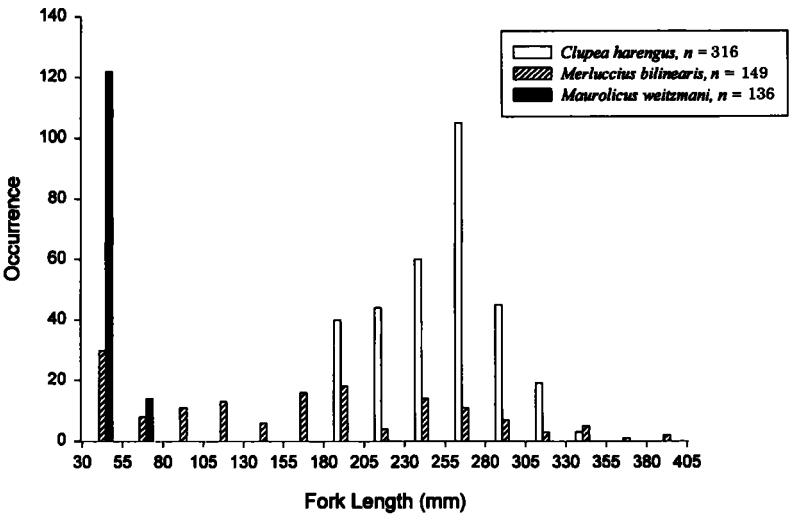


**Figure 2**

Length-frequency distributions of *Clupea harengus* (Atlantic herring), *Merluccius bilinearis* (silver hake), and *Maurolicus weitzmani* (pearlsides) eaten by harbor porpoises during autumn (1989–94) in the Gulf of Maine.

## Diet of sex and maturity categories

The stomach contents of calves differed substantially from those of nutritionally independent porpoises. Pearlsides, silver hake, and euphausiids each occurred in more than half (7/13) of the calf stomachs (Table 4). Pearlsides (72%) and silver hake (26%) were the most numerous prey in calf stomachs and accounted for 53% and 27% of the calf diet by proportion of total mass, respectively. Only 11% of the ingested mass in calf stomachs comprised Atlantic herring (<1% of numerical abundance). Although euphausiids and milk were common in the calf diet, they were excluded from the analyses of

**Table 4**

Relative food importance, measured by frequency of occurrence (%FO), numerical proportion (%Num), and proportion of total mass (%Mass), in the autumn harbor porpoise diet. Numbers in parentheses refer to frequency of occurrence values found by Smith and Read (1992) for the summer calf diet of the same population in the Bay of Fundy portion of their range.

| | Calves ($n$=13) | | | Juvenile males ($n$=18) | | | Juvenile females ($n$=12) | | | Mature males ($n$=34) | | | Mature females ($n$=10) | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Food items | %FO | %Num | %Mass | %FO | %Num | %Mass | %FO | %Num | %Mass | %FO | %Num | %Mass | %FO | %Num | %Mass |
| *Bathypolypus arcticus* | 0 (0) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | <1 | <1 | 0 | 0 | 0 |
| *Clupea harengus* | 15 (4) | <1 | 11 | 89 | 8 | 44 | 75 | 38 | 66 | 79 | 6 | 66 | 70 | 20 | 35 |
| *Gadus morhua* | 0 (0) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 6 | <1 | 1 | 10 | 1 | 1 |
| *Illex illecebrosus* | 0 (0) | 0 | 0 | 0 | 0 | 0 | 17 | 1 | <1 | 3 | <1 | <1 | 20 | 1 | <1 |
| *Loligo pealei* | 0 (0) | 0 | 0 | 11 | <1 | 1 | 0 | 0 | 0 | 3 | <1 | 1 | 0 | 0 | 0 |
| *Maurolicus weitzmani* | 54 (0) | 72 | 53 | 39 | 42 | 1 | 17 | 3 | <1 | 41 | 87 | 7 | 30 | 7 | <1 |
| *Meganyctiphanes norvegica* | 54 (63) | — | — | 22 | — | — | 17 | — | — | 9 | — | — | 0 | — | — |
| *Merluccius bilinearis* | 54 (0) | 26 | 27 | 78 | 38 | 31 | 67 | 50 | 32 | 62 | 4 | 19 | 70 | 65 | 37 |
| *Myxine glutinosa* | 8 (0) | — | — | 0 | 0 | 0 | 8 | — | — | 3 | — | — | 40 | — | — |
| *Pandalus montagui* | 0(4) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Peprilus triacanthus* | 15 (0) | <1 | 2 | 11 | 1 | 1 | 8 | 1 | <1 | 21 | 1 | 1 | 0 | 0 | 0 |
| *Pollachius virens* | 0 (0) | 0 | 0 | 6 | <1 | 1 | 0 | 0 | 0 | 9 | 1 | 2 | 20 | 4 | 10 |
| *Scomber scombrus* | 0 (0) | 0 | 0 | 6 | <1 | 1 | 8 | 1 | <1 | 15 | <1 | 2 | 0 | 0 | 0 |
| *Sebastes* spp. | 23 (0) | 1 | <1 | 17 | 3 | <1 | 25 | 1 | <1 | 6 | <1 | <1 | 0 | 0 | 0 |
| *Urophycis* spp. | 15 (0) | 1 | 7 | 39 | 7 | 21 | 33 | 6 | 1 | 24 | 1 | 1 | 20 | 2 | 18 |
| Unknown fish | 0(8) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 10 | 2 | — |
| Milk | 23 (29) | — | — | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

numerical and mass proportions because it was not possible to quantify their contributions. To facilitate comparisons between seasons, Table 4 also contains data from Smith and Read (1992) on the summer diet of calves from the Bay of Fundy.

Significant differences in stomach contents existed among the five sex and maturity groups regarding the mass proportion of Atlantic herring (no. of cases=87, df=4, $K$ [the Kruskal-Wallis test statistic] =16.077, $P$=0.003), the number of Atlantic herring present (Table 5; $K$=18.313, $P$=0.001), and the existing mass of all stomach contents ($K$=11.594, $P$=0.021). The stomach contents of calves were the most divergent of these three categories and when the Kruskal-Wallis tests were repeated with calves excluded, none of the results were significant (Atlantic herring mass proportion: no. of cases=74, df=3, $K$= 4.284, $P$=0.232; number of herring: $K$=1.739, $P$=0.628; existing mass of stomach contents: $K$=0.270, $P$=0.855). No other significant dietary differences were noted between any of the sex and maturity groups at the $\alpha$ = 0.05 level.

Qualitative comparisons between lactating and nonlactating mature females revealed that the former had higher frequencies of occurrence for most prey (Table 6). The proportion of total reconstituted mass represented by herring was much higher in nonlactating females. The mass proportions of silver hake and red and white hake were higher in lactating females. It is also interesting to note that three of five lactating females ate hagfish, a frequency far greater than that of any other sex and maturity group.

## Discussion

Atlantic herring was the most important prey of harbor porpoises in the Gulf of Maine during autumn; silver hake, red and white hake, and pearlsides were of secondary importance. Although herring was the most significant prey for porpoises in autumn, it was not as dominant as in the summer diet in the Bay of Fundy (Recchia and Read, 1989). Recchia and Read (1989) found Atlantic herring in 88% of noncalf porpoise stomachs, contributing 64% of ingested prey mass; we found herring in 78% of stomachs from noncalves, contributing 44% of prey mass. The relative importance of silver hake, of red and white hake, and of pearlsides was greater in the autumn than in the summer. For example, pearlsides occurred in 38%

**Table 5**

Prey consumption by harbor porpoises of different maturity and reproductive conditions caught incidentally in Gulf of Maine sink gill nets during autumn 1989–94 (mean ± standard deviation). *Clup.* = *Clupea harengus*, *Maur.* = *Maurolicus weitzmani*, *Mer.* = *Merluccius bilinearis*, and *Uroph.* = *Urophycis* spp.

| Porpoise groups | Average mass of individual prey | | | | Average no. of individual prey | | | | Average mass of stomach contents | | Average no. of prey taxa |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | *Clup.* | *Maur.* | *Mer.* | *Uroph.* | *Clup.* | *Maur.* | *Mer.* | *Uroph.* | Existing | Reconstituted | |
| Calves | 57 ±40 | 0.92 ±0.16 | 19 ±30 | 42 ±59 | 0.3 ±0.9 | 106.5 ±269.6 | 38.2 ±74.2 | 1.5 ±5.0 | 33 ±23 | 209 ±327 | 2.4 ±1.4 |
| Juvenile males | 131 ±35 | 0.95 ±0.20 | 51 ±56 | 108 ±105 | 4.2 ±5.0 | 21.3 ±46.8 | 19.1 ±38.7 | 3.6 ±10.8 | 284 ±288 | 1304 ±1036 | 3.2 ±1.3 |
| Juvenile females | 140 ±37 | 0.95 ±0.01 | 82 ±78 | 23 ±41 | 6.9 ±7.5 | 0.6 ±1.7 | 9.0 ±19.5 | 1.0 ±1.8 | 363 ±356 | 1389 ±1166 | 2.8 ±2.4 |
| Mature males | 125 ±30 | 0.95 ±0.05 | 73 ±103 | 50 ±46 | 8.1 ±10.6 | 117.0 ±372.3 | 5.6 ±9.5 | 0.6 ±1.6 | 274 ±285 | 1506 ±1526 | 2.9 ±1.5 |
| Mature females | 107 ±28 | 0.87 ±0.13 | 77 ±65 | 339 ±360 | 4.4 ±7.6 | 1.6 ±3.2 | 14.3 ±35.0 | 0.5 ±1.3 | 343 ±371 | 1378 ±1996 | 2.8 ±1.4 |

of porpoise stomachs in the autumn, representing 67% of numerical abundance and 3% of food mass but were absent from the summer diet. Recchia and Read (1989) found 11 prey taxa in the stomachs of 127 noncalf porpoises; we found 15 taxa in 82 noncalf stomachs. These results suggest that the diet of this population becomes more diverse as porpoises move out of the Bay of Fundy and into the Gulf of Maine. At the present time, we do not know whether these changes reflect seasonal differences in prey availability, interannual variability in prey populations, or choice on the part of foraging porpoises. Nevertheless, Atlantic herring remains the single most important prey of harbor porpoises in the Gulf of Maine during the autumn.

The size range of prey in the noncalf porpoise diet is larger in fall than in summer (Recchia and Read, 1989). Porpoises continue to eat large prey during autumn, such as adult herring and silver hake, but also eat a substantial number of smaller herring, silver hake, pearlsides, and red and white hake. The large standard deviations in Tables 2 and 5 reflect the wide range of prey sizes eaten.

With the exception of calves, the diet of porpoises did not vary significantly with age or sex. None of the comparisons of forestomach content mass, individual prey mass, or numbers of prey among the four noncalf categories yielded significant differences. Although previous studies of other marine mammal species have found measurable dietary differences between lactating and nonlactating adult females (Bernard and Hohn, 1989; Cockcroft and Ross, 1990; Cheal and Gales, 1991; Kastelein et al., 1993; Young and Cockcroft, 1994; Hobson et al., 1997; Robertson and Chivers, 1997), small sample sizes in this study prevented detailed investigation of potential dietary changes associated with changes in female reproductive condition. Therefore, the findings on diets of lactating and nonlactating mature females should be viewed with caution.

**Table 6**

Relative food importance, measured by frequency of occurrence (%FO), numerical proportion (%Num), and proportion of total mass (%Mass), in the autumn diets of lactating and nonlactating mature female harbor porpoises.

| Prey | Lactating ($n$=5) | | | Nonlactating ($n$=5) | | |
|---|---|---|---|---|---|---|
| | % FO | % Num | % Mass | % FO | % Num | % Mass |
| *Clupea harengus* | 80 | 7 | 14 | 60 | 52 | 71 |
| *Gadus morhua* | 20 | 1 | 1 | 0 | 0 | 0 |
| *Illex illecebrosus* | 40 | 1 | <1 | 0 | 0 | 0 |
| *Maurolicus weitzmani* | 0 | 0 | 0 | 60 | 25 | <1 |
| *Merluccius bilinearis* | 80 | 87 | 52 | 60 | 13 | 10 |
| *Myxine glutinosa* | 60 | — | — | 20 | — | — |
| *Pollachius virens* | 20 | 1 | 5 | 20 | 11 | 19 |
| *Urophycis* spp. | 40 | 3 | 28 | 0 | 0 | 0 |

At four to seven months of age (Read and Hohn, 1995), calves eat a variety of solid foods and continue to supplement their diet by nursing. The large standard deviations for calves in Table 5 may be an indi-

cation that some porpoise calves begin weaning sooner than others. The species composition found in the stomachs of calves in autumn begins to resemble that of older animals. However, the proportions of prey types and sizes of prey differ from those of adults. In autumn, calves eat a greater proportion of pearlsides and euphausiids than do older animals, and the sizes of Atlantic herring and silver hake are smaller than those eaten by older porpoises. Pearlsides, euphausiids, juvenile silver hake, juvenile herring, and juvenile red and white hake appear to be important in the "transitional diet" of calves, as they learn to forage independently. Calves eat a larger quantity and greater diversity of solid food in autumn than in the summer (Smith and Read, 1992). Our observations support and extend the findings of Smith and Read (1992), who suggested that porpoise calves eat euphausiids while their mothers are feeding on other euphausiid predators.

Although harbor porpoises prey on some of the groundfish species targeted by the sink gillnet fishery in the Gulf of Maine, these species contribute just a small fraction of the overall diet. Furthermore, the size range of groundfish consumed by porpoises is much smaller than that targeted by the gillnet fishery because porpoises feed on only the juvenile age classes of those commercial species. The prey that represent the bulk of the porpoise diet (i.e. Atlantic herring, silver hake, and pearlsides) are important forage items for groundfish targeted by the sink gillnet fishery (Langton, 1982). These dietary similarities may lead to overlap between the distributions of groundfish and porpoises, leading both to be caught in the same nets. Silver hake found in porpoise stomachs were highly digested (only 0.1% of silver hake were intact), indicating that they had been consumed some time prior to entanglement. In contrast, herring were often found in a relatively undigested state (15.8% were intact), indicating that many porpoises had been feeding on herring at, or just before, the time of entanglement.

Several potential biases should be kept in mind when interpreting these results. First, all the porpoises we examined had been killed in gill nets anchored to the ocean floor. This capture method may have led to a bias towards demersal prey and against pelagic prey. Without comparable samples collected near the surface, it is not possible to fully address this potential bias. The samples of Recchia and Read (1989) and Smith and Read (1992) may be similarly biased because both studies also obtained samples from porpoises killed in sink gill nets. Second, differential digestion and retention of hard parts are unavoidable in studies of marine mammal stomach contents. Consequently, the importance of species that are resistant to digestion, or that accumulate in porpoise stomachs, will be overestimated. Without empirical data on digestion times for each prey species, it is not possible to evaluate this potential bias fully.

A third potential source of bias arises from the difficulty in discriminating between primary prey (consumed by porpoises) and secondary prey (consumed by porpoise prey). For example, it is possible that small organisms, such as pearlsides, euphausiids, and juvenile silver hake, were secondarily introduced into the porpoise stomach contents. Careful examination of species co-occurrences in porpoise stomachs can provide insights into whether these small organisms were actually eaten by the porpoises. Because many porpoise prey are euphausiid predators (Bigelow and Schroeder, 1953; Langton, 1982; Scott and Scott, 1988), it is difficult to evaluate the likelihood of secondary consumption of euphausiids. However, two calves had euphausiid remains but no other solid food in their stomachs, indicating that they had consumed the euphausiids directly. One calf had pearlsides remains and a herring in its stomach; herring are not considered predators of pearlsides (Bigelow and Schroeder, 1953; Scott and Scott, 1988). Five calves had remains of pearlsides together with juvenile red, white, and silver hake less than 57 mm in length, too small to be predators of pearlsides. We interpret the co-occurrence of pearlsides and juvenile gadiforms in stomachs of calves as an indication of their preference for small prey, rather than as the presence of predators and secondary prey in their stomachs. Among older porpoises, one individual had pearlsides with no other food remains; four had pearlsides and herring; one had 13 pearlsides (totaling 16 grams), a 14-gram butterfish, and a herring; and one had 1100 pearlsides (1052 g) and one butterfish (6 g). Therefore, it is apparent that porpoises do indeed prey directly on euphausiids, pearlsides, and juvenile gadiforms.

In conclusion, the seasonal movements of harbor porpoises are accompanied by changes in diet. Seasonal movements of porpoises may, in fact, be driven by their need to maintain proximity to sufficient concentrations of prey. Assuming that there have not been any major shifts in prey availability between the previous study in the Bay of Fundy (Recchia and Read, 1989) and the present study, the diet of harbor porpoises in the Gulf of Maine during autumn appears to be more diverse than that of harbor porpoises in the Bay of Fundy during summer. The winter ecology of this population probably differs also because many porpoises are believed to leave the Gulf of Maine and Bay of Fundy region during this season. Further information on the diet of this popula-

tion in the winter and spring is required before we can fully assess the ecological relations between harbor porpoises and their prey in this system. We also suggest that further investigation of the ecological relations among Atlantic herring, groundfish, and harbor porpoises may provide information that will allow improved understanding of the causes of porpoise entanglement in gill nets and that will perhaps offer some insight into measures that may mitigate this problem.

## Acknowledgments

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# A comparison of two underwater census methods for estimating the abundance of the commercially important blacklip abalone, *Haliotis rubra*

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**Abstract.**—The blacklip abalone, *Haliotis rubra*, fishery is the most commercially important in Victoria, Australia. Two underwater census methods have been used to survey the status of its stocks. Collection rates from timed searches and counts from radial transects were used to estimate abalone abundance at various locations along the Victoria coast. Radial transect surveys provided precise estimates of abalone abundance; these did not vary significantly between research divers under controlled conditions. During stock monitoring, there were no significant differences among nine of twelve research divers' estimates of abalone abundance from 1339 radial transects sampled at 60 sites during 1992–94. Monte Carlo simulations, used to estimate the probability of detecting annual changes in abalone abundance with each method, provided evidence that radial transects have the potential to detect smaller annual changes in abalone abundance than do timed searches. We suggest that radial transects provide a credible alternative to timed searches and are less subject to potential biases that affect the latter.

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Most analyses of fish stocks are based on catch per unit of effort (CPUE) as a measure of abundance. There appears, however, to be consensus among investigators of abalone that fisheries-dependent methods are inadequate for the estimation of the abundance of abalone stocks. Reasons for this are well documented (Breen, 1992; McShane and Smith, 1992; Prince and Guzmán del Próo, 1993) and include difficulties in estimating the true catch (due in no small part to the prevalence of illegal harvesting) and hyperstability in catch rates despite stock reduction (Hilborn and Walters, 1992). The latter stems from the highly efficient searching behavior of abalone divers who, by targeting large aggregations of abalone, may serially deplete substocks (Prince and Guzmán del Próo, 1993).

Victoria, Australia's second largest abalone-producing state, yields a total annual quota of 1440 metric tons (t) of abalone from approximately 121 km$^2$ of commercially productive reef complexes distributed along approximately 1500 km of coast (McShane et al., 1986). The Victorian abalone fishing grounds are subdivided into central, eastern, and western zones (Fig. 1), each with its own total allowable catch (TAC). Abundance estimation methods used to survey such an extensive distribution of abalone stocks must be simple so that they may be applied under often adverse sea conditions and so that several sites may be sampled per day.

A reliable survey method for the estimation of abalone abundance has yet to be determined although several diving-based methods are currently used to assess the status of stocks in southern Australia and New Zealand. These include timed searches (McShane, 1994), transect surveys, patch-size estimates (McShane, 1996), change-in-ratio (Nash et al., 1994), and Petersen mark-recapture surveys (Hart and Gorfine, 1997) to provide measures of relative abundance. The intention of such surveys is to provide trends in relative abundance necessary for assessment of stock status. These methods have the advantage of being fishery independent.

However, underwater census methods are characterized by variation between research divers. In particular, relative abundance estimates from timed searches must be standardized between research divers to achieve uniformity in the base sampling unit (10 minutes). Standardization of many research

divers, each represented in the data for relatively few years of a long time series, is problematic. Strip transects can be time consuming and may traverse nonabalone habitat, such as sand; however they provide a consistent base sampling unit among research divers. Patch-size estimates have the advantage of providing a measure of the number and size of aggregations of abalone but are disadvantaged by difficulties in selecting appropriate patch-size categories and maintaining consistency in the area searched during surveys. Change-in-ratio (CIR) has the advantage of not being dependent upon a particular base sampling unit, such as time or area. However, CIR requires that there is no change in one of the two animal categories in the ratio, in this instance prerecruits. This means that the time interval between surveys must be sufficiently short that the effects of growth and natural mortality on the relative abundance of prerecruit abalone can be considered negligible. Mark-recapture (M-R) surveys are time consuming, require that many abalone be tagged, require an estimate of tag loss, may incur incidental mortality due to tagging, assume that the tagged abalone will disperse randomly within the untagged population, and can be affected by migration to and from the study site and into and out of cryptic habitat. If these limitations can be overcome, then M-R can be an effective abundance estimation technique that is free from the research diver effects that characterize other methods.

We introduce a new radial transect survey method for estimating the abundance of abalone and furnish the results of a preliminary comparison with timed searches previously used in Victoria. This new method was developed as an alternative to timed searches because 1) standardization of the effects of research divers who conducted surveys prior to 1992 with those involved in surveys from 1992 onwards was not possible and 2) the depths at many of the reefs surveyed were sufficient to warrant limiting the number of ascents made by research divers each day in order to reduce the divers' risk of decompression illness. We present an analysis of investigations into the effect of research divers on abundance estimates and the probability of detecting interannual changes in abundance with both survey methods. In Victoria, trends in interannual abundance for each management zone have been used as part of an adaptive management strategy. Several successive years of decrease in abundance will trigger consideration for decreasing annual quotas and similarly consideration will be give to increasing quotas where trends in abundance appear to be increasing. Whether quotas are changed and by how much will largely depend on the size of the change in abundance. It is anticipated that this approach will lead to the achievement of quotas that will minimize interannual changes in abalone abundance and thereby optimize sustainable yields from the fishery.

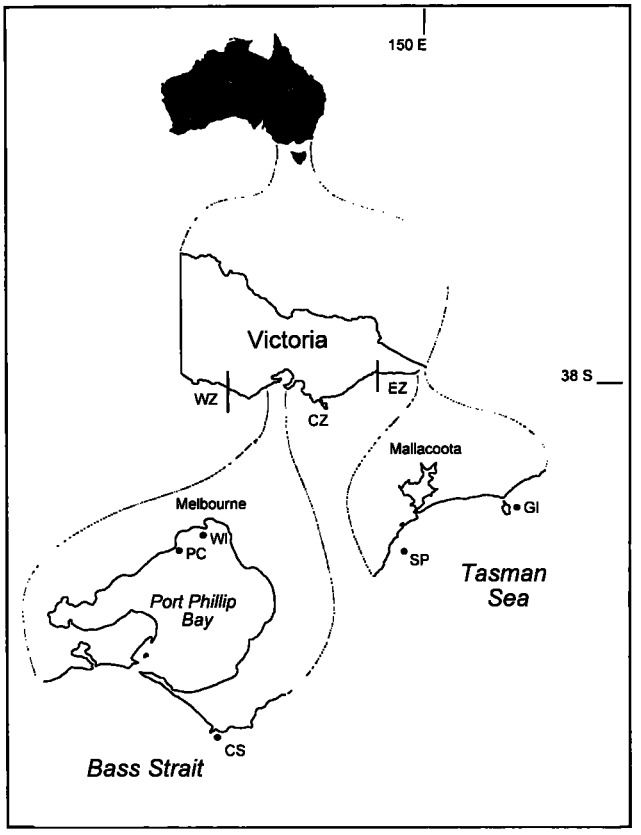


**Figure 1**

Location of study sites and management zones along the Victorian coast. CS = Cape Schanck; GI = Gabo Island; PC = Point Cook; WI = Williamstown (includes Sticks Reef); SP = Sandpatch Point; CZ = central zone; EZ = eastern zone; WZ = western zone.

## Materials and methods

### Survey methods

**Radial transects** Estimates of abalone abundance with radial transects were performed by research divers. At a particular site, a buoyed shot-line (a 20-mm-diameter line anchored by a 20-kg lead weight) was deployed. A stainless steel ring and swivel were used to connect a 35-m long transect-line of 20-mm-diameter line marked at 5-, 15-, and 20-m distances to the lead weight. The transect lines were made from a form of nylon rope that tends to float to the surface, thus decreasing the likelihood of the lines becoming tangled. Dives were made with a surface-sup-

plied breathing apparatus (SSBA) with an umbilical length of 100 m.

Prior to a dive, each diver was randomly allocated three or four compass bearings. On the bottom, each diver oriented himself towards the appropriate compass bearing and tucked the floating transect-line under his arm. Each diver was instructed to use a plastic laboratory tally counter to count, or an abalone iron to collect (depending on the study), emergent abalone larger than 50-mm shell length within an approximately 1-m wide strip from the 5-m mark laterally along the transect line. Abalone smaller than 50 mm were ignored because previous experience had shown that these juveniles were difficult to locate and were likely to be subject to large sampling errors among divers. Where estimates of the abundance of juvenile abalone were required, cryptic habitat within the transect was searched thoroughly by overturning boulders and examining crevices. These searches for juveniles were relatively time consuming. The width of the transect was constrained by the distance from the transect line under the diver's armpit to the hand of the outstretched arm on the opposite side of the diver's body. When abalone were not collected, separate counts of prerecruit abalone, i.e. those individuals smaller than the legal minimum length (LML), and of postrecruited abalone (larger than the LML) were made with a simple measuring gauge for discrimination. Each diver covered a linear distance of 30 m to survey an area of about 30 $m^2$ per transect. Any part of an aggregation of abalone falling outside the designated 1-m width was not included in the count. Underwater counts were made in instances where the removal of abalone would have interfered with further surveys of the study sites. However, during routine stock monitoring, abalone were collected and taken aboard the research vessel to obtain length-frequency data.

Each diver made additional collections in different directions radiating from the same point before surfacing. Total bottom time for each dive was usually between 30 and 60 minutes.

**Timed searches** The timed search method was the same as that described by McShane (1994), where each diver made timed searches at randomly selected subsites within each site previously surveyed by radial transects. Commencing at the research vessel's anchor, a pair of divers independently collected as many abalone as possible within a subsite in 10 minutes, using a nylon mesh catch bag and an abalone iron for removing the abalone off rocky substrata. Divers were free to search as much area as their surface air supply hose would allow (about a 100-m radius from the research vessel).

## Operator effects on methods

**Diver effects on radial transects** Variation among divers and each diver's precision with radial transects were investigated at Gabo Island near Mallacoota (Fig. 1). Precision was defined as the level of congruency among an individual diver's repeated counts of the same transect. A team of four scientific divers, each experienced in radial transects, completed two experiments at a fixed site. The objective of the first experiment was to estimate the precision of abalone counts by each diver. This was done by randomly assigning three transects from a set of twelve to each diver and by having them repeat abalone counts along the three allocated transects four times. Precision estimates for each diver were obtained as the quotients of the standard errors of the four counts for each transect divided by their mean count and were compared between divers by a one-way analysis of variance.

The second experiment compared differences among divers' abundance estimates. Each of the four divers completed counts along each of the twelve transects used in the first experiment. An analysis of variance was performed to test the hypothesis that differences among divers' mean abalone counts were not significantly different.

During both experiments, the reference shot-line remained undisturbed. Sea conditions were consistent throughout the day. Surge was slight and horizontal underwater visibility was about 10 m. The study site provided bottom topography that ranged from high relief with deep crevices to open ground with scattered boulders.

**Comparison of diver effects on radial transect and timed search survey methods** Timed search and radial transect methods were compared during abalone abundance surveys conducted on reefs at Cape Schanck, Point Cook, and Williamstown (Fig. 1). These reefs were selected to provide variety in topography, sea conditions, and abalone population structure. One site was selected at random on each of the three reefs. We tested the hypothesis that there were no significant differences in abalone abundance estimates between research divers for either sampling method. Sea conditions at each site were consistent between sampling methods but varied between the sites. In Port Phillip Bay (Point Cook and Williamstown) wind was slight, swell height was negligible, there was no surge, and horizontal underwater visibility was less than 3 m, whereas at Cape Schanck there was considerable surge (swell height 1–2 m) and underwater visibility was about 6 m.

Two experienced scientific divers, each expert in one of the techniques (>300 dives) but neither hav-

**Table 1**

Analysis of variance in density estimates, made from radial transect collections, among fifteen sites nested within three locations and among four divers for each of three size classes of *H. rubra* (type IV SS). ns = nonsignificant; * = $P<0.10$; ** = $P<0.05$; *** = $P<0.01$). $\omega^2$ = relative magnitude of variance estimate (%). MS = mean square.

| Class | Source | df | MS | *F* | *P* | $\omega^2$ | Significance |
|---|---|---|---|---|---|---|---|
| Juvenile | Location | 2 | 0.14 | 2.42 | 0.1312 | 14 | ns |
| | Diver | 3 | 0.05 | 1.92 | 0.1593 | 14 | ns |
| | Location × diver | 4 | 0.04 | 1.36 | 0.2822 | 3 | ns |
| | Site (location) | 12 | 0.06 | 1.69 | 0.0904 | 41 | * |
| | Diver × site (location) | 20 | 0.03 | 0.75 | 0.7631 | 25 | ns |
| | Residual | 63 | 0.04 | | | | |
| Prerecruit | Location | 2 | 2.36 | 19.24 | 0.0002 | 44 | *** |
| | Diver | 3 | 0.06 | 1.10 | 0.3723 | 0 | ns |
| | Location × diver | 4 | 0.08 | 1.32 | 0.2936 | 2 | ns |
| | Site (location) | 12 | 0.12 | 3.56 | 0.0003 | 37 | *** |
| | Diver × site (location) | 21 | 0.06 | 1.70 | 0.0475 | 18 | ** |
| | Residual | 81 | 0.03 | | | | |
| Postrecruit | Location | 2 | 2.60 | 9.98 | 0.0028 | 43 | *** |
| | Diver | 3 | 0.33 | 3.16 | 0.0461 | 16 | ** |
| | Location × diver | 4 | 0.14 | 1.30 | 0.3027 | 3 | ns |
| | Site (location) | 12 | 0.26 | 1.95 | 0.0393 | 27 | * |
| | Diver × site (location) | 21 | 0.10 | 0.78 | 0.7390 | 11 | ns |
| | Residual | 90 | 0.13 | | | | |

ing previously used the other method, performed both techniques to census abalone populations at each study site. Abalone counts in four radial transects and four timed collections of 10-min duration were made by each diver at each site so that the effects of divers and methods were fixed and the design balanced. Timed searches were performed after transect counts in each instance to avoid disturbance due to removal of abalone during timed searches.

Separate analyses for each method were made with general linear models to determine the significance of the effects of diver and site on abundance estimates. A combined analysis was not possible because of the different base sampling units for each method. Where Cochran's test indicated significant heterogeneity of variance, data were log-transformed prior to analysis to achieve homoscedasticity (Winer, 1971). Diver × site interaction was omitted from the analyses presented in Table 1 because preliminary analyses showed this effect to be nonsignificant.

## Trial stock surveys

The effects of divers on the detection of differences in abundance were further investigated during trial surveys of substocks at Gabo Island and Sandpatch Point near Mallacoota and Sticks Reef near Altona in Port Phillip Bay (Fig. 1). These surveys were aimed at determining how well variation among several locations was detected with this method when it was applied over a spatial scale comparable to that used in routine stock surveys.

Five sampling sites were randomly selected at each location, and for each site, three out of five divers were selected to undertake the sampling depending on their availability and fitness to dive. Two to three sites at each location were sampled during each day of the surveys. At each site, each diver made three replicate radial transect collections of emergent prerecruit and postrecruited abalone. Each diver also collected juvenile abalone (<80 mm) in one of their three assigned transects by searching cryptic habitat and turning over small boulders. All abalone collected were brought on board the research vessel, and the maximum shell length of each was measured to the nearest mm.

Analysis of variance of the mixed linear model was used to test the effects of locations, sites nested within locations, and divers on abundance estimates. The SAS® general linear model (GLM) procedure was used (SAS Institute, Inc., 1989). Separate analyses were performed for three size classes of abalone (juvenile <80 mm, 80-mm ≤ prerecruit < LML, and postrecruit ≥ LML). Data were converted to number per $m^2$.

The relative treatment magnitude, omega squared ($\omega^2$), for each effect in the GLM was calculated (Keppel, 1991).

### Design of stock monitoring program

Abundance estimates of abalone stocks in Victoria were made annually at 60 sites, using radial transects during 1992 to 1994. These estimates were made during routine stock surveys for the Victorian program for abalone stock assessment. At each site, nine replicate abalone collections were made. Sites were selected from abalone habitat with commercial quantities of abalone. During 1992, sites for radial transect surveys were initially chosen at random from between the 5-m and 18-m isobaths to avoid the wave-break zone and to minimize hyperbaric exposure. Accurate navigational fixes were made at each site with a global positioning system (GPS). During successive years each site was resurveyed after having been located with GPS. This mixed sampling design has been shown to have greater power than nested designs for benthic monitoring and avoids the potential bias of fixed designs (Van der Meer, 1997).

### Application of methods to stock monitoring

An analysis of variance was applied to results from stock monitoring surveys to determine the interannual variation in abundance for each zone. This was in the form of a mixed linear model in the SAS® general linear model procedure.

The relative treatment magnitude for each effect in the GLM was calculated with the same procedure as that used in the trial stock surveys.

The effect of differences between research divers on abalone abundance estimates from radial transects was further investigated (with two- and three-way interactions omitted) across all zones from an analysis of 1992–94 stock surveys. During each field survey of a group of adjacent sampling sites, the dive team was composed of three or four out of a possible twelve divers. Differences in the composition of dive teams between surveys occurred for logistical reasons. At each site three divers performed three radial transects each where the allocation of directions for these transects among divers was random. Differences among divers were compared by using Ryan's test (Day and Quinn, 1989), and the effect of diver experience on abundance estimates was determined by regressing divers' mean collections of abalone per transect against the number of transects each diver performed.

### Power to detect changes in abundance

Monte Carlo simulations were made to estimate the probability of detecting cumulative annual changes in abundance. The simulations were based on data from stock surveys conducted during 1992 and 1993 that employed radial transects as well as data from 1989 and 1991 surveys based on timed searches. Scenarios involving different combinations of annual change increments (increases) and number of years sampled were each simulated 200 times for each management zone (i.e. central, eastern and western; Fig. 1). Divers were randomly selected from those who participated in the surveys, and the abundance estimates for each radial transect were adjusted for the diver factor and variation within each site, whereas the abundance estimates for timed searches were standardized by using a linear regression between pairs of divers (McShane, 1994). The respective analyses of variance used to analyze the stock survey data for each method were applied to each simulation, and the proportion of tests that showed a significant ($\alpha$=0.05) annual change in abundance (year effect) was calculated. The proportion of significant results for each management zone was then plotted against the number of years simulated for each increment level. A smoothing function was applied to each curve to eliminate fluctuations due to changes in confidence levels among years in the series.

## Results

### Operator effects on methods

**Diver effects on radial transects** During the first experiment at Gabo Island, the precision (SE/$\bar{x}$) of the divers' abalone counts for each transect ranged from 0.04 to 0.27. Cochran's test showed the divers' variances of precision to be homoscedastic ($\alpha$=0.01). Differences among divers' mean precision values were not significantly different ($F$=1.43; df=3, 8; $P$>0.10). Collectively, the four groups of twelve estimates of abundance represent four identical surveys of the same site which yielded similar mean abundance estimates on each occasion (Fig. 2). Estimates of mean abalone abundance for the site during the second experiment were also similar (Fig. 3) and no significant differences were detected among the four divers ($F$=0.01; df=3, 33; $P$>0.10).

**Comparison of diver effects on radial transect and timed search survey methods** There were no significant differences between the two divers when using radial transects ($F$=0.19; df=1, 2; $P$>0.10) nor were there significant differences when using timed searches ($F$=7.31; df=1, 2; $P$>0.10). Notably, the differences between the divers' mean abundance estimates (Fig. 4) were much smaller for radial transects

(effect size=9%) than for timed searches (effect size=44%); thus power in the analysis was likely to be low.

### Trial stock surveys with radial transects

There were significant differences in density between all locations for the prerecruit and postrecruit size classes, but locations were not significantly different for juvenile abalone (Table 1). Locations and sites within locations accounted for most of the variation in density of pre- and postrecruit abalone. Significant differences between divers occurred for postrecruits, but the magnitude of the variance effect for divers was only about one third of the variance effect for sites. Sites varied significantly within locations for each size class; for juveniles and post recruits this was at the 10% confidence level, and for prerecruits at the 1% confidence level. Only one interaction effect, diver × site (location) for prerecruit density, was significant.

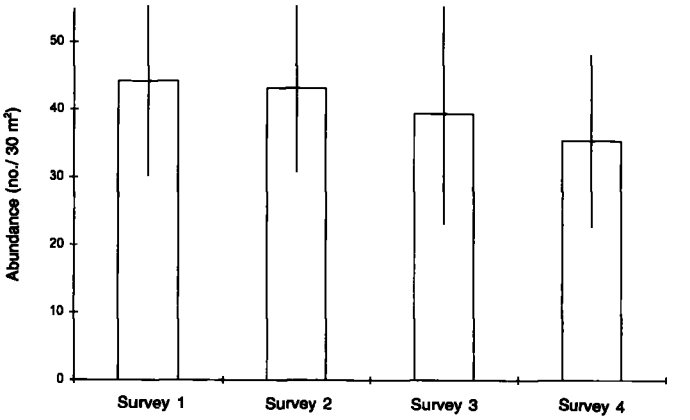


**Figure 2**

Comparison of mean abundance estimates of *H. rubra* at Gabo Island among surveys using radial transects. Error bars are 95% confidence limits.

### Application of methods to stock monitoring

Variation in abalone abundance estimates from both methods showed significant diver effects in two out of three instances (Tables 2 and 3). However, the only significant year effect detected was for estimates from radial transect surveys in the central zone of the fishery. The lack of a significant diver effect in this instance may have increased the power to detect a year effect. Consistent with the high spatial variability that characterizes abalone populations, site effects were significant in all instances. Year × site interactions were significant in two instances for each method, indicating that interannual changes in abundance varied among sites within the affected zones. Only one year × diver interaction was significant and because some divers were not represented in each year, the interpretation of this effect in this instance is problematic.

For each method only a relatively small amount of the variation in abundance could be attributed to the effect of year. Sites generally accounted for most of

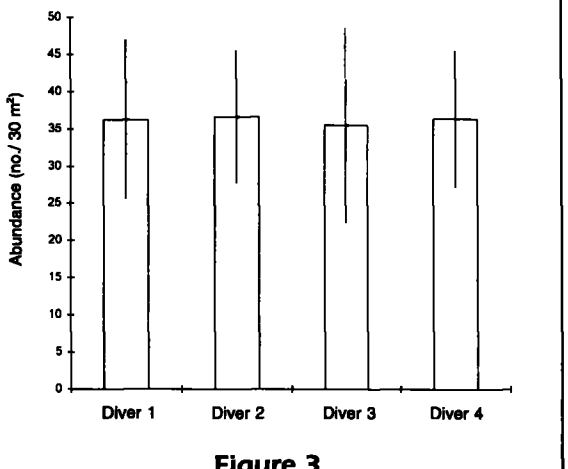


**Figure 3**

Comparison of mean abundance estimates of *H. rubra* at Gabo Island among divers using radial transects. Error bars are 95% confidence limits.

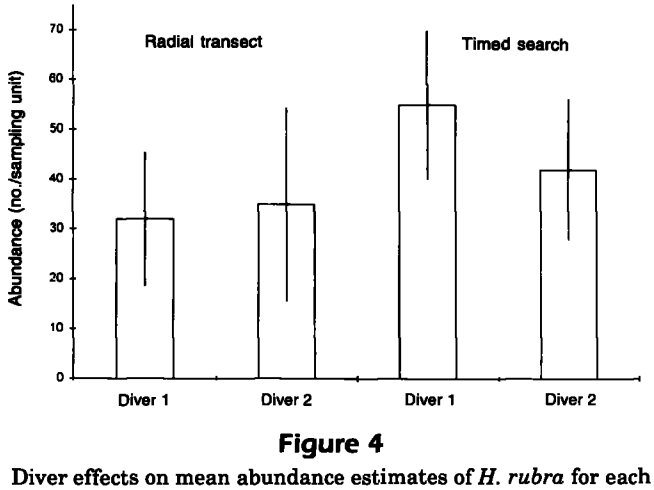


**Figure 4**

Diver effects on mean abundance estimates of *H. rubra* for each survey method. Error bars are 95% confidence limits; base sampling units were 30 $m^2$ for radial transects and 10 min for timed searches.

**Table 2**

Analysis of variance for interannual differences in abundance estimates of *H. rubra* for each of Victoria's fishery management zones, made from timed collection surveys, during 1989–91 (type IV SS). (ns = nonsignificant; * = $P<0.10$; ** = $P<0.05$; *** = $P<0.01$). $\omega^2$ = relative magnitude of variance estimate (%).

| Management zone | Source | df | MS | $F$ | $P$ | $\omega^2$ | Significance |
|---|---|---|---|---|---|---|---|
| Central | Year | 2 | 136.60 | 0.69 | 0.5141 | 1 | ns |
| | Site | 28 | 286.04 | 2.42 | 0.0008 | 45 | *** |
| | Diver | 16 | 205.08 | 1.73 | 0.0525 | 13 | * |
| | Diver × site | 83 | 92.85 | 0.79 | 0.8714 | 20 | ns |
| | Year × site | 21 | 198.87 | 1.68 | 0.0468 | 16 | * |
| | Year × diver | 4 | 25.70 | 0.19 | 0.9404 | 4 | ns |
| | Year × site × diver | 10 | 138.32 | 1.17 | 0.3207 | 2 | ns |
| | Residual | 98 | 118.28 | | | | |
| Eastern | Year | 2 | 203.64 | 1.30 | 0.2914 | 1 | ns |
| | Site | 13 | 181.97 | 1.99 | 0.0230 | 18 | ** |
| | Diver | 8 | 54.01 | 0.59 | 0.7863 | 5 | ns |
| | Diver × site | 71 | 77.91 | 0.85 | 0.7872 | 15 | ns |
| | Year × site | 24 | 156.81 | 1.71 | 0.0241 | 24 | ** |
| | Year × diver | 4 | 60.83 | 1.59 | 0.1961 | 3 | ns |
| | Year × site × diver | 41 | 38.34 | 0.42 | 0.9993 | 34 | ns |
| | Residual | 224 | 91.66 | | | | |
| Western | Year | 2 | 160.84 | 1.40 | 0.2814 | 1 | ns |
| | Site | 15 | 836.77 | 5.32 | 0.0001 | 67 | *** |
| | Diver | 5 | 779.21 | 4.95 | 0.0008 | 20 | *** |
| | Diver × site | 43 | 186.48 | 1.18 | 0.2755 | 8 | ns |
| | Year × site | 13 | 114.87 | 0.73 | 0.7262 | 4 | ns |
| | Year × diver | 0 | — | — | — | — | — |
| | Year × site × diver | 0 | — | — | — | — | — |
| | Residual | 54 | 157.38 | | | | |

the variation in the ANOVA model. For timed searches the variance estimate for diver effects was about one third that for sites; however for transects, the relativity between diver and site variance effects was more variable. The values for the relative magnitude of variance estimates attributable to divers were similar between the two methods.

Mean abundance estimates from radial transects during stock monitoring surveys varied significantly among divers; divers 4 and 5 in particular collected relatively fewer abalone per transect and diver 8 collecting more than the other divers (Table 4). Ryan's test did not reveal a significant difference between the remaining nine divers' mean relative abundance estimates (Table 4). A regression of the divers' mean relative abundance estimates against the respective numbers of radial transects performed ($r^2$=0.01, $n$= 1339) showed that the slope of the relationship was not significantly different from zero ($P>0.10$).

### Power to detect changes in abundance

The number of years of sampling required for an 80% or greater predicted probability of detecting a significant cumulative change in abundance with radial transects ranged from 1–3 years for all zones. The western zone required 3 years for 2.5% and 5% increments to become significant on 80% of occasions and 2 years for the 10% increment. The other two zones required only one year for all increments to become significant (Fig. 5A).

In contrast, timed searches (Fig. 5B) required three years to detect a cumulative annual increase of 10% in the central zone with 80% probability, and five years for the same size change in both the eastern and western zones. In the eastern zone the probability of detecting increases with timed searches was similar to that for the central zone with transects. In this instance only one year was required to have an 80% probability of detecting each increment of change.

## Discussion

Radial transects provided precise estimates of abalone abundance and did not vary significantly between different divers in three of the investigations made during this study. However, the importance of selecting scientific divers with aptitude for these types of surveys is underscored by the fact that three

**Table 3**

Analysis of variance for interannual differences in abundance estimates of *H. rubra* for each of Victoria's fishery management zones, made from radial transect surveys, during 1992–94 (type IV SS). ns = nonsignificant; * = $P<0.10$; ** = $P<0.05$; *** = $P<0.01$. $\omega^2$ = relative magnitude of variance estimate (%).

| Management zone | Source | df | MS | *F* | *P* | $\omega^2$ | Significance |
|---|---|---|---|---|---|---|---|
| Central | Year | 2 | 515.43 | 4.08 | 0.0222 | 3 | ** |
| | Site | 29 | 378.00 | 5.04 | 0.0001 | 54 | *** |
| | Diver | 10 | 93.24 | 1.24 | 0.2611 | 1 | ns |
| | Diver × site | 123 | 47.16 | 0.63 | 0.9989 | 21 | ns |
| | Year × site | 56 | 126.36 | 1.69 | 0.0022 | 18 | *** |
| | Year × diver | 5 | 31.23 | 0.49 | 0.7842 | 1 | ns |
| | Year × site × diver | 35 | 64.17 | 0.86 | 0.7066 | 2 | ns |
| | Residual | 479 | 75.00 | | | | |
| Eastern | Year | 2 | 130.23 | 0.87 | 0.4312 | 0 | ns |
| | Site | 14 | 801.99 | 5.33 | 0.0001 | 38 | *** |
| | Diver | 5 | 1170.54 | 7.78 | 0.0001 | 21 | *** |
| | Diver × site | 46 | 274.05 | 1.82 | 0.0021 | 23 | *** |
| | Year × site | 28 | 150.21 | 1.00 | 0.4728 | 0 | ns |
| | Year × diver | 4 | 301.05 | 5.22 | 0.0057 | 11 | *** |
| | Year × site × diver | 18 | 57.69 | 0.38 | 0.9899 | 7 | ns |
| | Residual | 242 | 150.48 | | | | |
| Western | Year | 2 | 36.54 | 2.30 | 0.1214 | 1 | ns |
| | Site | 12 | 261.00 | 7.14 | 0.0001 | 41 | *** |
| | Diver | 7 | 100.08 | 2.74 | 0.0096 | 7 | *** |
| | Diver × site | 40 | 47.61 | 1.30 | 0.1201 | 7 | ns |
| | Year × site | 24 | 147.51 | 4.03 | 0.0001 | 40 | *** |
| | Year × diver | 6 | 65.70 | 1.31 | 0.3016 | 1 | ns |
| | Year × site × diver | 18 | 50.04 | 1.37 | 0.1201 | 4 | ns |
| | Residual | 225 | 36.54 | | | | |

divers' mean transect collections differed significantly from the remaining nine divers during three annual abalone stock surveys. During routine monitoring, two divers (4 and 5) consistently collected less abalone than the others and frequently aborted dives after having failed to complete all their allocated transects. Reasons given for terminating their dives included problems with middle ear equalization, difficulty coping with the surge and backwash created by waves, and fouling of lines and air hoses due to entanglement. These observations concur with Shepherd (1985) who found that surge and kelp density were two significant factors affecting research diver efficiency in underwater censuses of abalone populations. In contrast to divers 4 and 5, diver 8 consistently collected more abalone than the other research divers. However, diver 8 participated only in those parts of the study conducted in the eastern zone, where abalone stocks are generally more abundant. Also, as an ex-abalone diver, diver 8 could reasonably be expected to possess a superior ability in performing abalone searches and collections that may have biased his estimates.

These observations suggest that some divers may not possess the aptitude required to conduct underwater censuses and highlight the need for understanding the nature of research being conducted. The ability to work at sea in often arduous conditions, discipline in adherence to sampling protocols, and

**Table 4**

Mean number (least squares) of *H. rubra* collected per transect by each diver during 1992–94 Victorian abalone stock surveys. Vertical bars in "ns" column indicate groups of means that were not detected as significantly different by Ryan's test ($\alpha$=0.05). ls = least squares; SE = standard error of the least squares means.

| Diver | *n* | ls mean | ± SE | ns |
|---|---|---|---|---|
| 8 | 36 | 19.48 | 1.92 | |
| 9 | 147 | 16.03 | 0.95 | |
| 1 | 467 | 12.62 | 0.53 | |
| 12 | 38 | 12.00 | 1.87 | |
| 3 | 408 | 11.26 | 0.57 | |
| 11 | 66 | 10.74 | 1.42 | |
| 7 | 6 | 10.50 | 4.71 | |
| 6 | 17 | 10.03 | 2.80 | |
| 2 | 119 | 10.02 | 1.06 | |
| 10 | 15 | 9.73 | 2.98 | |
| 4 | 107 | 7.83 | 1.12 | |
| 5 | 12 | 3.58 | 3.33 | |

the importance of avoiding a competitive atmosphere in which bagging the most abalone becomes the objective are essential characteristics of an effective abalone survey team. The problem of competition implies that nondestructive sampling, such as counting, may reduce potential bias associated with col-

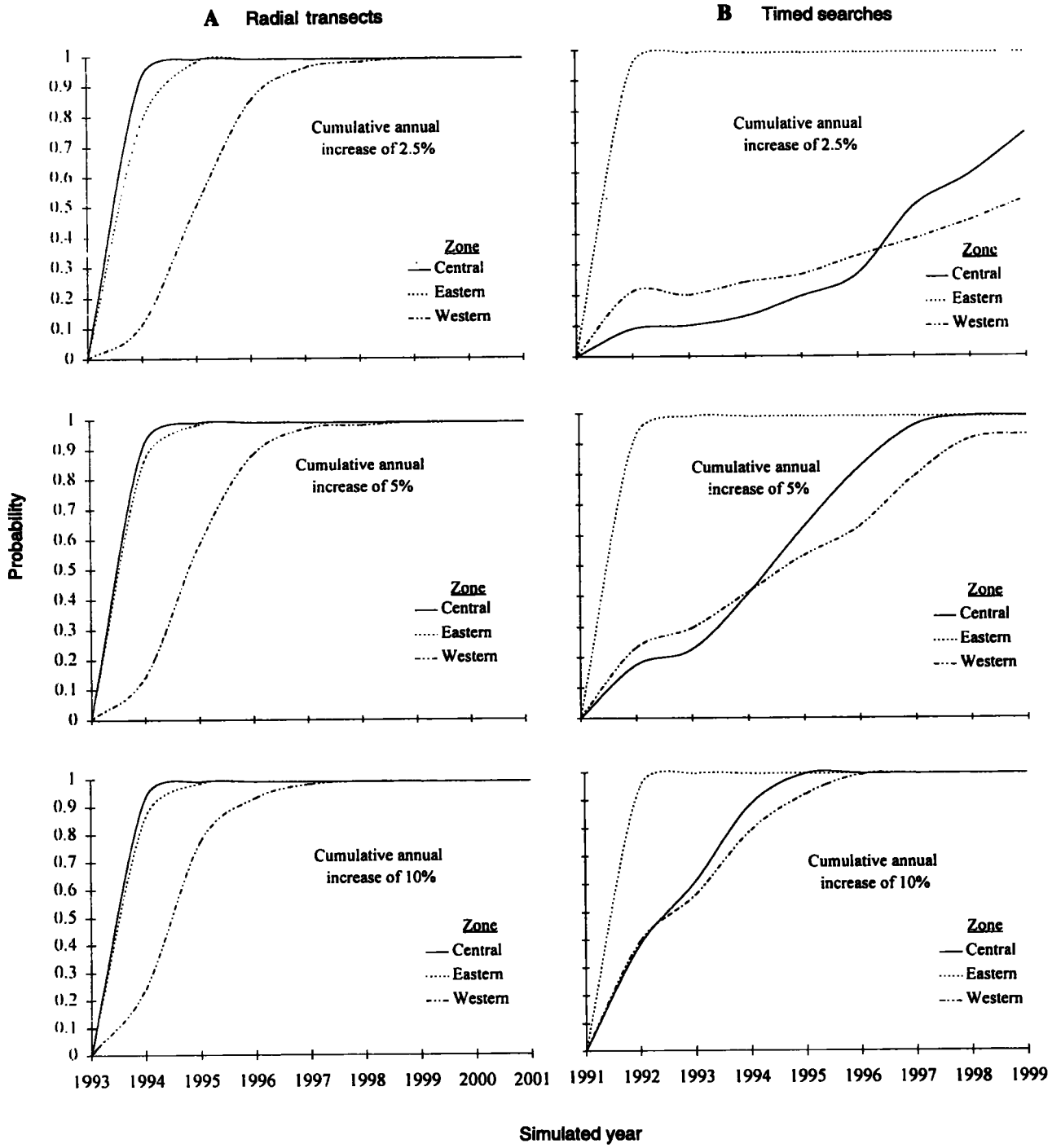


**Figure 5**

Predicted probabilities for detecting cumulative annual changes in *H. rubra* abundance from (**A**) radial transect surveys and (**B**) timed searches.

lecting. Indeed, the diver who consistently collected more abalone from transects during routine stock surveys was not significantly different from other members of the dive team when only counts of abalone were required. Similarly, McShane (1995) found that by reducing the handling time involved with the collection of large numbers of abalone from dense aggregations he reduced the operator bias in the estimation of patch frequency. Counting also has the advantage of considerably reducing the time needed to complete each transect. However, collecting becomes necessary when length-frequency data are required because in-situ measurements are impractical under the surgy conditions commonly encountered.

Experience in the radial transect method did not have a significant influence on the number of abalone estimated despite the fact that the number of transects completed per diver varyied over a wide range (6–438 transects). Differences among divers are expected when those who sampled at only a few locations are compared with divers who sampled over a larger range of abalone populations. This expectation is supported by the lower standard deviations associated with the mean collections per transect of the less experienced divers.

The standard deviations of the divers' mean relative abundance estimates from radial transects were relatively large, especially for those divers who had completed many such transects. This large range reflects the high spatial variability in abalone densities both within and between sampling sites which is evident from the relatively large proportion of variance contributed by location and site effects. During the trial stock surveys, variation among sites within locations was mostly similar to the variation among locations (except for juveniles). Although higher precision in abundance estimates may be obtained by sampling on a small scale, our results support the notion that abalone distributions are variable over the range of spatial scales commonly used to census abalone populations. Under these circumstances stratification of sites may provide little increase in the power of population surveys to detect interannual changes in abundance. The higher proportion of variance between sites in relation to locations with sampling juvenile abalone was not unexpected because of the smaller number of replicates and the greater degree of difficulty in observing this cryptic size class (Nash et al., 1994). The importance of adopting a sampling design that minimizes spatial effects is highlighted by the low proportion of the total variation attributable to the year effect. The mixed design we used provided a compromise between the advantages offered by fixed designs in reducing within-site variability and those offered by random designs in improving the precision of estimates of site means. The consequent increase in power over a random design has allowed us to economize on the number of sites sampled annually.

The use of transects to estimate the abundance of abalone stocks has been criticized (McShane, 1994) as a time-consuming approach that does not allow for the patchy nature of abalone distributions over relatively small spatial scales. However, strip transects provide an objective and reproducible approach to population surveys that appear to be somewhat less affected by research diver differences than are observations made against time. Our results demonstrate that variability among most scientific divers in the use of both radial transects and timed searches generally has a relatively small effect on variation in abalone abundance estimates. This finding suggests that standardization of abundance data from underwater censuses of abalone populations may be unnecessary. Because adaptive approaches to the setting of TACs require a time series of abundance indices, it is unlikely that all scientific dive team members will be retained for the required period. Thus effects of variation between diver and year will confound abundance estimates and interannual variation in abundance. The general linear model we used to analyze abalone abundance data includes the effect of variation among divers. For both methods, diver effects were smaller than site effects. Previous analyses of timed search estimates involved standardization to eliminate diver effects, with the assumption that all differences between within-site replicates were due to diver variation (McShane and Smith, 1990). With this approach there is a risk of underestimating the variances of mean abalone abundances because variation between divers is confounded with intrasite variation. Another problem with standardization of data to eliminate diver effects prior to analysis is the resulting confidence levels associated with performing multiple regressions between different diver pairs. The greater the number of divers the lower the level of confidence. This finding contrasts with the higher confidence level provided by the general linear models procedure, which takes account of diver × site interaction, thereby requiring only one comparison among divers.

The radial transect method is a credible alternative to timed searches for the conduct of underwater census of abalone. The notion that transect surveys are inefficient and time consuming ignores the importance of how the transects are applied. The number of radial transects that can be completed in a typical day of sampling compares favorably with the number of timed searches that can be completed within the same period. When timed searches were

used to survey Victorian abalone stocks, about 20–28 samples were completed daily; the radial transect method provides 27 samples during a typical day and requires only one-third the number of ascents per diver, reducing the risk of decompression illness (Marks and Fallowfield, 1994; Oxer, 1994). As with timed searches, the radial transect method has been successfully applied under rough sea conditions typical of the exposed coastal reefs colonized by abalone.

McShane and Smith (1990) identified the similarity between the timed search method and the techniques employed by commercial abalone divers to target aggregations of abalone. From this similarity one can reasonably infer that in some instances the abalone collection rate of research divers may exhibit (albeit over a smaller spatial scale) the hyperstability that characterizes the catch per unit of effort of commercial abalone divers. Indeed, in a study involving intensive experimental fishing McShane and Smith (1989) could not detect a significant difference between pre- and postfishing abundance estimates of postrecruited abalone from timed searches despite a 50% decrease in CPUE. In his discussion of a patch-frequency estimation method, McShane (1995) noted the bias in timed searches when a large proportion of the search time is spent collecting abalone from dense aggregations. Radial transects target a specific area (30 $m^2$); consequently handling time does not affect the numbers of abalone counted or collected and divers are unable to target aggregations to the exclusion of more sparsely distributed abalone. Therefore it is reasonable to expect that surveys based on radial transects more accurately reflect true abalone abundance than do those based on timed searches.

Although there is no doubt that dense patches of abalone are important with respect to fishing and the maintenance of profitable catch rates (McShane, 1995), recent work on *H. rubra* in Victoria (Officer[1]) has demonstrated the importance of postfishing movement and reaggregation in maintaining these patches. The Victorian studies also showed that dense patches contributed most of the variation in abundance estimates and that the standard deviations of samples of sparsely distributed abalone were relatively small. It is from these sparsely distributed abalone, and those occupying cryptic habitat, that reaggregation appears to have occurred. Further research is required to determine the relative importance of sparsely distributed abalone in assessing the impact of fishing. Abundance estimates from transect sampling may prove to be more effective indicators of the size of stocks if dense aggregations are excluded from surveys.

Because the application of radial transects avoids targeting some emergent abalone to the exclusion of others, there is less potential for divers to bias their sample towards larger abalone as may occur with timed searches. By measuring the length of each abalone collected, separate estimates of abundance for prerecruit (shorter than the legal minimum length) and postrecruit (recruited to the stock) abalone can be made. Timed searches do not necessarily permit this separation of prerecruits from postrecruits because of the potential for divers to collect larger, more accessible abalone at the expense of smaller abalone. Timed search estimates of abundance reported in McShane and Smith (1989) show an almost threefold increase in prerecruits after fishing, suggesting that abundances of prerecruits may have been underestimated prior to fishing because of the prevalence of postrecruits.

Our trial stock surveys provided evidence that the transect method has the power to detect differences in abalone abundance (among locations and sites) and is robust in respect to differences in divers' abilities to perform the method. Moreover, annual stock surveys based on radial transects were able to detect a significant change in abundance between consecutive years and had a high power of detecting smaller effect sizes over 2–3 years, thus showing their usefulness as an effective stock monitoring tool. The radial transect method as it is currently applied for monitoring Victorian abalone stocks should have sufficient power to detect changes in abundance of about 10% after 3 years sampling. Monte Carlo simulations showed that surveys based on timed searches generally would require several years of sampling and consequently would have lower power than radial transect surveys in detecting the same rate of change. The simulation results for the eastern zone, where it was predicted that only one year would be required for a 2.5% change, proved to be the only exception. However, unlike the timed search sampling of the central and western zones, all sites in the eastern zone were sampled twice annually during 1989–91. This additional sampling would be expected to increase substantially the statistical power to detect changes in abundance.

Surveys based on radial transects have been used to monitor *H. rubra* stocks in the Victorian abalone fishery since 1992 with the objective of establishing a temporal series of abundance data to assist managers in determining sustainable levels of fishing. In monitoring Victoria's abalone stocks, the aim is to detect an overall change in abundance across a man-

[1] Officer, R. 1997. Marine and Freshwater Resources Institute, PO Box 114, Queenscliff, Victoria 3225, Australia. Unpubl. manuscript.

agement zone against a background of increases and decreases at different sites within that zone. Although the Monte Carlo simulations predict that, with the use of transects, such overall changes should become detectable within several years, it is obvious that a much longer time series than three years is required to determine if significant interannual changes form part of a trend in abundance. In addition to the temporal scale required for effective monitoring of abalone stocks, there is also the issue of selecting an appropriate spatial scale over which to sample. Many abalone fisheries are managed in spatial units involving several hundreds of kilometres of coastline, and the relatively high cost of fishery-independent surveys ensures that compromises must be made to maximize the benefits from stock assessment programs. Consequently, the biologist investigating abalone is faced with selecting between a limited number of intensive surveys of substocks over small spatial scales and extensive surveys that are less detailed but at the scale over which the fishery is managed (McShane et al., 1994). In their discussion of the design of surveys for abundance indices, Hilborn and Walters (1992) favored extensive surveys with low sampling intensities that cover the entire fishing grounds. Their preference for many sampling stations and minimal effort per station has recently been supported by Van der Meer's (1997) study. This is the approach we are currently using to survey abalone stocks in Victoria, although we maintain relatively high within-site replication to allow greater precision for site means. Whether power is traded off against precision depends on the extent to which inferences are to be drawn regarding individual sites.

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# Age, growth, and mortality of black drum, *Pogonias cromis*, in the Chesapeake Bay region

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**Abstract.**—We used otolith ageing to describe the population dynamics of black drum, *Pogonias cromis*, collected over a three-year period from the Chesapeake Bay region's commercial and recreational fisheries. Black drum average age, total length, and weight were 26 years, 109.5 cm, and 22.1 kg respectively. The oldest fish was 59 years and fish older than 50 years were present in the catch from 1990 to 1992. Growth in length slowed by age 20, whereas growth in weight did not slow until age 45. A von Bertalanffy growth function was fitted to our data ($L_\infty$= 117.3 cm, $K$=0.105, $t_0$=–2.3 yr) and was similar to that for northeast Florida, but dissimilar to that for the Gulf of Mexico. Fish grow slower but reach larger sizes in the Atlantic than in the Gulf. Estimates of instantaneous total mortality, $Z$, from maximum age and catch-curve analyses were low, 0.08–0.13, indicating that fishing mortality is also low in the Chesapeake Bay region. Studies to date lend support to the hypothesis that black drum from the east coast of the United States are from a common stock. The fishery of the Chesapeake Bay region is made up of old, large migrants from that larger population and should be managed accordingly.

Manuscript accepted 28 October 1997.
Fishery Bulletin 96:451–461 (1998).

Black drum, *Pogonias cromis*, is the largest member of the family Sciaenidae in the western North Atlantic Ocean. Black drum range in U.S. waters from New England south through Florida and across the northern Gulf of Mexico, with Chesapeake Bay being near the northern end of the breeding range (Welsh and Breder, 1923; Hildebrand and Schroeder, 1928). Black drum support important recreational and commercial fisheries throughout their range in the United States. Their population abundance has been historically greater on the Florida coast than northward (Welsh and Breder, 1923), but the degree of stock unity along the east coast of the United States has not yet been determined.

Black drum is migratory in the Chesapeake Bay region. Frisbie (1961) speculated that juveniles move offshore and southward in the fall. Richards (1973) reported that black drum were absent from marine waters off Virginia during winter. Although occasionally caught inshore during winter, black drum generally move inshore to spawn in spring and offshore to overwinter in the fall. The migratory behavior of this fish complicates interpretation of the biological characteristics of the Atlantic coast fishery.

Proper management of the black drum population depends on knowledge of their basic biology throughout their range, particularly their resilience to harvesting. Yet much is unknown about their adult life history and biology in the Chesapeake Bay region where studies have concentrated on early life history. Initial studies of eggs, larvae, and juveniles (Frisbie, 1961; Joseph et al., 1964; Richards and Castagna, 1970) failed to clarify the geographic extent of the spawning and nursery regions. A recent study by Daniel and Graves (1994) concluded that egg production of black drum had been overestimated because of misindentification and that previously reported egg distributions (Joseph et al., 1964) may be incorrect.

Little work has been directed at adult black drum in the Chesapeake Bay region, aside from general faunal studies like that of Hildebrand and Schroeder (1928), and only one study is recent. Studies of early life history by Frisbie (1961) and Joseph et al. (1964) provide little information that can be used in yield modeling to evaluate resilience to harvest. The only studies that provide information specifically useful for modeling include Richards (1973) and Desfosse (1987), both on age and growth. Desfosse (1987) reported ages of 4–15 years with 10-year-olds predominant in the catch, whereas Richards (1973) estimated

maximum age at 35 years. Unfortunately, these studies relied on scales to age black drum. Furthermore, Beamish and McFarlane (1983) reported that scales were not a reliable hard part to age older fish of many species. Hence, the use of scales for ageing black drum in the Chesapeake Bay region may give unreliable results.

Only one recent study of black drum life history has focused on the Chesapeake Bay region; more work has been done in Florida and Gulf of Mexico waters. Pearson (1929) first described the early life stages for black drum in Texas waters. Egg and larval distributions have been reported (Jannke, 1971; Holt et al., 1985; Ditty, 1986), as well as adult distributions (Cody et al., 1978; Ross et al., 1983). Recent studies, based on otolith ageing, report maximum ages of 43 years in the northern Gulf of Mexico (Beckman et al., 1990) and 58 years off the northeast coast of Florida (Murphy and Taylor, 1989). Although Pearson (1929) described spawning migrations of fish over 80 cm, most young fish show little movement between embayments (Osburn and Matlock, 1984).

This paper describes fundamental biological characteristics of black drum in the Chesapeake Bay region that support stock unity of east coast fish. These data can be used as a basis for yield modeling and evaluation of black drum's resilience to harvest. We present the first otolith-based age determination for Chesapeake Bay black drum, which includes characteristics of catch, growth, and mortality. We compare these life history parameters with those derived from other geographic regions.

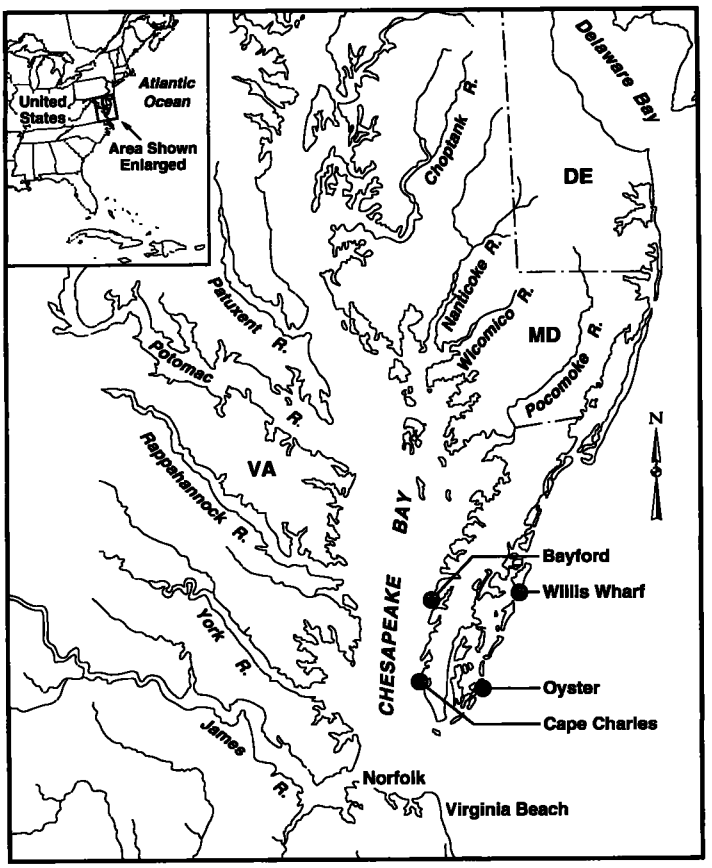


**Figure 1**
Map of Chesapeake Bay showing Chesapeake Bay region sampling sites.

## Methods

Black drum ($n$=853) were collected March through June, 1990–92, from commercial and recreational fisheries on the eastern shore of Virginia where more than 90% of the catch is landed (Jones et al., 1990). Commercial landing sites were located at Willis Wharf, Oyster, and Bayford; recreational sites were at Cape Charles and Cherrystone Point (Fig. 1). Fishermen were asked for the location of their catches. Collection sites were visited daily once the first landings were made. Additionally, in the fall of 1990 and 1992, we obtained juveniles ($n$=10) from special sampling of pound nets near the bay mouth.

Fish were sexed and measured for total length (TL), standard length (SL), total weight (TW), gonad weight (GW), girth at the preopercle (G1), and maximum girth (G2). Sagittal otoliths, dorsal spines, and fin rays were taken from each specimen. One otolith, chosen randomly from each pair, was transversely sectioned through the core on a Beuhler low-speed Isomet saw. Three sections of about 300-m thickness were mounted with Flo-texx mounting medium on a slide and read under a dissecting microscope (10×) with transmitted light and bright field. Dorsal spines and fin rays were processed similarly (10–40×) but sectioned perpendicular to the long axis of the growth plane, close to the base. To compare hard parts, we read random sections without knowledge of length or collection date of specimen.

Ages were assigned on the basis of counts of annuli. We call them presumptive annuli in this paper because we have not completed validation of ages 44–59. However, otolith annuli have been validated to age 43 in the Gulf of Mexico through marginal increment analysis (Beckman et al., 1990; Fitzhugh and Beckman[1]), and we have recently shown corre-

[1] Fitzhugh, G. R., and D. W. Beckman. 1987. Age, growth and reproductive biology of black drum in Louisiana waters. Coastal Fisheries Institute, Center for Wetland Resources, Louisiana State University, Final Report of Funded projects FY 1986–1987, 89 p.

spondences between bomb radiocarbon chronologies from the atmosphere and those from otolith cores of black drum (Campana and Jones, 1998). Average birth date was arbitrarily taken to be 1 January (Jearld, 1983). To assess ageing precision, all hard parts ($n$=30) were read twice by each of two readers, and agreement between and within readers was evaluated by percent agreement methods (Beamish and Fournier, 1981; Chang, 1982). Disagreements were resolved by a third reading.

To evaluate changes in otolith size in relation to fish total length and age, otoliths from 300 fish (1990 collections; ages 0–57; 22.9–130.0 cm TL) were measured for maximum length (otolith length [OL] ±0.01 mm), radius along the sulcal grove (otolith radius [OR] ±0.001 mm), maximum thickness (otolith width [OWID] ±0.01 mm), and weight (otolith weight [OWT] ±0.001 g). Relation between otolith measurements and fish TL and age were evaluated by simple linear regression analysis.

To evaluate growth, observed individual lengths-at-age were fitted to the von Bertalanffy growth function, VBGF (Ricker, 1975), by using nonlinear regression, SAS NLIN procedure DUD method (SAS, 1988). Likewise, individual weights-at-age were fitted to the VBGF. Model parameters were the following: $L_\infty$, the mean asymptotic length; $W_\infty$, the mean asymptotic weight; $K$ and $K'$, respectively; the Brody growth coefficient on length and weight; and $t_0$ and $t'_0$, the theoretical age at which the fish would have zero length on length and weight (Ricker, 1975). Growth curve parameters were compared between years and sexes with maximum likelihood ratio tests (Kimura, 1980).

Linear regression was used to determine length-weight relationships for fish ranging from 22.9 to 130.0 cm TL and 0.6 to 49.4 kg TW. Differences between sexes were tested with Rawlings' (1988) tests of homogeneity of slopes and intercepts by using PROC REG in SAS (Littell et al., 1991). The hypothesis of isometric growth (Ricker, 1975) was tested with a $t$-test.

Instantaneous total annual mortality rates, $Z$, were estimated from maximum age with Hoenig's pooled regression equation (Hoenig, 1983), by calculating a theoretical total mortality for the entire life span following the reasoning of Royce (1972), and with the regression method, i.e. with a catch curve combining $\log_e$-transformed recreational and commercial abundance data. In the latter method, mortality estimates were based on data from ages 21–43 and 21–59. Younger ages were truncated because the age group at the apex of the catch curve (age 20) may not have been fully recruited to the fishery (Everhart and Youngs, 1981). Older ages were truncated at the first age class (age 44) with fewer than five fish following Chapman and Robson (1960). Data from 1990 to 1992 were combined to minimize effects of variation in year-class strength (Robson and Chapman, 1961). The right limb of the catch curve was tested for deviation from linearity by analysis of variance (ANOVA). Estimates of $Z$ were converted to total annual mortality rates ($A$=1–$e^{-z}$; Ricker, 1975).

All statistical analyses were performed with SAS (SAS, 1988). Rejection of the null hypothesis was based on $\alpha = 0.05$, $F$-tests in ANCOVA were based on type-III sum of squares (Freund et al., 1986), and assumptions of linearity were checked with residual plots (Draper and Smith, 1981). Data were $\log_{10}$-transformed to correct for nonlinearity and heterogeneity of variance when necessary. Log-transformed data are presented in graphs and tables in original units, unless otherwise stated. Variables that could not be normalized were compared with Wilcoxon's two-sample test or a Kruskal-Wallis test for more than two samples, and large-sample approximate $z$-scores or $\chi^2$ were reported.

## Results

### Hard part comparisons

All hardparts showed regular, concentric marks that could be interpreted as annuli. However, marks were not equally clear or consistent between all hard parts. Otoliths were the clearest and most precise of the hard parts to interpret. One hundred percent of otoliths, 36.7% of dorsal spines, and 63.7% of fin rays had marks clear enough to read. Between-reader precision was 100% for otoliths, 27.3% for dorsal spines, and 47.4% for fin rays. Compared with otoliths, dorsal spines and fin rays underestimated age; this underestimation worsened with increasing age (Kruskal-Wallis distribution-free multiple comparison test, MSD=15.81, $P$<0.05). Underageing was especially marked with dorsal spines. On the basis of these results and otolith growth patterns (see next section), we deemed otoliths the clearest, most reliable hard part, and used them for all ageing.

### Otolith size relationships to fish size and age

Black drum otoliths continue to increase in size with fish length and age, apparently throughout life. All measures of otolith size—OL, OWT, OR, OWID—were significantly and positively related to fish length and age. Although black drum otoliths continue to increase in size, the relations of various otolith sizes to fish length and age were not consistent. Relations

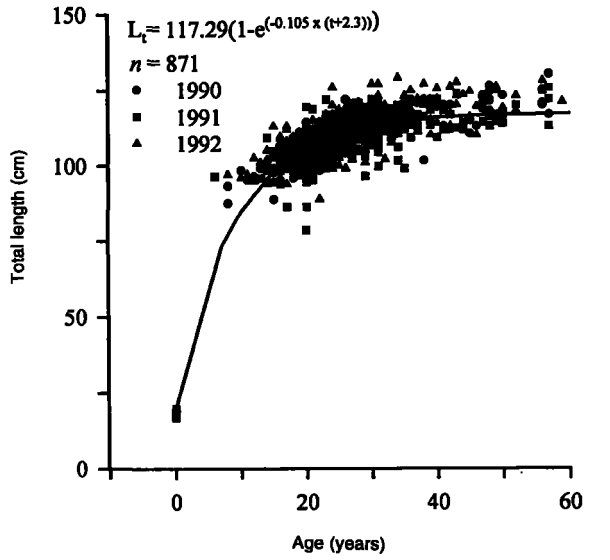


**Figure 2**

Observed lengths-at-age and fitted von Bertalanffy regression lines for black drum from the Chesapeake Bay region, 1990–92.

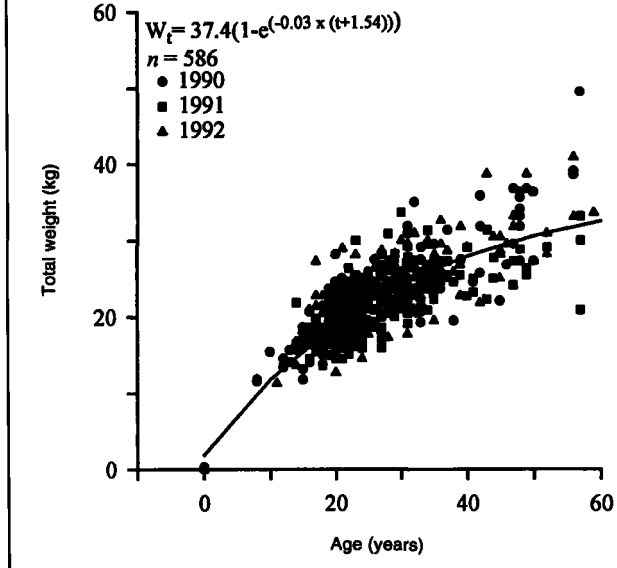


**Figure 3**

Observed weights-at-age and fitted von Bertalanffy regression line for black drum from the Chesapeake Bay region, 1990–92.

between fish total length and otolith maximum length ($OL$=2.69 + 0.20$TL$), and otolith maximum width ($OWID$=2.69 + 0.14$TL$), were isometric, reasonably linear, and therefore were useful for back-calculation of fish lengths. Other relations between total length and all relations on age were exponential functions ($OWT$=1.72 × $10^{-5}$ $TL^{2.66}$; $OR$=6.02 × $10^{-3}TL^{1.46}$; $OL$=10.78 $Age^{0.256}$; $OWID$=8.71 $Age^{0.231}$; $OWT$=0.231 $Age^{0.025}$; $OR$=0.964 $Age^{0.541}$ ).

Annuli on black drum otoliths continue to be deposited with increasing fish size. Annuli counts were significantly and positively related to fish length (Fig. 2) and weight (Fig. 3). Fitted regression lines and data plots indicate counts continue to increase most clearly with weight. However, they also increase with length even though there is a leveling off at greater numbers of annuli. Although usually used merely to describe growth patterns, Figures 2 and 3 provide evidence—usually not stated—that otolith age is valid.

## Age and size compositions

The Chesapeake Bay fishery generally captures old black drum. Mean age was 26 years (Fig. 4). Ages ranged from 6 to 59 years in the regularly sampled catch, but several juveniles were obtained from sampling pound nets. Median age in the catch was consistent from year to year (1990=25.0, 1991=23.0, 1992=24.0; Kruskal-Wallis $\chi^2$=4.53, $P$>0.05) and between sexes ( ♂ = ♀ =24.0; Wilcoxon $z$=1.01, $P$>0.05). Age at the 95$^{th}$ percentile was 48 years, indicating that many older fish were landed. The youngest fish

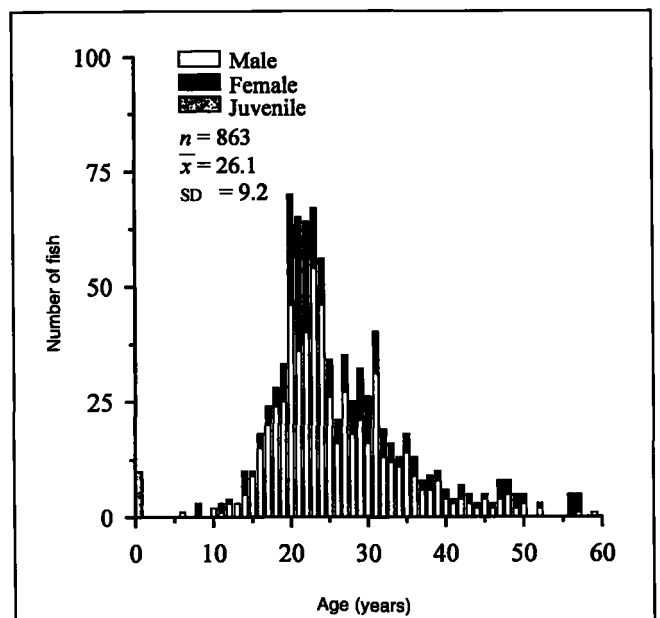


**Figure 4**

Overall age distribution of black drum in the Chesapeake Bay fishery, 1990–92. Juveniles were taken in the fall of 1990 and 1992 in special sampling of the pound nets.

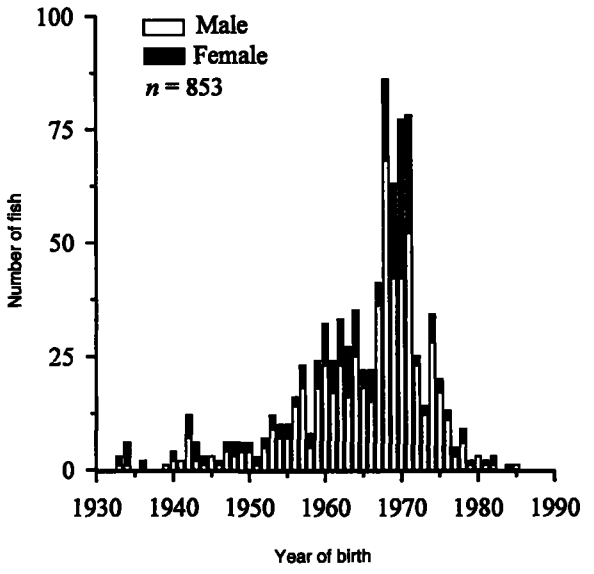


**Figure 5**

Year class distribution of black drum in the Chesapeake Bay fishery, 1990–92; juveniles excluded.

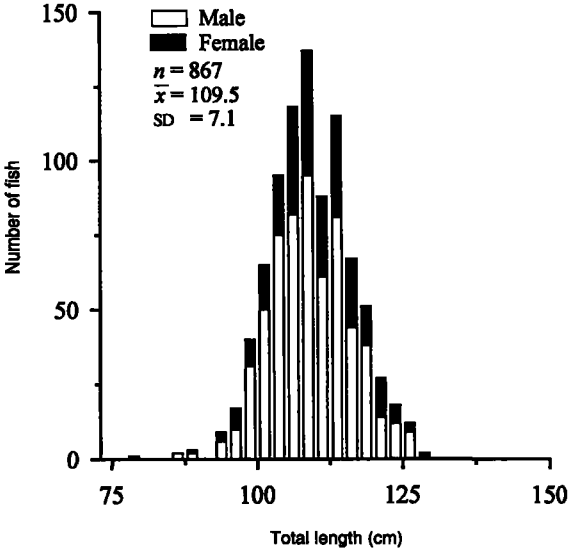


**Figure 6**

Distribution of total lengths of black drum in the Chesapeake Bay fishery, 1990–92.

caught, apart from young-of-the-year, was age 6, and age at the 5th percentile was 16 years. No fish between 1 and 5 years were found. Recruitment to the gear appears to be complete by age 20 or 21.

Black drum recruitment in Chesapeake Bay is characterized by occasional, dominant year classes (Fig. 5). Exceptionally large year classes occurred in 1934 and 1942, demonstrated in an abundance that fell above the 95% confidence band of expected year class strength around the catch curve. Abundant, but not exceptional, year classes occurred in 1933, 1943, and 1968. Poor year classes, those that fell below the lower 95% confidence interval, occurred in 1939, 1946, 1951, and 1958. We lack information on recruitment after 1972 because black drum are not fully recruited to the bay fishery until age 21.

Total length of adult black drum in Chesapeake Bay averaged 109.5 cm, ranging from 78.7 to 130.2 cm (Fig. 6). Median length (cm) in the catch was not significantly different from year to year (1990=109.2, 1991=108.0, 1992=110.5; Kruskal-Wallis $\chi^2$=4.52, $P$>0.05), although females were slightly longer than males (♂=109.2, ♀=109.5, Wilcoxon $z$=2.06, $P$<0.05). Length at the 95th percentile was 121.9 cm, indicating that many large fish were landed.

Mean total weight of adult black drum in Chesapeake Bay differed slightly between sexes and among years. Total weight of adults averaged 22.1 kg over the period 1990–92 and ranged from 11.3 to 49.4 kg

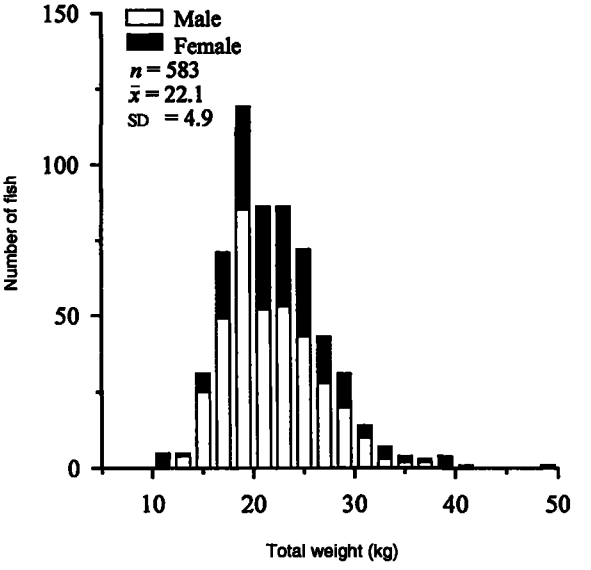


***Figure 7***

Distribution of total weights of black drum in the Chesapeake Bay fishery, 1990–92.

(Fig. 7). Females were slightly heavier (ANOVA, $F$=8.23, $P$<0.05), probably due to their reproductive product. The difference between sexes, 1.1 kg, amounts to only 5% of average total weight. Fish in

1990 (23.0 kg) were slightly heavier (ANOVA, $F$=4.67, $P$<0.05) than those landed in 1991 (21.4) and 1992 (22.3 kg). Again, the difference among years is only 7% of average total weight.

## Comparisons between areas and gears

Black drum collected in Chesapeake Bay and coastal waters did not differ in simple biological attributes. Catches from the two areas showed no significant differences in age (bay=25.8 yr, coastal=26.8 yr, $Z$=–1.21, $P$>0.05), total weight (bay=21.7 kg, coastal=22.4 kg, $Z$=–1.32, $P$>0.05), or total length (bay=109.5 cm, coastal=109.5 cm, $Z$=0.09, $P$>0.05). Hence, data from both areas were pooled in all other analyses.

Recreational and commercial catches showed statistically significant differences in total length ($Z$=2.13, $P$<0.05), but not in total weight (commercial=22.1 kg, recreational=22.2 kg, $Z$=0.76, $P$>0.05), or age (commercial=26.3 yr, recreational=26.9 yr, $Z$=1.60, $P$>0.05). Mean TL of the commercial catch was 109.0 cm ($n$=698, SE=8.7 cm), and recreational mean TL was 110.4 cm ($n$=166, SE=8.6 cm). Mean, median, ranges, and quantile measures of TL are almost identical for these two fisheries. Although the differences in TL are statistically significant because of large sample size, they are not biologically meaningful. Hence, data from these fisheries were pooled to analyze growth and mortality.

## Growth

Observed lengths varied greatly within age (Fig. 2). Growth was rapid before 15 years of age but slowed by age 20. Lengths thereafter varied asymptotically about the mean. Black drum have achieved 58% of $L_\infty$, by age 6, when fish are first caught in the bay, and have achieved 90% by age 20, after which they are fully recruited to the gears. Apparently growth was very rapid in the first 5 years, ages absent from our collections. The VBGF equation for data pooled over the period 1990–92 is

$$L_t = 117.3\left(1-e^{-0.105(t+2.3)}\right).$$

No differences were found in growth curve parameters in length between the sexes ($P$>0.05) or years ($P$>0.05 ). We observed large numbers of fish at older age, permitting a good estimate for $L_\infty$ ($n$=871; includes juveniles, $r^2$=0.998). However, because we observed no fish between 1 and 5 years, our estimate of $K$ is not optimum. Parameters estimated and asymptotic standard errors are given in Table 1.

Observed weights of Chesapeake Bay black drum varied greatly within age (Fig. 3). As with age-length data, growth was rapid for the first 6 years. Although it slowed thereafter, fish still grew appreciably in weight until growth slowed substantially at 45 yr. Black drum have reached 22% of $W_\infty$ by age 6 when they first appear in the bay as adults, 51% of $W_\infty$ by age 20, and 78% by age 45. Hence, they grew more slowly in weight than in length. The VBGF equation for data pooled over the period 1990–92 is

$$W_t = 37.4\left(1-e^{-0.03(t+1.5)}\right).$$

We observed large numbers of older fish, permitting a good estimate for $W_\infty$ ($n$= 586, $r^2$=0.977). However, because we observed no fish between ages 1 and 5, our estimate of $K'$ is not optimum. Parameters estimated, asymptotic standard errors, and 95% confidence intervals are given in Table 1.

No differences were found in weight-growth curve parameters between the sexes ($P$>0.05). However, pairwise comparisons showed parameters differed between the years 1990 and 1991 (1990: $W_\infty$=57.2 kg, $K'$=0.018/yr, $t'_0$=–2.24 yr; 1991: $W_\infty$=29.8 kg, $K'$=0.052/yr, $t'_0$=0.06 yr, likelihood ratio test: $\chi^2$= 10.54, $P$< 0.05). Fish captured in 1991 weighed less at older ages than in 1990 and 1992. We have no explanation for this; causes could be minor, i.e. sampling error, a slightly greater proportion of older fish that had completed spawning in 1992, or perhaps fish that were in worse condition in 1991.

A pooled length-weight regression was developed (Fig. 8) with the equation

$$TW = 1.01 \times 10^{-2}\, TL^{3.11} \qquad (r^2=0.97;\ n=599;\ P<0.01).$$

The slope of the regression line ($b$=3.11; SE=0.03) was significantly different from 3.00 ($t$-test; $t$=3.75; $P$<0.05), indicating allometric growth.

**Table 1**

Summary of parameter estimates for the von Bertalanffy growth equation on total length (cm) and total weight (kg) of Chesapeake Bay region black drum, *Pogonias cromis* (199092).

| | | | 95% confidence intervals | |
|---|---|---|---|---|
| Parameter | Estimate | SE | Lower | Upper |
| $L_\infty$ | 117.3 | 0.4 | 116.5 | 118.1 |
| $K$ | 0.105 | 0.003 | 0.099 | 0.111 |
| $t_0$ | –2.3 | 0.2 | –2.7 | –1.9 |
| $W_\infty$ | 37.4 | 1.7 | 34.0 | 40.8 |
| $K'$ | 0.033 | 0.003 | 0.027 | 0.039 |
| $t'_0$ | –1.5 | 0.9 | –3.3 | 0.3 |

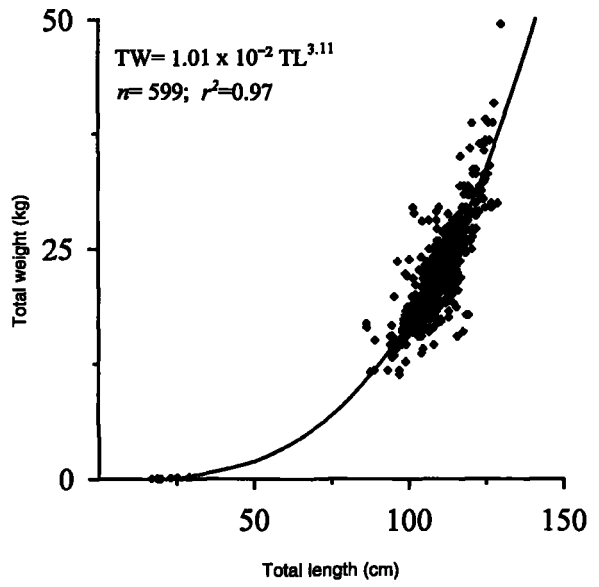


**Figure 8**

Pooled length-weight relationship of black drum in the Chesapeake Bay region, 1990–92.

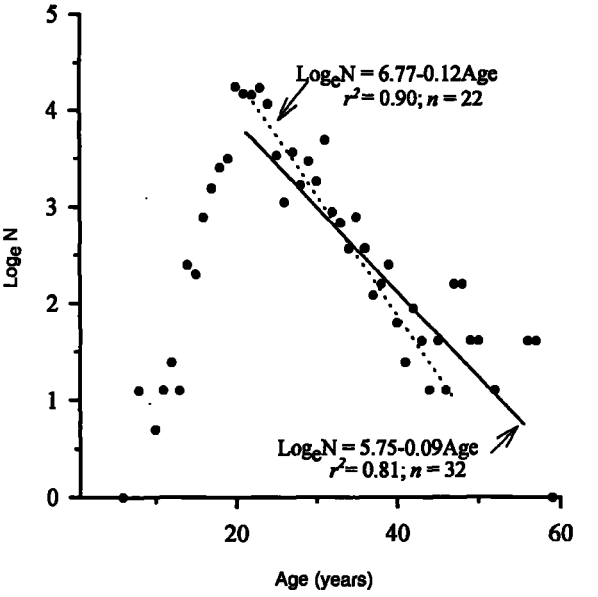


**Figure 9**

Catch curve for black drum in the Chesapeake Bay region, 1990–92. Fish are not fully recruited to the gears until age 21. Estimates of $Z$ was obtained from fish ages 21–59 (—) and fish ages 21–43 (---).

### Mortality

Mean instantaneous total mortality rates, $Z$, ranged from 0.08 to 0.13. Estimates obtained from a maximum observed age of 59 years, and for age truncated at the 95$^{th}$ percentile—48 years, were 0.08 ($A$=8%) and 0.09 ($A$=10%) with Hoenig's (1983) method, and 0.08 ($A$=8%) and 0.10 ($A$=10%) with Royce's (1972) method. A regression estimate obtained from the slope of a catch curve truncated at older ages (Fig. 9) was 0.12 ($A$=13%) with 95% confidence intervals of 0.11 ($A$=12%) and 0.13 ($A$= 14%). This regression line did not deviate significantly from linearity (ANOVA; $F$=1.18; $P$> 0.05). A regression estimate obtained from the slope of the full catch curve, i.e. with all older cohorts even when $n$<5, was 0.09 ($A$=9%) with 95% confidence intervals of 0.08 ($A$=8%) and 0.09 ($A$= 10%). This regression line, too, did not deviate significantly from linearity (ANOVA; $F$=1.29; $P$> 0.05).

## Discussion

### Age determination methods

We believe otoliths are the preferred, most reliable hard part to use for ageing black drum. Reasons for this include high precision and readability of otoliths, their continued growth with increase in fish size and age, the increase in the number of annuli with size, and validation over most of the life span. Otolith annuli are extremely clear and easy to read, even out to 59 annuli, and agreement between readings was absolute, 100%. In contrast, fin rays and spines often produced unreadable sections, and fewer bands were counted than on otoliths, especially at older ages.

We have not yet been able to validate black drum otolith ages completely in the Chesapeake Bay region with marginal increments or other analyses. However, evidence from other regions indicate that black drum otoliths are valid throughout much of their life. For example, Fitzhugh and Beckman,[1] and Beckman et al. (1990) used marginal increment analysis to validate otolith annuli formation in black drum to age 43 from Louisiana. However, because most of their fish were age 5 to 27, they had to group the few fish at older ages. Our putative ages extend an additional 15 years beyond the range these authors described. Other evidence indicates members of the family (Sciaenidae) consistently produce annuli throughout life. Beckman et al. (1989) used marginal increment analysis to confirm annulus formation to age 37 in red drum, *Sciaenops ocellatus*. Ross et al. (1995) confirmed annuli formation in two red drum aged 38 and 40 through oxytetracycline marking of otoliths. Although we have not yet fully

validated ages from 44 to 59 years, we have found (see above) that black drum otoliths satisfy the criteria of Van Oosten (1929) for annuli: the number of rings increased with mean size, rings were consistently located on otoliths of different putative ages, and otolith radii correlated highly with putative age.

Although we did not evaluate scales because of their problematic use in ageing, we believe there is direct evidence that they underestimate black drum age in the Chesapeake Bay region. Beamish and McFarlane (1983) documented the tendency of scales to underestimate age, especially at older ages. Richards (1973) and Desfosse (1987) estimated maximum ages for Chesapeake Bay region black drum of only 35 and 10 yr, respectively, using scales. Considering that size composition has not changed over the intervening years (Desfosse, 1987; Hutchinson and Rogers[2]), these ages are much younger than we observed. Richards should have seen maximum ages of at least 41, Desfosse at least 57. We therefore argue against using scales for ageing black drum.

## Implications of age structure

Although we had only three years of data, the long lives of black drum allowed our collections to represent a history of recruitment of over 50 years—as was the case with Pereira et al. (1995) for freshwater drum, *Aplodinotus grunniens*. Our data show that recruitment of black drum from the Chesapeake Bay region generally appears to be low, with only occasional strong year classes that persist for many years, for example the 1934 and 1942 cohorts. Moreover, low average recruitment is anticipated for a species with a long reproductive lifespan (20 years at the age of capture), high batch fecundity (1–14 million eggs), and several batches in a spawning season (Wells, 1994), especially when the population remains at low abundance throughout the years.

Our recruitment history of black drum also showed an absence of fish ages 1 to 5, which is consistent since at least the 1960s. There are several possible causes: 1) low abundance of black drum young that is hard to measure, 2) recent complete recruitment failure, 3) gear specificity, and 4) migration southward during this life stage and later northward migration. We review the evidence in support of these alternatives briefly.

Given its demography, this stock should have a low survival rate during the early life stages that is difficult to distinguish from zero. Black drum's potential lifetime production of 60–840 million eggs requires mortalities of at least $10^6$ or $10^7$ during larval and juvenile stages to maintain stable populations. Hence, the high mortality seen in the field (Cowan et al., 1992) is predictable and is difficult, if not impossible, to differentiate from 100% in the field during early life.

The absence of several year classes in the catch of a fishery could also signify complete recruitment failure. Yet indirect evidence does not support this throughout the east coast range. Frisbie (1961) noted the virtual absence of young black drum in the bay and Richards (1973) stated that "black drum of more than 220 to less than 800 mm in length were not readily available . . .". These observations correspond to cohorts from the late 1950s and 1960s which, seen retrospectively in modern catches, showed normal recruitment levels. Even though fish of the expected size of 1–5 year-olds are not typically seen in the bay, these young fish are not missing from the entire geographic range. Fish ages of 1–4 years are found in bycatch from northeast Florida (Murphy and Taylor, 1989). Hence, examination of the catch argues against complete recruitment failure throughout the stock's range.

Fishing gear and practices used for black drum in Chesapeake Bay target large fish and may exclude small fish. The commercial fishery uses anchored and drifted gill nets with 33-cm stretch mesh, which allow smaller fish to escape. Likewise, recreational anglers use hooks that target large fish. Hence, we can explain some of the absence of smaller fish by gear selectivity in the directed fishery. However, if these fish were present in the bay, we would expect to see them in other fisheries, but fishermen have told us that they have never seen these fish in their gear—gear such as pound nets and gill nets of 7.6–15.2 cm (3–6 inch) stretch mesh that would retain these smaller sizes.

Perhaps the strongest alternative explanation for missing 1–5 year-olds lies in the migratory patterns seen in many sciaenids. Specifically, black drum undergo long-range migration along the coasts of the southeast states. Although black drum have been noted as far north as Canada (Welsh and Breder, 1923; Silverman, 1979), they occur more commonly from Delaware south to Florida. Even in the Chesapeake Bay, however, black drum are not resident year round. Frisbie (1961) suggested a southward migration of young fish from Chesapeake Bay in the fall, and the same pattern of fall emigration of juveniles has been shown for Delaware Bay (Thomas and Smith, 1973). Thereafter, only larger and older fish migrate into the bay in the spring—with few younger than six years. In contrast with the Chesapeake Bay pattern, Murphy and Taylor (1989) found that only 20% of their sample from Florida included fish older than age four. Our adult catch data could be ex-

[2] Hutchinson R., and C. Rogers. 1969. Salt water fishing in Virginia. Dep. Conserv. and Econ. Devel., Richmond, VA, 41 p.

plained by the differential seasonal migration northward of older, larger fish from a population centered farther south, as was first postulated by Welsh and Breder (1923). Finally, two fish tagged in northeast Florida were captured about four months later at the mouth of Chesapeake Bay; thus long-range migrations do occur (Murphy[3]).

In summary, migration and gear selectivity are likely explanations of the age structure of the Chesapeake Bay fishery and the apparent absence of age 1–5 fish in this region. However, given our data, we cannot rule out local recruitment failure. Movement and exchange is supported by similar sizes-at-age in fish from Florida and Chesapeake Bay (Table 2): mean maximum length is 117.2 cm TL for Florida, 117.3 cm TL for Virginia; maximum ages along the east coast are 58 for Florida (Murphy and Taylor, 1989), 46 for Georgia (Music and Pafford, 1984), and 59 for Virginia (this study).

## Stock unity

Several lines of evidence suggest that black drum on the U.S. east coast are from a common stock. Fish throughout the area appear to have similar growth. Von Bertalanffy growth function parameters that we estimated for the Chesapeake Bay region ($L_\infty$=117.3 cm; $K$=0.105/yr; $t_0$=-2.3 yr) were similar to those that Murphy and Taylor (1989) found in northeast Florida ($L_\infty$=117.2 cm; $K$=0.124/yr; $t_0$=–1.29 yr). In contrast, black drum from the Gulf of Mexico grow more quickly, are smaller at age, and have a smaller maximum size (Table 2). Mitochondrial DNA evidence also suggests a common stock in the western North Atlantic Ocean. No significant differences in frequency of mtDNA haplotypes were found in fish taken from Virginia and the east coast of Florida (Gold[4]). However, Atlantic east coast fish differed from those sampled in the northern Gulf of Mexico (Gold et al., 1995). Finally, limited tagging data directly suggest black drum move between Chesapeake Bay and Florida (as noted previously).

## Implications of mortality estimates

The long life we found in black drum indicates a low mortality rate for larger fish and a stock that cannot support heavy fishing pressure. Our greatest estimate of instantaneous total mortality, $Z$, converts to an annual total mortality ($A$) of less than 13%. As $Z = F + M$, natural mortality must also be less than 13%. Because black drum do not completely recruit to the fishery until age 21 in the Chesapeake Bay region, our estimates of total mortality apply to the period of 21 years ago and earlier. For our estimates to be valid today, fishing mortality on young fish must still be low throughout the stock's range. Values of $Z$ have important implications for management. Stocks with high $M$ generally can withstand the highest fishing mortality because fishing simply takes fish that would otherwise die from natural causes. In contrast, stocks with low $M$ (like black drum) do not have a potential for such "excess" natural mortality that can be diverted into fishing mortality (Gulland, 1983; Murphy and Taylor, 1989).

## Life history strategy

Black drum have an unusual life history for a long-lived fish. They achieve a large size quickly—84% of

[3] Murphy, M. D. 1995. Florida Marine Research Institute, Department of Environmental Protection, 100 Eighth Ave. S.E., St. Petersburg, FL 33701. Personal commun.

[4] Gold, J. R. 1995. Center for Biosystematics and Biodiversity, Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843. Personal commun.

**Table 2**

Estimates of von Bertalanffy growth function parameters from various studies of black drum. Standard errors in parentheses (when available).

| Area and study | Growth parameters | | | Sample size | Total length range (cm) |
|---|---|---|---|---|---|
| | $L_\infty$ (cm) | $K$ | $t_0$ | | |
| Atlantic coast | | | | | |
| Murphy and Taylor (1989) | 117.2 (0.9) | 0.124 (0.003) | –1.29 (0.08) | 397 | 20.2–127.5 |
| Northeast Florida | | | | | |
| Present study | 117.3 (0.4) | 0.105 (0.003) | –2.3 (0.2) | 871 | 22.9–130.2 |
| Gulf of Mexico | | | | | |
| Doerzbacher et al. (1988), Texas | 79.8 (4.2) | 0.219 (0.027) | — | 383 | 20.3–99.1 |
| Beckman et al. (1990), Louisiana | 110.0 | 0.038 | –16.42 | 1072 | — |

their total potential growth is accomplished in only 20% of their life span. Moreover, they become sexually mature at age 5–6 years (Murphy and Taylor, 1989) and appear reproductively active over a potential lifespan of some 60 years. Life history theory indicates that species that have an early age at first reproduction and fast growth tend to be short lived (Begon et al., 1990; Charnov, 1993). Typically, long-lived fishes grow slowly and mature late, like sturgeons (Jenkins and Burkhead, 1993) and redfishes, *Sebastes* (Scott and Scott, 1988; Beverton, 1992). Black drum are as long-lived as these fishes but have faster early growth and a relatively early age of first reproduction. This strategy may give black drum a capacity to maintain population stability greater than that seen in similarly long-lived fishes in the presence of heavy fishing.

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# Stock structure and movement of tagged sablefish, *Anoplopoma fimbria*, in offshore northeast Pacific waters and the effects of El Niño-Southern Oscillation on migration and growth

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**Abstract.**—Sablefish in the northeast Pacific are found in commercial quantities from the Bering Sea, the Aleutian Islands, throughout the Gulf of Alaska, and south along the west coast of Canada and the U.S. to Baja California. Tag-recovery data support a two-population hypothesis throughout the North American range: an Alaska population ranging from the Bering Sea, including the Aleutian Islands and extending down through the Gulf of Alaska to northwest Vancouver Island, Canada; and a west coast population extending from southwest Vancouver Island to Baja California. Tag recoveries indicate that these two populations mix off southwest Vancouver Island and northwest Washington, and to a lesser extent off southern Washington and Oregon.

Alaska sablefish, which commonly migrate over 500 n mi, are more mobile than west coast sablefish. Tag recoveries for sablefish tagged in Alaska have shown strong mutual exchanges between nearly all areas. In contrast, west coast sablefish have shown far less migratory behavior. Tagging data with respect to bathymetry are difficult to interpret in both regions owing to the fact that tagging and recovery effort do not cover the full bathymetric range of adults.

Results of analysis of tag-recapture growth data were consistent with patterns observed for several other pelagic and demersal species. That is, El Niño-Southern Ocean Oscillation events appeared to retard the growth of sablefish along the west coast and to enhance growth of Alaska sablefish. The timing of recoveries from sablefish tagged off Alaska and recovered off southwest Vancouver Island and Washington–Oregon suggests that movement south correlates positively with strong upwelling in this southern area. Although sablefish trap-index surveys show a north to south cline in the percentage of large sablefish (>60 cm, and possibly of Alaska origin) sampled in length frequencies along the west coast, we were unable to correlate annual fluctuations in these percentages with upwelling strength.

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Adult sablefish have a proclivity for great depths (200–1500 m) where the ocean environment is relatively constant over extensive geographic distances and consequently can be found from central Baja California along the Pacific coast through the Gulf of Alaska and Aleutian Islands, along the Bering Sea slope to the Russian coast, and down the Kamchatka Peninsula all the way to southern Japan (OCSEAP, 1986; Allen and Smith, 1988).

The marked absence of sablefish eggs and larvae from the Bering Sea above 55°N is usually attributed to an intolerance to low (<2°C) temperatures (OCSEAP, 1986). Sablefish occurrence in the Bering Sea and Aleutian Islands is thought to be dependent on egg and larval drift from the northeast Pacific, principally through westward transport from the Gulf of Alaska by the Alaskan Stream (OCSEAP, 1986). Although sablefish occur along the coast of Asia, only adult fish (>2 yr) are found (Kodolov, 1968) and they are believed to have been recruited from the northeast Pacific stock. Ocean currents from the western Bering Sea favor dispersal of sablefish along the Asian coast by means of the East Kamchatka and Oyashio Currents.

Commercial catches of sablefish appear to be absent off Japan (Chikuni, 1985). We do not know if commercial catches of sablefish occur off Russia, although Kodolov (1968) describes the adult distribution of sablefish as extending from the Bering Sea all along the Kamchatka Peninsula. In contrast, sablefish is an important commercial species throughout the northeast Pacific with average annual landings (1984–93) of 2150 t for the eastern Bering Sea, 2405 t for the Aleutian Islands, 22,590 t for the Gulf of Alaska, 4835 t for British Columbia, Canada, and 11,129 t for the U.S. West Coast.[1]

Sablefish fecundity is determinate and eggs are spawned in three or four batches (Hunter et al., 1989; Macewicz and Hunter, 1994); eggs are semipelagic (McFarlane and Beamish, 1992) and have been found at depths ranging from 200 to 800 m (Thompson, 1941; Kodolov, 1968; Moser et al. 1994). Age-0 (yr) larvae initially inhabit offshore surface waters (McFarlane and Beamish, 1992), move inshore during the

[1] Aleutian Islands and eastern Bering Sea catches (Lowe, 1995), Gulf of Alaska catches (Fujioka, 1995), Canadian west coast catches (Saunders et al., 1995), U.S. west coast catches (Methot et al., 1994).

summer of their first year (still 0-yr-old) (Rutecki and Varosi, 1997a), and usually become demersal in outer coastal waters during their second year of life at age 1 yr (Rutecki and Varosi, 1997a, 1997b). From there, it is believed that they undergo a protracted ontogenetic migration to greater depths (Saunders et al., 1997).

Adult sablefish recruit to offshore demersal fisheries at about age 3–4 yr (Sasaki, 1985; McFarlane and Saunders, 1997). Routine trawl, longline, and trap surveys by the National Marine Fisheries Service principally cover depths from 200 to 1000 m (Parks and Shaw, 1988; Lauth et al., 1998). These surveys in Alaska, and along the west coast typically indicate sablefish are abundant at the maximum depths fished. Spawning off California occurs at depths beyond 800 m (Hunter et al., 1989). In Monterey Bay, Parrish[2] measured dissolved oxygen and noted that peak longline catches occurred in the oxygen-minimum zone at around 730 m. A special longline survey targeting deeper waters (Wilkins[3]) and deep trap sets (Parks and Shaw, 1988) has shown that sablefish along the west coast occur to depths of up to ~1500 m. Beamish et al. (1979) reported exploratory catches of sablefish to depths of 2740 m. Pearcy et al. (1982) noted the occurrence of sablefish in the Astoria and Cascadia abyssal plains down to a depth of 2560 m. Deepwater trawl and photographic work by Wakefield (1990) showed that sablefish occur as far down as ~1500 m but appear to become scarce beyond this depth. Former naval dumping sites off San Francisco, at depths from 2000 to 3200 m, showed an absence of sablefish (Cailliet et al.[4]). A reasonable interpretation might be that although sablefish can occur at depths beyond 1500 m, sablefish abundance can be expected to decline considerably beyond this depth.

Because of the many interesting questions raised by their broad geographic and bathymetric distributions, sablefish have become one of the most tagged demersal fish species in the northeast Pacific. On the basis of tagging studies, authors have emphasized both the resident nature of some sablefish (Wespestad, 1983; Beamish and McFarlane, 1983, 1988; Maloney and Heifetz, 1997) and the proclivity of other sablefish to be highly migratory (Bracken, 1983; Dark, 1983; Heifetz and Fujioka, 1991; McFarlane and Saunders, 1997). Generally fish tagged inshore, off the west coast of Vancouver Island, or off the U.S. west coast were more likely to be characterized as resident and nonmigratory.

In this paper we examine several hypotheses concerning the movement of sablefish, using recapture data gathered from offshore tagging of sablefish from throughout the northeast Pacific Ocean. The first hypothesis is that sablefish off Alaska and Canada, i.e. north of 50°N latitude, are a separate population from the sablefish south of 50°N latitude found along southern Canada and the U.S. west coast. The second hypothesis is that Alaska sablefish tend to migrate much farther than west coast sablefish. Another question is whether sablefish migrate to greater depths as they become older. Such hypotheses are of practical importance because they can affect the way resource assessment survey results are interpreted.

A study in which growth curves were estimated from a sablefish tag data set has been completed (Kimura et al., 1993). In that study differences in the growth curves of Alaska and west coast populations were reported. In this paper, we examine the effects of El Niño-Southern Oscillation (ENSO) events on the growth of sablefish in the northeast Pacific Ocean.

Finally, we examine the migration of fish tagged in Alaska to areas along the west coast. Upwelling along the west coast (42–48°N latitude) appears to be positively correlated with these migrations, and possible explanations are given for why a correlation exists.

## Materials and methods

In this paper we analyze tag recoveries of the sablefish tagging program conducted by the National Marine Fisheries Service (NMFS). Tagging occurred during surveys designed to measure relative abundance of sablefish throughout its range in offshore U.S. waters. From 1971 to 1993, approximately 218,255 fish were captured with trawl, trap, and longline gears and later released after having been tagged with anchor tags (Table 1). With the exception of Canadian waters, sablefish were tagged from southern California to the Bering Sea. Analyses of sablefish tagged in Canadian waters have been previously reported (e.g. Beamish et al. 1979; Beamish and McFarlane, 1983, 1988; McFarlane and Saunders, 1997).

[2] Parrish, R. H. 1975. The relationships of oxygen concentration and depth of capture with size and abundance of sablefish (*Anoplopoma fimbria*) in Monterey Bay, California. Current address: Pacific Fisheries Environmental Lab., 1352 Lighthouse Ave., Pacific Grove, CA 93940. Unpubl. manuscript.

[3] Wilkins, M. E. 1997. RACE Division, Alaska Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA 98115. Personal commun.

[4] Cailliet, G. M., W. W. Wakefield, G. Moreno, and K. Rhodes. 1992. The deep-sea fauna from the proposed navy ocean disposal site, using trap, otter and beam trawl, and camera sled samples. Navy CLEAN Contract No. N62474-88-D-5086, prepared for PRC Environmental Management, San Francisco, CA, and Honolulu, HI, 69 p.

From 1971 to 1976, sablefish were tagged and released through a cooperative program involving the NMFS, California Department of Fish and Game, Oregon Department of Fish and Wildlife, and research vessels from Russia and the Republic of Korea. Trawls, traps, and longlines were the predominate gears used to capture sablefish, accounting for approximately 99% of the tag releases.

In Alaska from 1978 to 1993, the U.S.-Japan Cooperative Longline Survey was the primary source of sablefish tag releases; a few releases were made from NMFS trap and trawl surveys. Along the U.S. west coast from 1979 to 1993, most tagged sablefish were released through NMFS sablefish trap index surveys and the remaining fish were released during NMFS trawl surveys.

Tagging from 1971 to 1976 was carried out mainly on the west coast and in southeastern Alaska (Tables 2 and 3). In 1978, tagging operations expanded into the Gulf of Alaska; in 1979, into waters off the Aleutian Islands; and by 1982, into the eastern Bering Sea. Tag releases from 1982 onward has been fairly consistent in all areas.

## Tagging

All sablefish were tagged with anchor tags (Floy FD-68). The vinyl tubing (yellow, orange, or blue) on each tag was 60 mm long, 2 mm in diameter, and bore a unique number and a legend of where to return the tag.

Captured sablefish were routinely put into "live" tanks supplied with fresh running sea water immediately after the catch was brought on board. Anesthetics were not used. Usually within 15 minutes of completion of each haul, sablefish were dipped from

**Table 1**

Releases and recoveries by gear and region of release. Also shown are the proportion of recoveries for each combination of gear and region of release. Bottom table shows tag recoveries by gear and region of recovery. Tag types were all anchor tags.

| Gear of release | Alaska | West coast | Total |
|---|---|---|---|
| Tag releases by gear and region of release | | | |
| Trawl | 10,920 | 28,899 | 39,819 |
| Trap | 7248 | 30,722 | 37,970 |
| Longline | 136,077 | 0 | 136,077 |
| Unknown | 4206 | 183 | 4389 |
| Total | 158,451 | 59,804 | 218,255 |
| Tag recoveries by gear and region of release | | | |
| Trawl | 717 | 1320 | 2037 |
| Trap | 977 | 3717 | 4694 |
| Longline | 7987 | 0 | 7987 |
| Unknown | 166 | 19 | 185 |
| Total | 9847 | 5056 | 14,903 |
| Recovery proportions by gear and region of release | | | |
| Trawl | 0.0657 | 0.0457 | 0.0512 |
| Trap | 0.1348 | 0.1210 | 0.1236 |
| Longline | 0.0587 | — | 0.0587 |
| Unknown | 0.0395 | 0.1038 | 0.0422 |
| Total | 0.0621 | 0.0845 | 0.0683 |
| Tag recoveries by gear and region of recovery | | | |
| Trawl | 552 | 1863 | 2415 |
| Trap | 1331 | 1856 | 3187 |
| Longline | 6342 | 826 | 7168 |
| Unknown | 1209 | 603 | 1812 |
| Total | 9434 | 5148 | 14,582 |

**Table 2**

We divided the northeast Pacific into 27 areas based on the criteria described below (Fig. 1). The historic regions: eastern Bering Sea (EBS), Aleutian Islands (AI), Gulf of Alaska (GOA), and west coast (WC) essentially maintain their integrity. Nominally, Alaska includes EBS, AI, and the GOA; whereas the west coast includes only WC. Areas are defined in decimal degrees of longitude and latitude.

| Area number and region | Area definition | |
|---|---|---|
| | Longitude | Latitude |
| 1. EBS | 170°E–175°E | Above 55°N |
| 2. EBS | 175°E–180°E | Above 55°N |
| 3. EBS | 175°W–180°W | Above 55°N |
| 4. EBS | 170°W–175°W | Above 55°N |
| 5. EBS | 165°W–170°W | Above AK Pen. |
| 6. EBS | 160°W–165°W | Above AK Pen. |
| 7. AI | 170°E–175°E | 50–55°N |
| 8. AI | 175°E–180°E | 50–55°N |
| 9. AI | 175°W–180°W | 50–55°N |
| 10. AI | 170°W–175°W | 50–55°N |
| 11. GOA | 165°W–170°W | Below AK Pen. |
| 12. GOA | 160°W–165°W | Below AK Pen. |
| 13. GOA | 155°W–160°W | Below AK Pen. |
| 14. GOA | 150°W–155°W | Below AK Pen. |
| 15. GOA | 145°W–150°W | |
| 16. GOA | 140°W–145°W | |
| 17. GOA | 135°W–140°W | |
| 18. GOA | | 52.5°N –60°N |
| 19. GOA | | 50°N–52.5°N |
| 20. WC | | 47.5°N–50°N |
| 21. WC | | 45°N–47.5°N |
| 22. WC | | 42.5°N–45°N |
| 23. WC | | 40°N–42.5°N |
| 24. WC | | 37.5°N–40°N |
| 25. WC | | 35°N–37.5°N |
| 26. WC | | 32.5°N–35°N |
| 27. WC | | 30°N–32.5°N |

**Table 3**

Tag releases tabulated by the area of release (rows) and year of release (columns). Areas are described in Table 2 and Fig. 1.

| Area of release | 1971 | 1972 | 1973 | 1974 | 1975 | 1976 | 1977 | 1978 | 1979 | 1980 | 1981 | 1982 | 1983 | 1984 | 1985 | 1986 | 1987 | 1988 | 1989 | 1990 | 1991 | 1992 | 1993 | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 288 | 181 | 89 | 71 | 167 | 96 | 34 | 102 | 78 | 48 | 12 | 3 | 1169 |
| 4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1495 | 897 | 549 | 287 | 319 | 370 | 179 | 194 | 113 | 29 | 35 | 5 | 4472 |
| 5 | 0 | 0 | 0 | 0 | 0 | 20 | 0 | 0 | 241 | 131 | 288 | 5070 | 4488 | 2642 | 1823 | 1594 | 1025 | 305 | 451 | 264 | 50 | 131 | 20 | 18,543 |
| 6 | 0 | 0 | 0 | 0 | 21 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 21 |
| 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 75 | 40 | 82 | 37 | 25 | 33 | 64 | 182 | 70 | 22 | 11 | 19 | 12 | 7 | 679 |
| 8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 191 | 68 | 101 | 215 | 332 | 283 | 251 | 390 | 450 | 119 | 196 | 31 | 59 | 25 | 9 | 2720 |
| 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 397 | 768 | 1130 | 1296 | 701 | 854 | 617 | 775 | 767 | 264 | 410 | 142 | 230 | 136 | 180 | 8667 |
| 10 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 314 | 307 | 1071 | 1015 | 366 | 538 | 526 | 255 | 394 | 126 | 236 | 86 | 33 | 57 | 48 | 5372 |
| 11 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 428 | 414 | 518 | 846 | 1303 | 863 | 0 | 149 | 148 | 473 | 167 | 190 | 181 | 134 | 104 | 0 | 5918 |
| 12 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 595 | 822 | 780 | 1466 | 1380 | 1532 | 0 | 351 | 370 | 489 | 302 | 503 | 258 | 148 | 226 | 0 | 9222 |
| 13 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 633 | 1258 | 1245 | 1796 | 2321 | 1793 | 137 | 476 | 448 | 482 | 824 | 465 | 383 | 180 | 430 | 351 | 13,222 |
| 14 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 1702 | 1820 | 1984 | 2133 | 2120 | 2166 | 321 | 516 | 380 | 588 | 725 | 607 | 497 | 378 | 511 | 470 | 16,920 |
| 15 | 0 | 0 | 0 | 0 | 34 | 0 | 0 | 693 | 1060 | 1938 | 2703 | 3316 | 2301 | 0 | 82 | 0 | 859 | 562 | 201 | 568 | 247 | 452 | 398 | 15,414 |
| 16 | 0 | 0 | 0 | 0 | 67 | 0 | 0 | 705 | 2112 | 2574 | 2462 | 2257 | 1340 | 0 | 0 | 0 | 805 | 0 | 0 | 0 | 0 | 0 | 0 | 12,322 |
| 17 | 0 | 0 | 1523 | 0 | 0 | 34 | 0 | 2441 | 7007 | 2868 | 4651 | 2454 | 1684 | 0 | 0 | 0 | 1131 | 0 | 0 | 0 | 0 | 0 | 0 | 23,793 |
| 18 | 0 | 2303 | 5408 | 0 | 0 | 108 | 0 | 501 | 2353 | 1958 | 4047 | 1730 | 1167 | 0 | 0 | 0 | 373 | 49 | 0 | 0 | 0 | 0 | 0 | 19,997 |
| 19 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 20 | 0 | 446 | 2046 | 0 | 263 | 0 | 0 | 0 | 802 | 903 | 494 | 0 | 119 | 0 | 102 | 38 | 618 | 0 | 462 | 0 | 0 | 167 | 0 | 6460 |
| 21 | 0 | 3897 | 1239 | 475 | 448 | 122 | 0 | 0 | 478 | 1097 | 1519 | 0 | 524 | 15 | 48 | 205 | 849 | 103 | 810 | 0 | 0 | 364 | 0 | 12,193 |
| 22 | 0 | 4144 | 1852 | 541 | 2259 | 0 | 0 | 0 | 437 | 1105 | 322 | 0 | 875 | 29 | 0 | 23 | 180 | 17 | 92 | 0 | 0 | 772 | 0 | 12,648 |
| 23 | 0 | 552 | 253 | 260 | 443 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 464 | 0 | 0 | 1007 | 0 | 1670 | 6 | 0 | 811 | 78 | 0 | 5544 |
| 24 | 634 | 155 | 0 | 740 | 902 | 0 | 0 | 0 | 0 | 647 | 0 | 763 | 177 | 0 | 0 | 249 | 11 | 968 | 16 | 0 | 93 | 232 | 0 | 5587 |
| 25 | 581 | 0 | 0 | 625 | 145 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1106 | 223 | 2576 | 110 | 0 | 805 | 42 | 0 | 6213 |
| 26 | 696 | 0 | 0 | 187 | 270 | 19 | 0 | 0 | 0 | 6455 | 800 | 475 | 0 | 0 | 0 | 0 | 9 | 0 | 2 | 0 | 0 | 11 | 0 | 8924 |
| 27 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 363 | 0 | 1008 | 0 | 0 | 864 | 0 | 0 | 2235 |
| Total | 1911 | 11,497 | 12,321 | 2828 | 4854 | 303 | 0 | 7698 | 19,706 | 25,421 | 25,869 | 27,580 | 22,007 | 5482 | 5332 | 7901 | 10,374 | 10,068 | 5075 | 2612 | 4128 | 3797 | 1491 | 218,255 |

the tank, placed in a padded tagging cradle, measured, tagged, and released. Each anchor tag was inserted between and engaged behind the pterygiophores of the dorsal fin. Fork length, tag number, capture depth, geographical position, and date of release were recorded for each fish. Only fish judged in viable condition were tagged. Sablefish of all sizes (20–110 cm) taken by the capture gear were tagged.

## Recovery

A recovery program was promoted through the use of posters, news releases, and letters explaining the research and enlisting the cooperation of those who might encounter tagged sablefish, particularly fishermen, fish processors, and members of state fisheries agencies. Individuals finding a tagged fish were requested to return the tag with information about the date, location, fishing gear, depth of capture, and fish length. A reward and the release history of the tagged fish were provided to those who returned tags.

By the end of 1993, 14,903 recoveries had been made (6.82%). The information garnered from these recoveries constitutes the core of this paper. Owing to the widespread geographic availability of sablefish and the broad coverage of the surveys and fisheries, tagged sablefish were released and recaptured from locations throughout its range in the northeast Pacific Ocean.

## Data analysis

Our philosophy in this paper is to present the data as they are and not to adjust the number of tag recoveries for exploitation rates. Such adjustments require knowing the catch and population biomass, or standardized effort measures, by area. If these are incorrectly specified, the data may be further distorted rather than corrected. When the recovery data are being adjusted over an extremely broad geographic range, where dominant gears are different and where even the same gears fish differently, such adjustments become particularly difficult.

Because of the high numbers and long time series of tag returns, basic descriptive tools appear to reveal large-scale migration and stock-structure patterns. Accordingly, we used basic descriptive tools such as mapping locations of tag recovery. Although such visual representations are useful, we also needed to aggregate the data so that general patterns could be more easily discerned. Therefore, we divided the range of sablefish (encompassing the eastern Bering Sea, the Aleutian Islands, Gulf of Alaska, and the west coast of the U.S. and Canada) into 27 areas of moderately small scale. We used large nominal regions (the eastern Bering Sea, the Aleutian Islands, and the Gulf of Alaska) to assist in these demarcations and also a straight line drawn down the Alaska Peninsula passing through 150°W, 60°N and 168.5°W, 53°N and continuing on to 170°W longitude. All areas west of 130°W longitude were divided into areas 5° wide in longitude, and areas east of 130°W longitude were divided into areas 2.5° wide in latitude (Fig. 1; Table 2). The habitat of adult sablefish includes the 400-m depth contour shown in Fig. 1.

Once these areas were described we were able to tabulate the tag recoveries in a table whose rows are the areas of release and whose columns are the areas of recovery. We feel this is the single most useful piece of information that can be garnered from any study of migration based on a tagging experiment. We also characterized net movements by mapping average positions of release and recovery. The average position of tagging and recovery was calculated for all fish tagged in area $i$, for each area $i$. An arrow was then drawn from the area of tagging to the area of recovery. The back end of the arrow was in area $i$, and the position of the arrow point provided some indication of the average movement of the tagged sablefish (i.e. the arrow points to where the tagged fish in area $i$ go). Similarly, the average position of tagged and recovered fish was calculated for all fish recovered in area $i$, for each area $i$. The pointed end of these arrows were in area $i$, and the back end of the arrow gave some indication of where these fish, on average, originated (i.e. the arrow indicated where the tagged fish recovered in area $i$ came from).

Distance traveled was examined by calculating a histogram and empirical cumulative distribution function (cdf) of the distance traveled between tagging and recovery. Movement of tagged fish in relation to depth was examined by simply tabulating the depth of tagging and the depth of recovery.

## Modeling ENSO growth effects

Modeling approaches to analyzing ENSO growth effects was difficult because the best model for this apparently simple task was unclear. Assuming an initial size at tagging of $S_1$, a size at recovery of $S_2$, and a time at liberty of $\Delta_t$, the most direct model would seem to be something like $S_2 = S_1 + \Delta_t\beta$. However, this model ignores the common sense notions that the growth increment per unit time would be expected to decrease as both $S_1$ and $\Delta_t$ increase and suggests the model $S_2 = S_1 + \Delta_t \exp(\beta_{enso} + \beta_1 S_1 + \beta_2 \Delta_t)$, where $\beta_{enso}$ represents an ENSO effect, and $\beta_1$ and $\beta_2$ can be presumed negative. A tagged fish was assumed exposed to ENSO if it was at liberty anytime during a recognized ENSO event: 1972–73, 1976–77, 1982–83, 1986–87, and 1991–93.

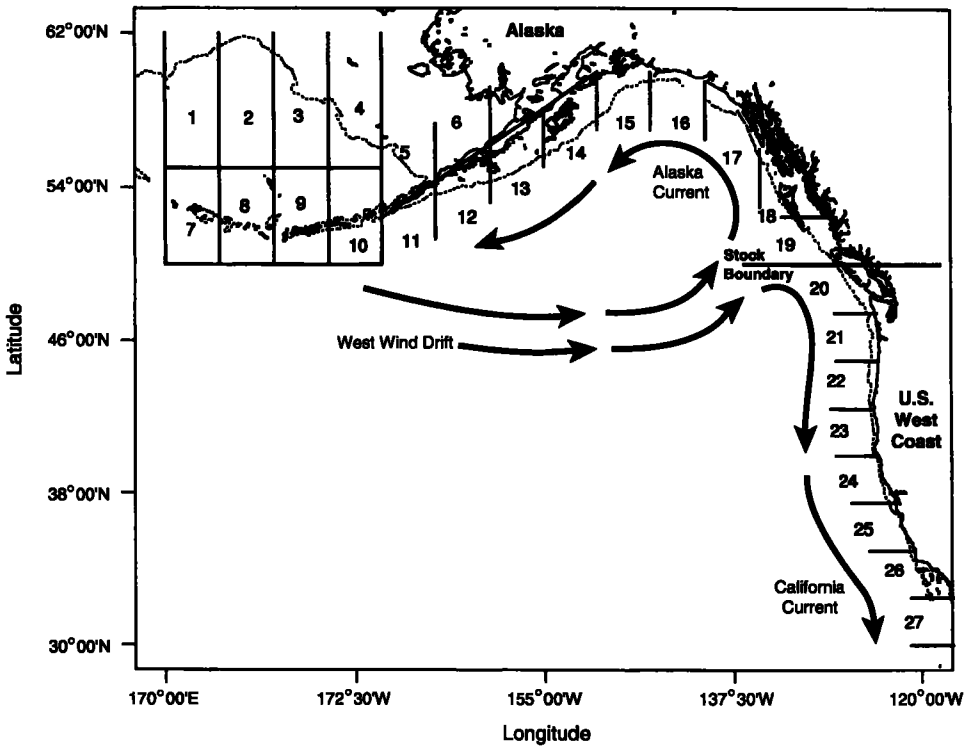


**Figure 1**

Map of 27 areas (described in Table 2) used in this paper to describe analysis of sablefish tag-recovery data. Principal regions are also described in Table 2. Also shown are the 400-m depth contour, which is the approximate habitat of adult sablefish, and the oceanographic circulation that are hypothesized to affect movements of sablefish.

### Migration from Alaska to the west coast

A well-defined sablefish migration seems to occur from Alaska to the northern portion of the west coast. To explore this phenomenon, we plotted the number of tag recoveries from Alaska, recovered along the west coast, against upwelling strength in the northern portion of the west coast. Length frequencies from Alaska and west coast sablefish trap index surveys (Parks and Shaw, 1983) were also used to examine the hypothesis that a substantial mixing of large (>60 cm) sablefish of Alaska origin occurs in west coast sablefish stocks from Vancouver Island and Washington State to California's San Francisco Bay.

## Results

### Descriptive results

Tag recovery rates by fishing gear type used for initial capture show that the tag recovery rate for trap gear (12.4%) is twice that for longline (5.87%) and trawl (5.12%) gears (Table 1). Because these results hold for fish tagged in Alaska and off the west coast, it is likely that the much higher tag recovery rate for trap gear is due to the superior condition of and presumably lower mortality rate for trap-caught fish.

Tag recovery rates were remarkably consistent for all areas of tagging (Table 4). This finding would suggest that the exploitation rate for sablefish stocks are similar throughout the northeast Pacific. Recovery rates were higher along the west coast (8.4%) than from Alaska waters (6.0%). This is just about the magnitude that would be expected when taking into account the mixtures of gears used for tagging (i.e. if we apply both the recovery rates for trawl and trap caught fish observed from the west coast and the longline recovery rate observed in Alaska to the numbers released in Alaska, we would arrive at the 6% recovery rate that was actually observed in Alaska).

Sablefish are long-lived; ages over 40 yr are regularly documented (Kimura et al., 1993) and a maximum recorded age of 94 yr has been recorded at AFSC (Anderl[5]). The instantaneous natural mortality rate

[5] Anderl, D. M. 1997. Age and Growth Task, Alaska Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA 98115. Personal commun.

used for stock assessments is $M = 0.10$ or less (Methot et al., 1994). Thus fish tagged in the early 1970s were still contributing to recoveries as of 1993 (Table 5). It is also notable that sablefish tagged offshore are usually not recaptured immediately; recoveries are typically protracted over many years.

## Results related to population structure

Mapping the location of the 14,903 sablefish tag recoveries shows a geographic continuity in sablefish distribution and commercial fishing effort (Fig. 2). The few offshore recoveries in midocean were located on seamounts. If we plot the source of these seamount recoveries (Fig. 3), we see that they came from virtually all areas of release (see Shaw and Parks, 1997, for details).

Table 6 lists the area of release against the area of recovery for the 27 areas in Figure 1. The data show that sablefish tagged off Alaska north of 50°N latitude have a 96.5% chance of being recaptured north of 50°N. Similarly, sablefish tagged off the west coast south of 50°N latitude have a 95.6% chance of being recovered south of 50°N.

Table 6 suggests that Alaska sablefish mix in areas 1–19. It is noteworthy that all Alaska areas show reciprocal migrations to all other Alaska areas. Mixing is also suggested from the fact that the recovery rate for fish tagged in all these areas is similar (Table 4). In contrast, west coast sablefish (areas 20–27) largely confined their movements within the area of release (64.4% of west coast tag recoveries came from the same areas as their release compared with 35.8% for Alaska).

Tag recoveries indicate that Alaska sablefish on average move considerably further than west coast sablefish (Fig. 4). More than 30% of tagged Alaska

**Table 4**

Table showing the percentage of tags recovered from releases in each area. Also shown by size category are the percentage of tagged fish moving north or west, staying put, and moving east or south. Areas are described in Table 2 and Figure 1.

| Area | All sizes | Size less than 57 cm | | | Size greater than 57 cm | | |
|---|---|---|---|---|---|---|---|
| | Percent recovered | Percent north or west | Percent in area of tagging | Percent east or south | Percent north or west | Percent in area of tagging | Percent east or south |
| 1 | — | — | — | — | — | — | — |
| 2 | — | — | — | — | — | — | — |
| 3 | 5.4 | 0.0 | 11.8 | 88.2 | 0.0 | 2.2 | 97.8 |
| 4 | 6.3 | 0.0 | 24.4 | 75.6 | 0.4 | 13.0 | 86.6 |
| 5 | 6.2 | 2.4 | 32.7 | 64.9 | 1.8 | 20.9 | 77.3 |
| 6 | — | — | — | — | — | — | — |
| 7 | 3.8 | 0.0 | 0.0 | 100.0 | 0.0 | 29.2 | 70.8 |
| 8 | 5.3 | 0.0 | 28.6 | 71.4 | 2.9 | 28.3 | 68.8 |
| 9 | 5.5 | 9.1 | 30.5 | 60.4 | 4.1 | 26.8 | 69.1 |
| 10 | 5.8 | 20.0 | 16.5 | 63.5 | 10.6 | 18.5 | 70.9 |
| 11 | 6.1 | 26.6 | 21.3 | 52.1 | 4.8 | 15.6 | 79.6 |
| 12 | 6.8 | 17.4 | 31.3 | 51.4 | 10.5 | 18.8 | 70.7 |
| 13 | 5.8 | 19.3 | 27.4 | 53.3 | 10.9 | 17.9 | 71.2 |
| 14 | 5.4 | 20.5 | 36.6 | 42.9 | 9.8 | 29.2 | 61.1 |
| 15 | 4.9 | 34.9 | 29.5 | 35.7 | 15.2 | 43.4 | 41.5 |
| 16 | 4.9 | 46.4 | 34.0 | 19.6 | 25.9 | 42.8 | 31.3 |
| 17 | 6.3 | 41.9 | 36.7 | 21.3 | 24.2 | 56.8 | 19.0 |
| 18 | 7.9 | 40.9 | 42.7 | 16.4 | 29.2 | 59.3 | 11.6 |
| 19 | — | — | — | — | — | — | — |
| 20 | 8.0 | 10.7 | 74.5 | 14.8 | 6.4 | 76.0 | 17.6 |
| 21 | 7.6 | 22.5 | 66.6 | 10.9 | 19.5 | 71.4 | 9.1 |
| 22 | 6.0 | 16.1 | 73.6 | 10.4 | 18.3 | 70.7 | 11.0 |
| 23 | 14.8 | 17.6 | 64.9 | 17.5 | 18.9 | 67.1 | 14.0 |
| 24 | 8.4 | 31.5 | 61.9 | 6.6 | 38.7 | 55.5 | 5.9 |
| 25 | 9.1 | 41.3 | 54.3 | 4.5 | 32.9 | 64.4 | 2.7 |
| 26 | 8.8 | 44.6 | 54.4 | 0.9 | 53.6 | 46.4 | 0.0 |
| 27 | 6.7 | 36.3 | 63.7 | 0.0 | 57.7 | 42.3 | 0.0 |

## Table 5

Tag recoveries (1971–93) tabulated by the year of release (rows) and year of recovery (columns).

| Year of release | 1971 | 1972 | 1973 | 1974 | 1975 | 1976 | 1977 | 1978 | 1979 | 1980 | 1981 | 1982 | 1983 | 1984 | 1985 | 1986 | 1987 | 1988 | 1989 | 1990 | 1991 | 1992 | 1993 | Total tag recoveries |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 71 | 4 | 3 | 1 | 7 | 8 | 2 | 5 | 2 | 6 | 2 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 43 |
| 72 | — | 72 | 78 | 39 | 114 | 75 | 17 | 31 | 58 | 19 | 29 | 39 | 17 | 6 | 6 | 4 | 6 | 3 | 2 | 0 | 9 | 1 | 0 | 625 |
| 73 | — | — | 100 | 85 | 86 | 69 | 23 | 25 | 44 | 49 | 34 | 30 | 14 | 11 | 10 | 9 | 13 | 4 | 12 | 3 | 5 | 10 | 7 | 643 |
| 74 | — | — | — | 9 | 26 | 16 | 10 | 11 | 11 | 6 | 2 | 1 | 4 | 1 | 3 | 0 | 1 | 0 | 0 | 0 | 2 | 2 | 1 | 106 |
| 75 | — | — | — | — | 49 | 86 | 30 | 22 | 64 | 7 | 21 | 10 | 10 | 11 | 3 | 1 | 3 | 1 | 0 | 0 | 0 | 2 | 3 | 323 |
| 76 | — | — | — | — | — | 1 | 0 | 0 | 2 | 0 | 3 | 0 | 1 | 1 | 1 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 12 |
| 77 | — | — | — | — | — | — | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 78 | — | — | — | — | — | — | — | 18 | 98 | 50 | 65 | 28 | 37 | 21 | 21 | 13 | 12 | 12 | 3 | 11 | 10 | 13 | 15 | 427 |
| 79 | — | — | — | — | — | — | — | — | 116 | 219 | 236 | 160 | 135 | 112 | 96 | 76 | 48 | 59 | 37 | 47 | 40 | 35 | 31 | 1447 |
| 80 | — | — | — | — | — | — | — | — | — | 96 | 369 | 296 | 426 | 169 | 131 | 198 | 78 | 90 | 70 | 66 | 57 | 53 | 67 | 2166 |
| 81 | — | — | — | — | — | — | — | — | — | — | 102 | 310 | 247 | 146 | 173 | 146 | 100 | 101 | 77 | 84 | 74 | 48 | 61 | 1669 |
| 82 | — | — | — | — | — | — | — | — | — | — | — | 71 | 279 | 208 | 255 | 212 | 158 | 168 | 102 | 122 | 92 | 72 | 83 | 1822 |
| 83 | — | — | — | — | — | — | — | — | — | — | — | — | 74 | 237 | 279 | 204 | 157 | 152 | 112 | 134 | 89 | 88 | 68 | 1594 |
| 84 | — | — | — | — | — | — | — | — | — | — | — | — | — | 10 | 39 | 42 | 54 | 59 | 40 | 49 | 27 | 24 | 29 | 373 |
| 85 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 14 | 64 | 56 | 58 | 36 | 39 | 38 | 37 | 35 | 377 |
| 86 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 46 | 201 | 155 | 78 | 111 | 69 | 80 | 55 | 795 |
| 87 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 43 | 145 | 89 | 93 | 76 | 84 | 76 | 606 |
| 88 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 32 | 323 | 262 | 160 | 151 | 60 | 988 |
| 89 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 22 | 84 | 81 | 66 | 64 | 317 |
| 90 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 4 | 35 | 29 | 24 | 92 |
| 91 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 48 | 217 | 89 | 354 |
| 92 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 17 | 63 | 80 |
| 93 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 0 | 0 |
| Total | 4 | 75 | 179 | 140 | 283 | 249 | 85 | 109 | 399 | 448 | 861 | 945 | 1244 | 935 | 1031 | 1017 | 930 | 1039 | 1004 | 1110 | 912 | 1029 | 831 | 14,859 |

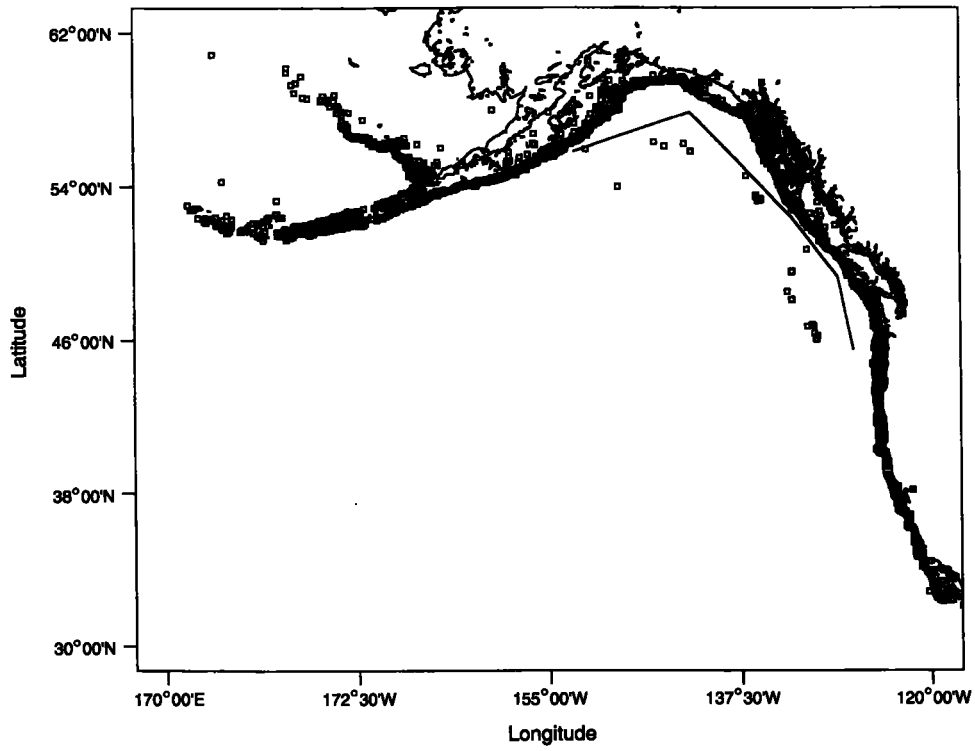


**Figure 2**

Position of recovery for 14,903 sablefish recovered from 1971 to 1993. Offshore recoveries, separated by line segments, were from seamounts.

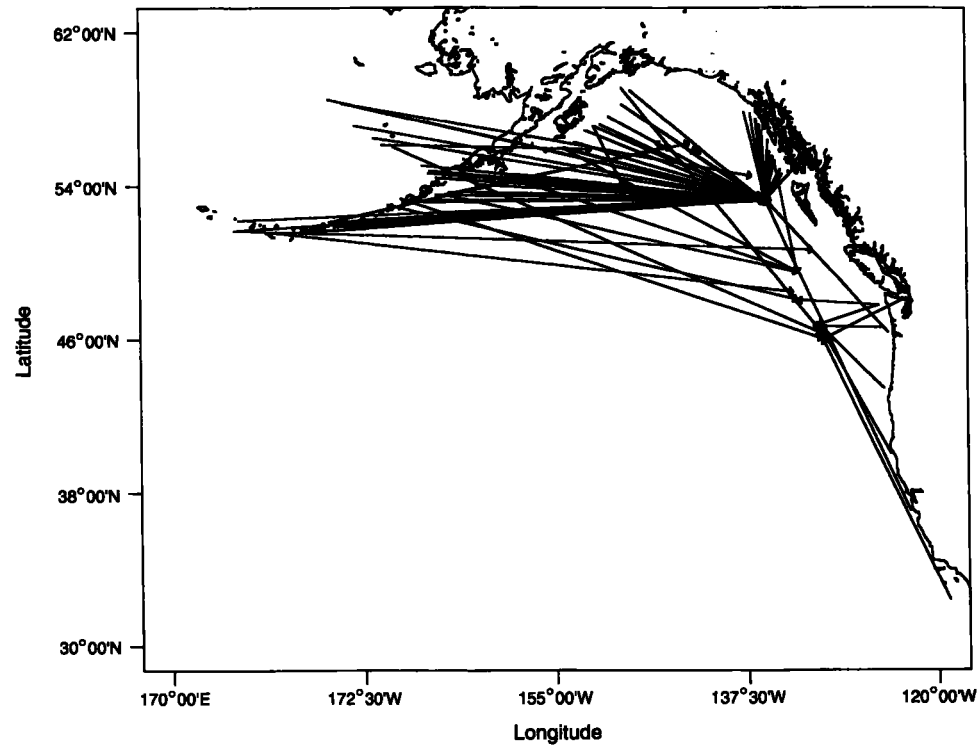


**Figure 3**

Source of seamount tag recoveries can be seen to be from almost all areas. Figure adapted from Shaw and Parks (1997).

## Table 6

Tag recoveries tabulated by the area of release (rows) and area of recovery (columns). Areas are described in Table 2 and Figure 1.

| Area of release | Area of recovery | | | | | | | | | | | | | | | | | | | | | | | | | | | Total tag recoveries |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 | 23 | 24 | 25 | 26 | 27 | |
| 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 3 | 0 | 0 | 3 | 6 | 5 | 0 | 0 | 1 | 2 | 1 | 1 | 3 | 0 | 1 | 9 | 2 | 16 | 7 | 3 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 63 |
| 4 | 0 | 0 | 1 | 42 | 18 | 1 | 0 | 1 | 8 | 9 | 2 | 8 | 13 | 17 | 46 | 23 | 42 | 29 | 14 | 6 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 283 |
| 5 | 0 | 0 | 5 | 18 | 284 | 1 | 2 | 5 | 28 | 19 | 26 | 60 | 46 | 84 | 143 | 115 | 149 | 109 | 39 | 4 | 3 | 3 | 1 | 0 | 2 | 0 | 0 | 1146 |
| 6 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 7 | 0 | 0 | 0 | 0 | 0 | 0 | 7 | 4 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 2 | 2 | 6 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 26 |
| 8 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 41 | 6 | 2 | 3 | 5 | 3 | 6 | 6 | 7 | 28 | 18 | 11 | 3 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 145 |
| 9 | 0 | 0 | 0 | 6 | 22 | 0 | 0 | 0 | 134 | 38 | 4 | 13 | 19 | 18 | 36 | 33 | 57 | 50 | 27 | 16 | 3 | 0 | 1 | 1 | 0 | 0 | 0 | 478 |
| 10 | 0 | 0 | 2 | 4 | 14 | 0 | 1 | 2 | 18 | 56 | 11 | 10 | 10 | 14 | 26 | 24 | 43 | 38 | 25 | 8 | 2 | 0 | 3 | 0 | 1 | 0 | 0 | 312 |
| 11 | 0 | 0 | 4 | 6 | 16 | 0 | 0 | 2 | 4 | 6 | 62 | 31 | 23 | 20 | 41 | 21 | 50 | 42 | 22 | 8 | 4 | 0 | 1 | 0 | 0 | 0 | 0 | 363 |
| 12 | 0 | 0 | 2 | 9 | 23 | 0 | 1 | 3 | 9 | 9 | 20 | 136 | 49 | 38 | 78 | 40 | 79 | 63 | 42 | 15 | 6 | 3 | 3 | 0 | 0 | 0 | 0 | 628 |
| 13 | 0 | 0 | 0 | 5 | 17 | 0 | 0 | 0 | 12 | 12 | 6 | 49 | 157 | 103 | 111 | 56 | 89 | 75 | 41 | 21 | 8 | 1 | 1 | 0 | 0 | 0 | 0 | 764 |
| 14 | 0 | 0 | 0 | 6 | 17 | 0 | 1 | 2 | 10 | 11 | 10 | 21 | 38 | 284 | 139 | 87 | 114 | 72 | 57 | 24 | 8 | 6 | 2 | 0 | 0 | 0 | 0 | 909 |
| 15 | 0 | 0 | 1 | 4 | 27 | 0 | 2 | 0 | 4 | 9 | 6 | 12 | 22 | 76 | 297 | 93 | 82 | 57 | 43 | 17 | 8 | 2 | 0 | 0 | 0 | 0 | 0 | 762 |
| 16 | 0 | 0 | 0 | 1 | 17 | 0 | 0 | 1 | 10 | 10 | 8 | 18 | 26 | 26 | 79 | 241 | 99 | 39 | 19 | 6 | 2 | 0 | 1 | 0 | 0 | 0 | 0 | 603 |
| 17 | 0 | 0 | 1 | 3 | 26 | 0 | 0 | 4 | 18 | 16 | 13 | 30 | 30 | 60 | 109 | 99 | 796 | 181 | 71 | 27 | 6 | 3 | 2 | 1 | 0 | 0 | 0 | 1496 |
| 18 | 1 | 0 | 0 | 1 | 13 | 0 | 0 | 0 | 17 | 6 | 1 | 14 | 13 | 48 | 34 | 54 | 299 | 879 | 115 | 62 | 9 | 8 | 3 | 1 | 1 | 0 | 0 | 1579 |
| 19 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 20 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 3 | 1 | 1 | 1 | 6 | 5 | 1 | 6 | 9 | 14 | 387 | 68 | 7 | 2 | 2 | 0 | 1 | 0 | 517 |
| 21 | 0 | 0 | 0 | 3 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 3 | 6 | 3 | 10 | 4 | 10 | 11 | 7 | 138 | 638 | 76 | 15 | 2 | 0 | 1 | 0 | 929 |
| 22 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 2 | 2 | 1 | 2 | 3 | 11 | 5 | 27 | 70 | 548 | 64 | 12 | 2 | 2 | 0 | 755 |
| 23 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 5 | 3 | 2 | 2 | 5 | 6 | 6 | 17 | 98 | 534 | 122 | 13 | 2 | 1 | 818 |
| 24 | 0 | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 2 | 2 | 2 | 0 | 3 | 2 | 4 | 11 | 35 | 89 | 282 | 27 | 2 | 1 | 468 |
| 25 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 5 | 1 | 1 | 2 | 8 | 28 | 55 | 123 | 314 | 16 | 8 | 565 |
| 26 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 2 | 3 | 0 | 3 | 5 | 7 | 15 | 8 | 57 | 106 | 64 | 84 | 414 | 6 | 779 |
| 27 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 1 | 4 | 6 | 12 | 15 | 14 | 9 | 13 | 120 | 197 |
| Total | 1 | 0 | 19 | 116 | 509 | 2 | 16 | 66 | 283 | 210 | 177 | 417 | 461 | 818 | 1180 | 910 | 1974 | 1711 | 572 | 802 | 889 | 887 | 900 | 625 | 453 | 451 | 136 | 14,585 |

sablefish were observed to move over 500 n mi from tagging to recovery, and more than 10% moved over 1,000 n mi. In contrast fewer than 10% of west coast sablefish moved over 500 n mi.

For the Gulf of Alaska, there is a strong proclivity for fish tagged in the southeast (areas 16–18) to move north and west and for fish tagged in the west (areas 3–14) to move east and south (Tables 4 and 6). It is convenient to define movement north or west as a recovery from an area number less than the area of tagging, and movement east or south as a recovery from an area number greater than the area of tagging (Fig. 1). Several authors (Fujioka et al., 1988; Heifetz and Fujioka, 1991) point out that these directional movements are most pronounced for fish tagged at less then 57 cm in southeast Alaska, and for fish tagged at greater than 57 cm in the western Gulf of Alaska. The greater intensity of these size-selective migrations are supported by our data (Table 4).

The patterns of migration can be illustrated visually by considering maps of average movement where tag recoveries are aggregated by the area of tagging or the area of recovery. Figure 5 shows the average position of tagging (tail of arrow) for each of the 27 areas for which sablefish were tagged (i.e. 23 areas) and the average position where subsequent recoveries occurred. Similarly, Figure 6 shows the average position of recoveries (head of arrow) in each area (i.e. 24 areas) where more than 2 recoveries occurred and the average position of tagging (tail of arrow) for each aggregation of tags.

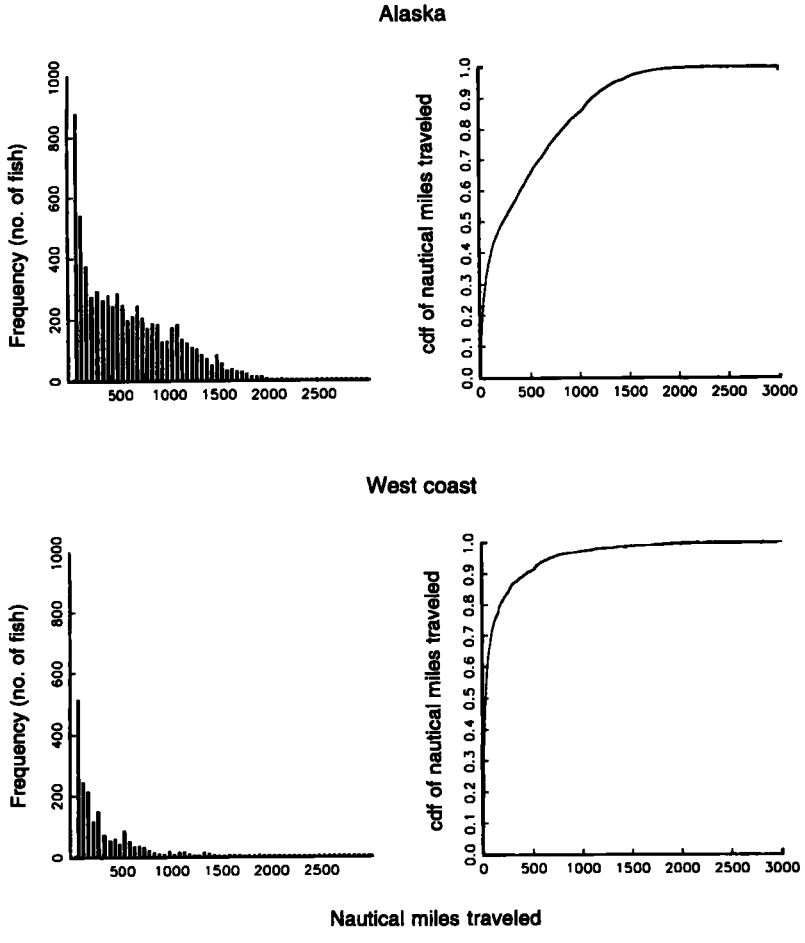


**Figure 4**

Histogram and cumulative distribution function (cdf) of the distance traveled (n mi) for sablefish that were tagged and recovered. Distances are straight line distances that are minimums; actual distance traveled must have been greater. Histograms are binned in 50 n mi intervals, with the 0–50 n mi bin not plotted so that more detail could be seen. For Alaska the 0–50 n mi bin count was 2744, for the west coast the 0–50 n mi bin count was 3075.

For the Alaska population, Figures 5 and 6 seem to show an expansion and return about the center of sablefish abundance in the central Gulf of Alaska. By this we mean that fish tagged away from the center of the Gulf of Alaska tend to be recovered toward the center of the Gulf, and fish recovered away from the center of the Gulf tend to have originated toward the center of the Gulf. Such a pattern could represent random movement throughout the Alaska range, with concentration of tagging and recovery effort (Tables 3 and 6) occurring in the central Gulf of Alaska. For the west coast population, the movement is more of a slight but steady northward shift whether the aggregation is by area of tagging or area of recovery. Such movement may be the result of migrations or may represent a biologically static situation, one in which recoveries are influenced by increasing fishing pressure towards the north.

As pointed out in the introduction, sablefish inhabit a very broad bathymetry. In order to try to learn something of sablefish depth migrations, we tabulated depth at release for all tagged sablefish and depth at release versus depth at recovery for sablefish that were tagged and recovered (Table 7). Fish that were tagged in Alaska and recovered off the west coast,

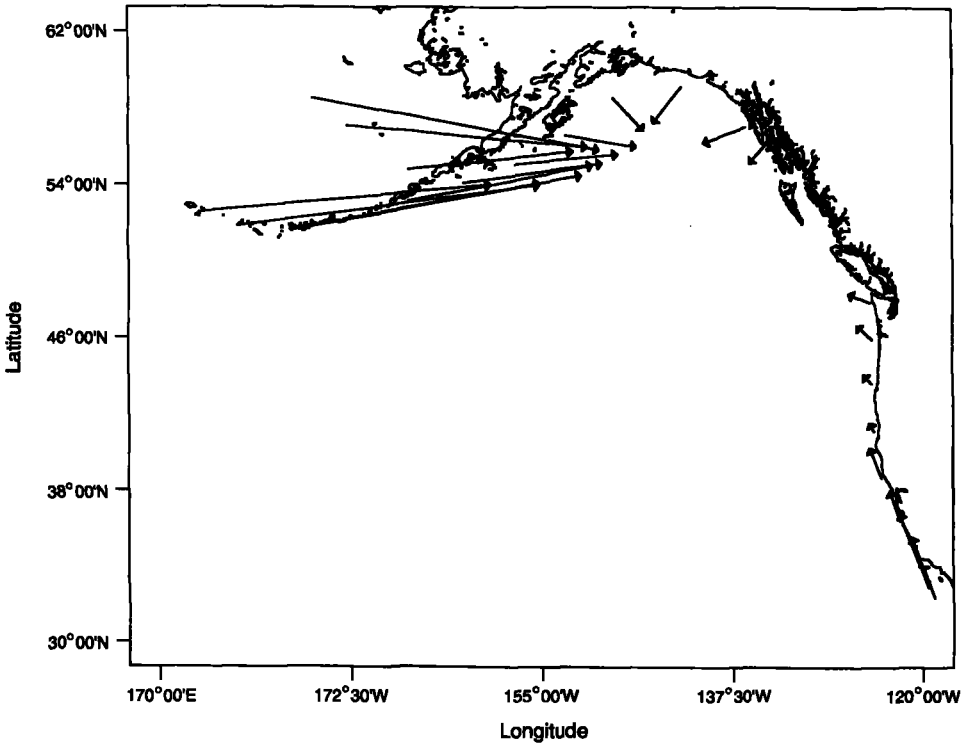


**Figure 5**

Average movement of tagged and recovered sablefish aggregated by area of tagging. Arrows point to the average location where sablefish tagged in a specified area were recovered (i.e. where fish were going). Tail of arrow originates in one of the 27 areas in which tagging occurred. Tagging did not occur in all areas.

or vice versa, were excluded from Table 7. For Alaska sablefish, the depth of tag recovery generally had the same distribution regardless of the depth of tagging. For west coast sablefish, recoveries tended to be in the same depth zone as the depth of tagging. However, few recoveries were made from the relatively large number of tags released in the 400–1000 m depth zone.

## Results related to ENSO events and migration from Alaska to the west coast

Global-scale El Niño-Southern Oscillation (ENSO) events are the strongest climatic feature occurring in the Pacific Ocean. Along the west coast it weakens upwelling and is known to lower food availability and to stunt growth of pelagic species (Bakun, 1996). To the north, off Alaska, ENSO may have the opposite effect, enhancing growth and biological productivity (Beamish and Bouillon, 1993; Bakun, 1996). A significant negative effect on sablefish growth due to ENSO events was detected ($P[|t|>3.973] < 7.2\times10^{-5}$, df=3666) off the west coast, and a significant positive effect on growth was detected ($P[|t|>2.604] < 0.01$, df=6030) for Alaska sablefish (Table 8). In this analysis growth increment data were used only if tagging and recovery occurred in the same region. Residuals histograms suggested a normal pattern of errors for the model fits (Fig. 7).

We found that sablefish that migrate from Alaska waters to the west coast appear to concentrate in areas off Vancouver Island, Washington, and Oregon. Area 20, between 47°30' and 50°N latitude (Fig. 1), is of particular interest because it is an area of mixing for Alaska and west coast sablefish (Table 6, column 20). The question arises whether we can detect factors that might influence the migration from Alaska to areas 20 and 21 off the west coast. One factor that seems to have a positive correlation with this migration south is the strength of upwelling in these southern areas (Fig. 8, two-tailed, sign. $\alpha$= 0.01).

Length frequencies from sablefish trap index surveys (1978–91), aggregated over all years, strongly distinguish between fish from Alaska (areas 17 and 18) and the west coast (areas 20–27) (Fig. 9A). However, the length frequencies for fish greater than 60 cm (Fig. 9B) suggest three groups: Alaska (areas 17 and 18), west coast north (areas 20–24), and west coast south (areas 25–27). The west coast north (ar-

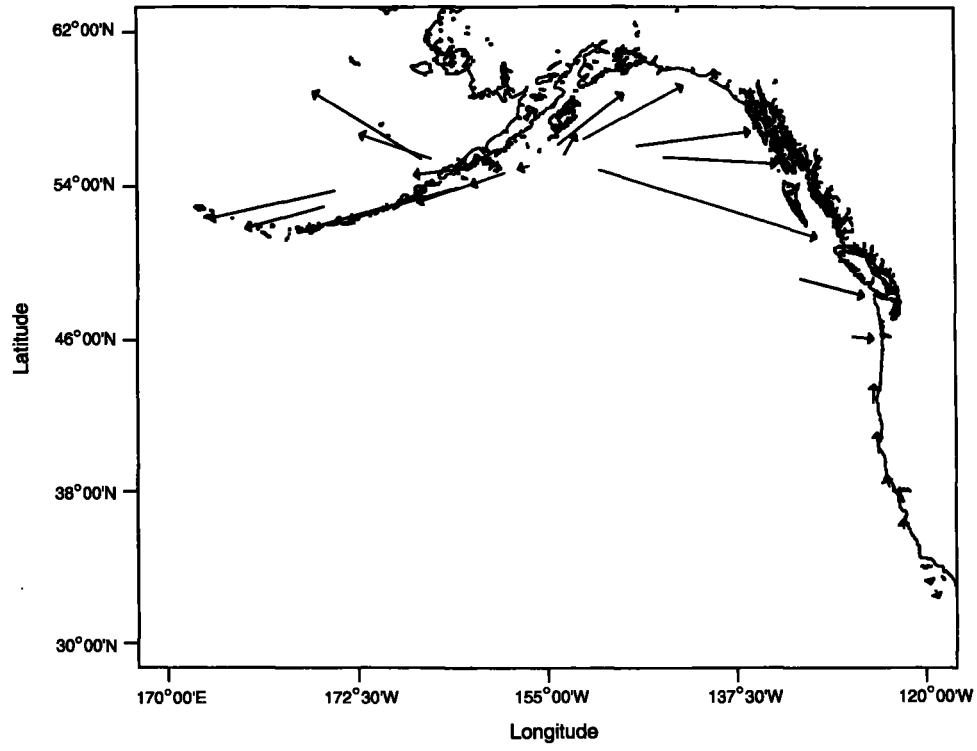


**Figure 6**

Average movement of tagged and recovered sablefish aggregated by area of recovery. Head of arrow lies in one of the 27 areas in which more than two tag recoveries occurred. Rear of arrows lies in the average location where sablefish were tagged (where fish were coming from).

eas 20–24) group appears to have an excess of large (>60 cm) sablefish, but we cannot be sure of their origin. We were unsuccessful in our attempt to correlate annual fluctuations in the abundance of large sablefish with upwelling, but this may have been due to limitations in the samples that were available on a biennial basis from the west coast north area.

## Discussion

### Comparison and interaction of Alaska and west coast populations

Our tag-recovery data alone provide compelling evidence (Table 6) that Alaska and west coast sablefish constitute separate populations that, for practical purposes, remain largely independent. In the long-term, approximately 3.5% of Alaska fish migrate to the west coast, and approximately 4.4% of west coast fish migrate to Alaska. Short-term migration rates will be small and justify the separation of these populations for fishery management purposes. However, biologically, these exchange rates are probably sufficient to consider sablefish a single biological population throughout its range, provided these populations are not reproductively isolated. Notice that these migration rates say nothing of net migration which is dependent on the absolute magnitude of the Alaska and west coast populations.

Stock assessment scientists have long felt that sablefish constitute two distinct stocks between Alaska and the U.S. west coast, largely because their von Bertalanffy growth parameters and size-at-maturity differ so dramatically (Table 9; McDevitt, 1990; Kimura et al., 1993). However, early genetic studies (Tsuyuki and Roberts, 1969; Wishard and Aebersold, 1979; Gharrett et al., 1983) indicate that although the northeast Pacific may support many "somewhat discrete" populations, a mechanism for gene transfer was expected to explain the observed polymorphism. In light of our strong evidence for migratory behavior in tagged sablefish, it is not surprising that significant gene flow occurs throughout the range.

The recapture rate for tagged sablefish appears to be remarkably similar for all areas of tagging (Table 4), especially if the differential survival rate from the fishing gears used for initial capture is taken into account. These recapture rates cannot tell us much

**Table 7**

Number of sablefish tag releases and recoveries by depth category (in meters). Proportions are proportion of total releases that were recovered and the proportion of recoveries that were made at each depth category. Alaska and the west coast was divided at 50°N latitude, with tagging and recovery occurring within the respective regions.

| Alaska | | Number recovered at depth | | | | | |
|---|---|---|---|---|---|---|---|
| Depth released | Total released | 0–200 | 200–400 | 400–600 | 600–800 | 800–1000 | Total recoveries |
| 0–200 | 11240 | 75 | 98 | 264 | 237 | 49 | 723 |
| 200–400 | 19334 | 73 | 365 | 704 | 568 | 116 | 1826 |
| 400–600 | 108131 | 51 | 268 | 866 | 856 | 208 | 2249 |
| 600–800 | 17572 | 11 | 41 | 206 | 312 | 64 | 634 |
| 800–1000 | 683 | 2 | 0 | 7 | 31 | 14 | 54 |

| Alaska | | Number recovered at depth | | | | |
|---|---|---|---|---|---|---|
| Depth released | Proportion recovered | 0–200 | 200–400 | 400–600 | 600–800 | 800–1000 |
| 0–200 | 0.064 | 0.104 | 0.136 | 0.365 | 0.328 | 0.068 |
| 200–400 | 0.094 | 0.040 | 0.200 | 0.386 | 0.311 | 0.064 |
| 400–600 | 0.021 | 0.023 | 0.119 | 0.385 | 0.381 | 0.092 |
| 600–800 | 0.036 | 0.017 | 0.065 | 0.325 | 0.492 | 0.101 |
| 800–1000 | 0.079 | 0.037 | 0.000 | 0.130 | 0.574 | 0.259 |

| West coast | | Number recovered at depth | | | | | |
|---|---|---|---|---|---|---|---|
| Depth released | Total released | 0–200 | 200–400 | 400–600 | 600–800 | 800–1000 | Total recoveries |
| 0–200 | 9208 | 376 | 386 | 34 | 3 | 0 | 799 |
| 200–400 | 15283 | 309 | 2054 | 339 | 12 | 0 | 2714 |
| 400–600 | 23624 | 6 | 108 | 118 | 7 | 0 | 239 |
| 600–800 | 6208 | 1 | 5 | 7 | 2 | 0 | 15 |
| 800–1000 | 4327 | 0 | 0 | 0 | 0 | 0 | 0 |

| West coast | | Number recovered at depth | | | | |
|---|---|---|---|---|---|---|
| Depth released | Proportion recovered | 0–200 | 200–400 | 400–600 | 600–800 | 800–1000 |
| 0–200 | 0.086 | 0.471 | 0.483 | 0.043 | 0.004 | 0.000 |
| 200–400 | 0.178 | 0.114 | 0.757 | 0.125 | 0.004 | 0.000 |
| 400–600 | 0.010 | 0.025 | 0.452 | 0.494 | 0.029 | 0.000 |
| 600–800 | 0.002 | 0.067 | 0.333 | 0.467 | 0.133 | 0.000 |
| 800–1000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 |

about the absolute exploitation rate on sablefish, because tag loss, survival of tagged fish, and reporting rates are unknown. However, the data seem to indicate that the relative exploitation rate of substocks is roughly of similar magnitude throughout their range.

Adult sablefish make two types of migrations that are quite striking in nature: migrations from the continental slope across abyssal plains to seamounts, and long-range migrations along the continental slope that can extend all the way from the Bering Sea to southern California in either direction. The mechanism for accomplishing these long-range migrations has been discussed very little in the literature, although Moser et al. (1994) suggest that migration to seamounts may be midwater over the abyss.

Because adult sablefish are demersal, one possible mechanism for accomplishing these long-range migrations is that sablefish follow the continental slope, or sea floor. Because these deep areas are in the low-oxygen zone (Bakun, 1996), this route would appear

to be a difficult and inefficient for long migrations. Also, it would seem that such migrations would take time, but several authors have noted that for tagged sablefish, there appears to be little relation between time at liberty and distance traveled (Bracken, 1983; Dark, 1983; Beamish and McFarlane, 1988). A second possibility is that sablefish are using the dominant ocean circulation patterns to redistribute themselves.

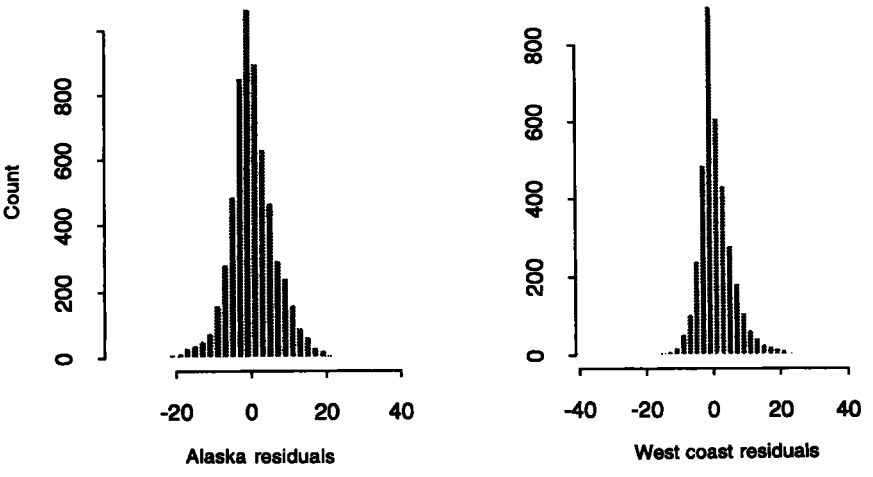


**Figure 7**

Histograms of residuals from fits to the growth model used to detect ENSO growth effects suggest that residuals from the model fits are approximately normally distributed.

The dominant circulation patterns in the northeast Pacific—the counter-clockwise Alaska Gyre (and Alaska Current) and the clockwise Central Pacific Gyre (and California Current)—suggest both a physical basis for separation and a mechanism for partial exchanges between Alaska and west coast stocks (Fig. 1). North of 50°N latitude, all life stages of sablefish occur in the counterclockwise rotating gyre. In contrast, south of 50°N latitude, adults live in a northward flowing undercurrent, and pelagic juveniles and benthic subadults live in the southward flowing surface current (i.e. the California Current).

Tag recoveries from midocean seamounts come from all areas of tagging and appear to demonstrate that sablefish routinely migrate on (and mix on) open ocean currents from release areas along the continental slope (Fig. 3). The Alaska Current (and Gyre) could provide a passive means for sablefish to make long migrations throughout the Gulf of Alaska. Similarly, the California Current (flowing offshore and southerly on the surface) and the California Undercurrent (flowing nearshore and northerly at depth) could provide the physical conveyance for sablefish to migrate passively up and down the North American west coast.

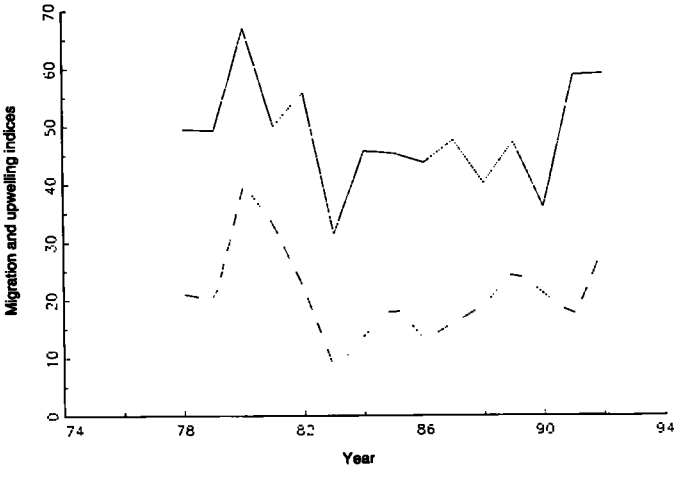


**Figure 8**

Plot showing correlation of the number of sablefish tagged off Alaska and recovered off the west coast (dash) with the strength of upwelling off the west coast (solid). One year was subtracted from the year of tag recovery, allowing time for the tag recovery to take place. The Bakun upwelling indices were mean coastal summer upwellings (April–August) from 42–48°N latitude (Mason and Bakun, 1986).

Our findings concerning exchanges among areas in Alaska stocks corroborate earlier findings (Sasaki, 1985; Fujioka et al., 1988; Heifetz and Fujioka, 1991). Perhaps the relative strength and general timing of prevailing currents available to Alaska sablefish are what allow them to migrate farther and with greater frequency than west coast sablefish (Fig. 4). The latitudinal range of the Alaska population is only 50–60°N, half that of the west coast population which is 30–50°N. Perhaps this narrower latitudinal range also facilitates migrations.

Earlier, we described how migrations from Alaska to the west coast are reciprocated by migrations from the west coast to Alaska. Although this is true, sablefish

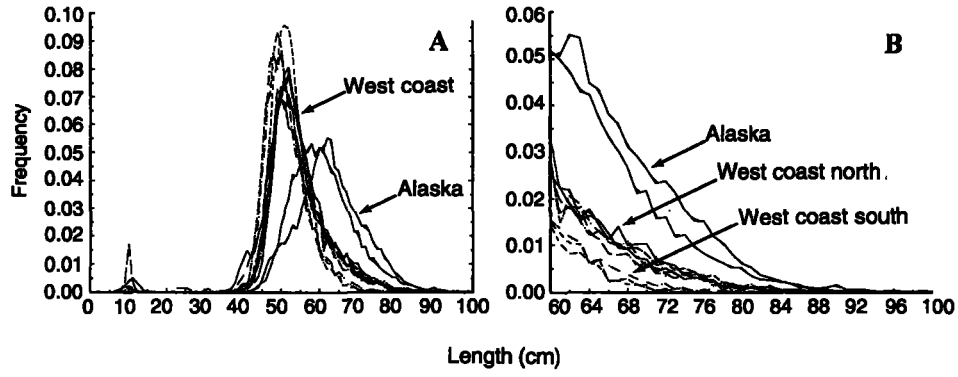


**Figure 9**

(**A**) Length frequencies from trap index surveys, plotted by areas, showing the dichotomy between Alaska (areas 17 and 18) and west coast (areas 20–27) sablefish. The two distributions shifted to the right are from Alaska. (**B**) The same length frequencies but only for sablefish with length greater than 60 cm. Top distributions are from Alaska (areas 17 and 18), the middle distributions are from the west coast north (areas 20–24), and the lower distributions are from the west coast south (areas 25–27).

migrating from Alaska to the U.S. west coast appear to concentrate in the northern area of the west coast (areas 20–22, Table 6).

Methot[6] recognized from fishery data that west coast sablefish varied greatly in size at age. He suggested that this was due to a commingling of southern California and Alaska "morphs." Extending this hypothesis, tag recoveries (Table 6) suggest that area 20 contains a substantial number of fish from Alaska, but that areas farther south contain substantially fewer migrants. Similarly, length frequencies of large fish from the NMFS trap index survey (Fig. 9B) suggest three populations: Alaska fish from areas 17 and 18; a mixture of Alaska and smaller southern California fish from areas 20–24; and small southern California fish from areas 25–27.

On the basis of size and age-at-depth data, adult sablefish are believed to inhabit greater depths as they grow older owing to a protracted, ontogenetic migration to greater depths (Fujioka et al., 1988; Saunders et al., 1997). Norris (1997) disagreeing with this view, conjectured that the broad bathymetric range was due to radiative evolutionary adaptation of enzyme systems to greater depths. Norris (1997) regarded the age-at-depth data as an artifact caused by varying size-selective fishing mortality with depth. He felt that reproducing populations inhabit various depth zones. Sigler et al. (1997) hypothesized that age-at-depth data could be explained by considering the movement of sablefish to greater depths as being a random walk (i.e. resulting from a sequence of random movements). From this point of view, greater age-at-depth could be viewed as an ontogenetic phenomenon resulting from statistical behavior.

**Table 8**

Parameter estimates and their statistical significance for a tag-recovery growth model intended to detect a growth effect due to ENSO events. Data were divided between Alaska and the west coast and the ENSO parameter was included when a particular tagged fish was at liberty during any ENSO event. The model used was $S_2 = S_1 + \Delta_t \exp(\beta_{enso} + \beta_1 S_1 + \beta_2 \Delta_t)$, where $S_1$ was the size of fish at the time of tagging, $S_2$ was the size of fish at time of recovery, $\Delta_t$ was the time elapse between tagging and recovery, and $\beta_{enso}$ represents an effect from any exposure to ENSO events. Both release and recovery were in the same region for the data used.

| Parameter | Estimate | SE | *t*-value |
|---|---|---|---|
| Alaska modeling results. | | | |
| Degrees of freedom for *t*–statistic=6,030. | | | |
| $\beta_{enso}$ | 0.05781 | $2.2200 \times 10^{-2}$ | 2.604 |
| $\beta_1$ | –0.08307 | $4.8603 \times 10^{-4}$ | –170.910 |
| $\beta_2$ | –0.00031 | $9.9375 \times 10^{-6}$ | –31.093 |
| West coast modeling results. | | | |
| Degrees of freedom for *t*-statistic=3,666. | | | |
| $\beta_{enso}$ | –0.12918 | $3.2513 \times 10^{-2}$ | –3.973 |
| $\beta_1$ | –0.09636 | $7.4322 \times 10^{-4}$ | –129.651 |
| $\beta_2$ | –0.00036 | $1.4059 \times 10^{-5}$ | –25.853 |

[6] Methot, R. D. 1993. Latitudinal and bathymetric patterns in sablefish growth and maturity off the U.S. West coast. Paper presented at the international symposium on the biology and management of sablefish, Alaska Fisheries Science Center, April 13–15, 1993.

**Table 9**

Von Bertalanffy growth parameters and lengths at maturity for Alaska (AK) and west coast sablefish. Growth parameters are based on age data (Kimura et al., 1993). Lengths at maturity for Alaska are from Sasaki (1985), and for the west coast are from Parks and Shaw (1983).

| Region | Location | Sex | $L_\infty$ (cm) | $K$ | $t_0$ (yr) | Length at maturity (cm) |
|---|---|---|---|---|---|---|
| Alaska | | male | 70.2 | 0.120 | –8.06 | |
| | | female | 86.7 | 0.106 | –6.15 | |
| | Bering Sea | male | | | | 65 |
| | | female | | | | 67 |
| | Aleutian Islands | male | | | | 61 |
| | | female | | | | 65 |
| | Gulf of AK | male | | | | 57 |
| | | female | | | | 65 |
| West coast | | male | 54.7 | 0.472 | –1.82 | |
| | | female | 61.0 | 0.499 | –0.81 | |
| | Bodega Canyon | male | | | | 52.7 |
| | | female | | | | 55.3 |
| | Patton Escarpment | male | | | | 54.8 |
| | | female | | | | 56.3 |

Depth-related tagging data for sablefish are very difficult to interpret for several reasons. First of all, surveys, and therefore tag releases, did not cover the full bathymetric distribution of sablefish. Second, commercial fishing, and therefore recovery effort, did not cover the full bathymetric distribution of sablefish. And finally, the bathymetric distribution of a species abundant across such a broad latitudinal range as sablefish, might be expected to vary by latitude.[7] Most of our evidence supports the hypothesis that sablefish seem to have a deeper, lower limit to their distribution off the west coast, compared with their distribution off Alaska.

The principal depth-related result for Alaska sablefish is that the depth distribution of recoveries is similar regardless of the depth of tagging (Table 7). Although the depth distribution of recoveries naturally follows recovery effort, it also suggests a certain amount of random movement in relation to depth over time. The depth-related data for west coast sablefish are even more difficult to decipher. These data show an extremely low recovery rate from fairly heavy tagging of fish from the 400–1000 m depth zone. The reason for this low recovery rate is unknown. Perhaps, the strongest conclusion to emerge from our study is that we still have more to learn about sablefish depth distributions.

## Effects of ENSO on migration and growth

It seems natural that the growth of pelagic species off the west coast, such as Pacific whiting (*Merluccius productus*) and Pacific salmon (*Onchorynchus* spp.), would be adversely affected by ENSO events (Beamish and Bouillon, 1993; MacLellan and Saunders, 1995). It is perhaps more interesting that along the west coast, the growth and somatic condition of adult rockfish have been negatively affected by ENSO (Lenarz et al., 1995). That the observed growth of a deepwater species, such as sablefish, can be negatively affected suggests that the feeding of many demersal species along the west coast may suffer some ill effects from ENSO. In the Gulf of Alaska, ENSO growth effects are thought to be opposite of those experienced off the west coast. Growth of salmon and groundfish species are thought to be significantly enhanced by ENSO events (Beamish and Bouillon, 1993; Bakun, 1996). Thus our findings that ENSO events retard growth of sablefish off the west coast but enhance growth of sablefish off Alaska are consistent with this literature. However, this may be the first documentation of this effect for a demersal species.

The question arises as to why there is a positive correlation between Bakun's upwelling index and west coast tag recoveries of Alaska fish (Fig. 8). Are

[7] One reviewer noted the term "latitudinal emergence," where deeper dwelling species are thought to have shallower upper limits on their bathymetric distributions in the more northern limits of their range. However, we did not find this term to be widely used in the literature.

migrating sablefish taking advantage of enhanced feeding opportunities presented by strong upwelling or are they displaced sablefish subject to irregular but recurring episodes of ocean-forcing events and passively entrained in strengthened currents southward?

Dorn (1992) noted two oceanographic phenomena that make west coast waters a highly productive region: coastal upwelling and the advection of cool, zooplankton-rich water from the Alaska Subarctic Gyre. These phenomena could be distinguished (Roesler and Chelton, 1987) and Hollowed and Wooster (1992) have pointed out that they are positively correlated.

Hollowed and Wooster (1992) noted that climate and ocean circulation in the northeast Pacific oscillates between a type-A pattern (i.e. weak Aleutian Low and Gulf of Alaska circulation, intensified California Current, and strong upwelling off the west coast) and type-B ENSO-associated conditions (i.e. intensified winter Aleutian Low and Gulf of Alaska circulation, weak California Current, and weak coastal upwelling). It is the more prevalent type-A scenario, with a strong California Current, that possibly facilitates the migration of sablefish south. Thus, the strength of migration from Alaska to the west coast would be negatively correlated with ENSO events. Dorn (1995) concluded that increased northward movements of Pacific whiting along the west coast during El Niño years were due to intensified northward currents. Whether or not a subset of Alaska sablefish follow enhanced feeding gradients, a strong California Current could deliver them to the west coast.

Because the California Current is a surface current and because there exists a natural boundary between the California Current and the Alaska Gyre, it is somewhat speculative to claim that a strong California Current plays an important role in the migration of Alaska sablefish to the west coast. Nevertheless, Alaska sablefish do make this migration, and the migrations coincide with an enhanced California Current and increased upwelling. It would seem difficult to conclude that these phenomena are totally unrelated.

One difficulty in discussing sablefish migration is that we cannot be sure that the larger fish found along the northern portion of the west coast are of Alaskan origin. A partial explanation could be that the strong upwelling zone from Cape Mendocino to Point Conception in central California, as measured by Ekman transport (Parrish et al. 1981), represents a physical barrier to larger (Alaska?) sablefish. This barrier seems plausible because large sablefish become relatively rare in the length frequencies for the areas where upwelling intensifies. The second part of this theory would tell us whether Alaska sablefish are able to reproduce in waters off Washington and Oregon. It is possible that the gross numbers of Alaska sablefish migrating to the west coast are not substantial enough to affect length frequencies directly but that the numbers may be substantial enough to affect the population genetically over a much broader geographic range. Bakun (1996) argued that the Southern California Bight and the Columbia River Plume offer two locations where fish larvae can survive the disruptions of a strong upwelling environment. These locations may correspond to those for northerly and southerly west coast sablefish populations.

However, Moser et al. (1994) believed that although sexually mature and spawning sablefish are encountered as far south as Baja California, virtually none of their reproductive potential survives below the Southern California Bight and they do not contribute to the standing stock in any meaningful way. They concluded that it is the advection of eggs and larvae from the north that ensures the stability of the population south of Pt. Conception. This hypothesis, that sablefish abundance off the west coast (and particularly California) is dependent on a steady "leakage" of eggs, larvae, or juvenile fish from more northern center(s) of abundance, parallels the hypothesis that Asian stocks are dependent on the migration of adult fish from northern and eastern areas of the Pacific.

Although the appearance of northern fish in the mixed-zone off the Washington–Oregon coast is well established, we cannot yet quantify the net contribution of immigrants. Also, we found little evidence of tagged adult fish migrating from areas north of central California to southern and Baja California. However, this does not preclude Moser et al.'s (1994) conjecture that the southern California population is dependent on eggs and larvae advected from the north. The dependence of sablefish stocks on spawning populations appears not to be well understood.

## Acknowledgments

We thank Heather A. Parker, LTJG/NOAA, Pacific Fisheries Environmental Group, for providing data on the Bakun upwelling indices, and Sandra A. Lowe for providing catch data and a careful review. Jeffrey T. Fujioka, Anne B. Hollowed, and William T. Peterson (Northwest Fisheries Science Center, Newport Laboratory) provided extremely helpful internal reviews. We would like to give special thanks to three referees who pointed out numerous errors in our manuscript. One referee in particular shared a great deal of his or her knowledge of sablefish biology and bathymetry. Because of divergent views ex-

pressed concerning sablefish biology and movement, it is important for us to state that the conclusions described here are those of the authors.

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**Abstract.**—Age and growth of *Alopias superciliosus* in waters off northeastern Taiwan were determined from vertebral band counts on 321 specimens (214 females and 107 males) and verified with a length-frequency analysis of 821 specimens (491 females and 330 males). Growth bands formed once a year according to marginal increment analysis and numbered up to 21 and 20 bands for females and males, respectively. The parameters of von Bertalanffy growth equations estimated from vertebral readings were the following: asymptotic precaudal length ($L_\infty$) = 224.6 cm, growth coefficient ($K$) = 0.092/yr, age at zero length ($t_0$) = –4.21 yr for females; and $L_\infty$ = 218.8 cm, $K$ = 0.088/yr, $t_0$ = –4.24 yr for males. The ages at maturity were estimated to be 12.3–13.4 yr for females, 9–10 yr for males. The largest female aged from vertebrae was 20 yr old, the largest male 19 yr old. Length-frequency analysis supported our vertebral ageing estimates.

# Age and growth estimates of the bigeye thresher shark, *Alopias superciliosus*, in northeastern Taiwan waters

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The bigeye thresher shark, *Alopias superciliosus* (Lowe), is circumtropical and subtropical in distribution (Compagno, 1984). It is found over the continental slope around Taiwan and is abundant at depths of 40–100 m in waters off northeastern Taiwan (Fig. 1). Based on daily catch data (1989–1994) from Nan Fan Ao fish market, near Suao, estimates of annual landings of bigeye threshers in number of fish are about 3300, and 220 metric tons (t) in weight, 13% of the total annual shark catch.

Biological information, particularly on reproduction, for bigeye thresher is abundant (Nakamura, 1935; Cadenat, 1956; Bass et al., 1975; Stillwell and Casey, 1976; Gruber and Compagno, 1981; Gilmore, 1983, 1993; Moreno and Moron, 1992; Chen et al., 1997) but little is known about age and growth. Other than Gruber and Compagno's (1981) preliminary estimation on the age and growth of bigeye threshers, no studies have been published. Accurate age structure of stocks is essential for stock assessment and fishery management. This study provides the first information concerning age and growth of bigeye threshers from waters off northeastern Taiwan. Age and growth, from vertebral band counts, were verified with length-frequency analysis.

## Materials and methods

Thresher sharks caught in northeastern Taiwan waters by commercial longlines were sampled at Nan Fan Ao fish market, from September 1993 to October 1994.

Precaudal length (PCL), fork length (FL), and total length (TL) (in cm) were measured and weighed at the fish market. Because caudal fins of bigeye thresher sharks are often damaged, PCL is used throughout this paper, unless otherwise noted. After specimens were gutted, a total of 371 (245 females and 126 males) precaudal vertebrae were removed for age determination. Vertebrae located under the first dorsal fin are often used for age determination (Casey et al., 1985; Branstetter and Stiles, 1987; Chen et al., 1990); samples from two specimens (166 cm and 171 cm PCL) were used to compare variations in banding patterns from centra at different locations along the vertebral column. Precaudal vertebrae had the same band counts as those under

the dorsal fin and were used for age analysis in this study because these are the only vertebrae readily available at market.

X-ray radiography (Cailliet et al., 1983; Cailliet, 1990; Joung, 1993) and staining of vertebrae (Stevens, 1975; Casey et al., 1985; Tanaka, 1991; Joung, 1993) are two methods commonly used to enhance the clarity of bands on vertebrae. The silver nitrate technique of Stevens (1975) was tried but no increase in clarity of bands was observed; hence, we did not use the technique. The x-ray method, which is simpler and yields better clarity of bands with a Java video image analysis system, was used.

A Rigaku industrial x-ray apparatus (model: radioflex 90 GSB) with Fuji industrial x-ray film (fine grain and high contrast) was used to take x-radiographs of vertebral centra. Banding patterns in every x-radiograph were counted three times by one of the authors during a three-month period; only those centra whose band counts were the same for at least two of the three readings were accepted for further analysis. Growth bands included fast-growth and slow-growth zones. The radii of each band and vertebrae were measured on a line from the nucleus (notochord) to the outer edge of each band and to the outer margin of each vertebrae with x-radiography and the Java video image analysis system (Fig. 2).

The time of band formation was estimated from monthly change of marginal increment (MI) with the following equation:

$$MI = (R - r_n)/(r_n - r_{n-1}),$$

where $R$ = the vertebral radius; and
$r_n$ and $r_{n-1}$ = radii of the ultimate and penultimate bands, respectively.

In addition, Tanaka and Mizue's (1979) method was used to identify the ultimate band on the basis of the following stages: opaque zone, narrow translucent zone (the width of translucent zone is smaller than half width of opaque zone), and wide translucent zone (the width of translucent zone is larger than half width of opaque zone).

The growth of bigeye thresher sharks was described with the von Bertalanffy growth equation (VBGE) as

$$L_t = L_\infty\left(1 - e^{-K(t-t_0)}\right),$$

where $L_t$ = the length at age $t$;
$L_\infty$ = the asymptotic length;
$K$ = the growth coefficient; and
$t_0$ = the theoretical age at zero length.

The parameters of VBGE were estimated from a Walford plot (Walford, 1946).

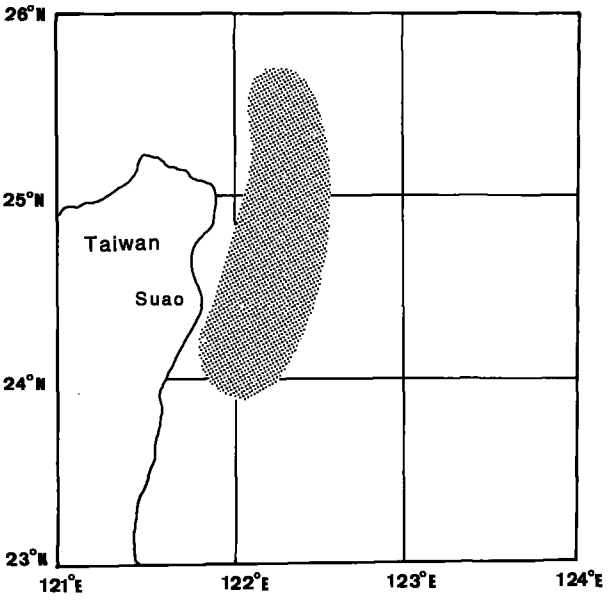


**Figure 1**
Sampling area for *Alopias superciliosus* in northeastern Taiwan waters.

The asymptotic weight was obtained by substituting $L_\infty$ into the weight-length relationship; the VBGE on weight can be expressed as

$$W_t = W_\infty\left(1 - e^{-K(t-t_0)}\right)^b,$$

where $W_t$ = the weight at age $t$;
$W_\infty$ = the asymptotic weight; and
$b$ = the exponent of the weight-length relationship.

Length-frequency distributions of 821 individuals (330 males, 491 females), grouped by season and sex, were analyzed with the computer package MULTIFAN (Fournier et al., 1990) to estimate the parameters of von Bertalanffy growth equations. Initial values of the $L_\infty$ and $K$ were adapted from those obtained in the previous section.

The relation between precaudal length and vertebral radius was tested with an $F$-test, and the difference in regression lines between sexes was tested with analysis of covariance.

## Results

The relation between precaudal length and vertebral radius showed a slightly curved trend for both sexes (Fig. 3) and was statistically significant ($P<0.05$).

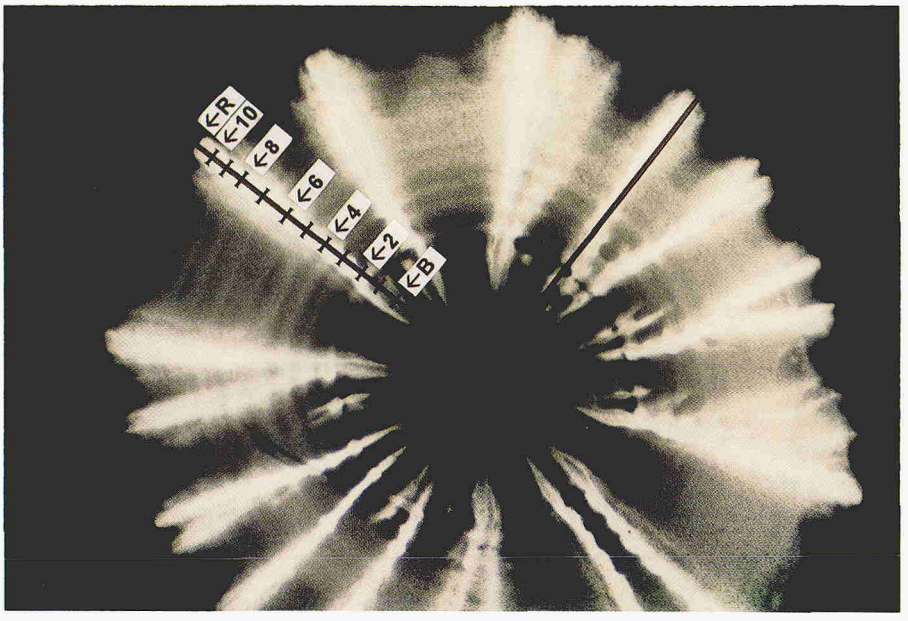


**Figure 2**

X-ray radiograph of *Alopias superciliosus* used for age determination. B = birth mark, R = vertebral centrum radius. Radiating bands are indicated in even years: 2,4,6,8, and 10.

Analysis of covariance indicated that there is significant difference in PCL-R relationships between female and male ($P<0.05$). Therefore, the PCL-R relationships were expressed by sex as follows:

female: $PCL = 50.84\ R^{0.494}$ ($r^2=0.75$, $n=214$),
male: $PCL = 48.91\ R^{0.492}$ ($r^2=0.75$, $n=107$).

Growth bands included two types of growth zones, as shown on the x-radiographs. These varied with season; usually a more calcified zone (translucent zones in Fig. 2) represented growth in summer (Casey et al., 1985; Cailliet et al., 1986; Branstetter and McEachran, 1986).

The vertebral bands numbered up to 21 and 20 for females and males, respectively. Owing to a lack of smaller specimens, the mean vertebral radii of bands I–III for females and I–V for males were interpolated from the relationship between vertebral radius and number of bands. The back-calculated length at band formation was able to be obtained by substituting the mean band radii ($r_i$) for R in the PCL-R relationship (Table 1).

The monthly change in vertebrae (MI) indicated that MI reached its peak in February, 0.60 for males, decreasing thereafter to its lowest value of 0.08 in June, and increasing thereafter (Fig. 4). This trend suggested that a vertebral band was formed once a year in the period April to July. A similar trend was found for females. Following Tanaka and Mizue's (1979) ageing criteria, we found that translucent zones (fast-growth zones) were formed between late spring and early summer, slow growth zones in winter, compa-

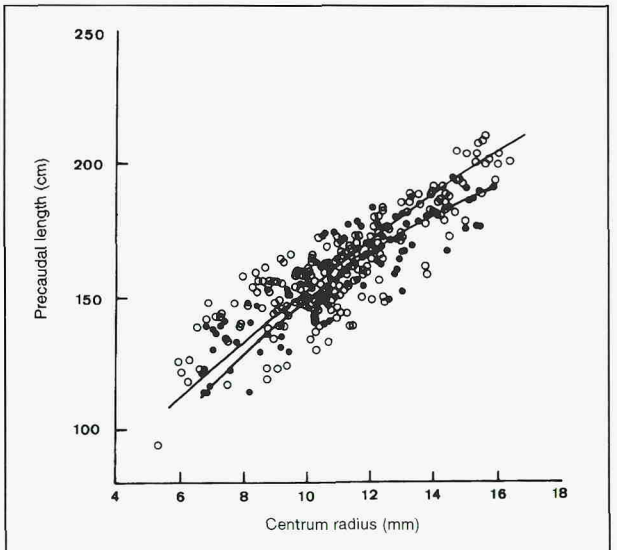


**Figure 3**

Relationship between precaudal length and centrum radius of *Alopias superciliosus*. ○ = female; ● = male.

## Table 1

Back-calculated precaudal length at time of band formation of female *Alopias superciliosus*. *n* = sample size, B = birth.

| | | Precaudal length (mm) | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Annulus | *n* | B | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 |
| B | 0 | 793.26 | | | | | | | | | | | | | | | | | | | | |
| 1 | 0 | 786.92 | 927.03 | | | | | | | | | | | | | | | | | | | |
| 2 | 0 | 780.53 | 921.27 | 1075.37 | | | | | | | | | | | | | | | | | | |
| 3 | 1 | 752.31 | 920.31 | 1054.06 | 1153.59 | | | | | | | | | | | | | | | | | |
| 4 | 3 | 769.59 | 910.14 | 1045.81 | 1146.52 | 1246.83 | | | | | | | | | | | | | | | | |
| 5 | 8 | 759.50 | 877.17 | 1009.42 | 1152.07 | 1239.09 | 1322.33 | | | | | | | | | | | | | | | |
| 6 | 5 | 729.61 | 891.97 | 1023.99 | 1131.02 | 1232.82 | 1317.7 | 1396.33 | | | | | | | | | | | | | | |
| 7 | 6 | 744.71 | 869.95 | 996.40 | 1146.30 | 1224.89 | 1310.77 | 1384.95 | 1463.29 | | | | | | | | | | | | | |
| 8 | 9 | 731.17 | 877.45 | 1024.23 | 1116.53 | 1210.93 | 1304.95 | 1378.55 | 1457.49 | 1532.69 | | | | | | | | | | | | |
| 9 | 11 | 722.11 | 846.30 | 1006.05 | 1109.22 | 1212.38 | 1311.24 | 1372.12 | 1470.92 | 1526.92 | 1590.91 | | | | | | | | | | | |
| 10 | 18 | 705.61 | 862.39 | 987.33 | 1054.89 | 1205.66 | 1272.9 | 1365.65 | 1445.58 | 1521.05 | 1585.60 | 1643.49 | | | | | | | | | | |
| 11 | 24 | 688.53 | 854.31 | 993.75 | 1110.68 | 1199.21 | 1286.75 | 1360.44 | 1418.36 | 1502.87 | 1580.65 | 1637.89 | 1683.24 | | | | | | | | | |
| 12 | 30 | 698.58 | 848.83 | 966.57 | 1089.96 | 1208.97 | 1166.43 | 1377.01 | 1420.21 | 1509.31 | 1567.64 | 1632.73 | 1684.05 | 1742.22 | | | | | | | | |
| 13 | 23 | 657.63 | 821.34 | 981.02 | 1083.27 | 1189.05 | 1275.83 | 1349.21 | 1429.56 | 1520.97 | 1552.99 | 1612.15 | 1678.74 | 1737.38 | 1788.94 | | | | | | | |
| 14 | 24 | 691.83 | 838.97 | 976.53 | 1078.4 | 1151.75 | 1270.93 | 1344.77 | 1423.62 | 1499.39 | 1563.67 | 1622.13 | 1658.14 | 1719.16 | 1783.74 | 1832.89 | | | | | | |
| 15 | 15 | 662.44 | 835.66 | 998.03 | 1074.09 | 1179.65 | 1259.09 | 1340.22 | 1419.59 | 1481.62 | 1559.21 | 1617.77 | 1667.62 | 1726.93 | 1778.81 | 1828.50 | 1870.77 | | | | | |
| 16 | 12 | 684.65 | 856.08 | 972.02 | 1088.92 | 1211.65 | 1262.65 | 1335.28 | 1410.00 | 1490.49 | 1570.17 | 1598.93 | 1662.70 | 1721.47 | 1789.36 | 1823.89 | 1865.81 | 1909.11 | | | | |
| 17 | 9 | 700.93 | 829.29 | 966.96 | 1068.47 | 1171.35 | 1258.29 | 1315.52 | 1410.53 | 1486.23 | 1551.14 | 1608.45 | 1672.07 | 1717.29 | 1769.03 | 1818.86 | 1853.57 | 1904.25 | 1942.43 | | | |
| 18 | 10 | 680.38 | 827.47 | 964.23 | 1064.71 | 1169.11 | 1254.72 | 1326.47 | 1355.76 | 1481.87 | 1546.01 | 1603.51 | 1653.05 | 1712.52 | 1764.76 | 1829.31 | 1856.97 | 1899.38 | 1938.22 | 1966.23 | | |
| 19 | 4 | 679.26 | 826.40 | 962.66 | 1062.00 | 1166.32 | 1252.12 | 1323.27 | 1402.74 | 1479.18 | 1542.23 | 1599.86 | 1649.74 | 1707.81 | 1760.82 | 1810.20 | 1852.30 | 1894.68 | 1933.50 | 1961.51 | 1981.34 | |
| 20 | 2 | 673.64 | 823.19 | 960.05 | 1058.21 | 1164.93 | 1252.12 | 1321.1 | 1401.32 | 1473.79 | 1538.35 | 1595.59 | 1646.88 | 1707.01 | 1759.62 | 1803.90 | 1822.67 | 1893.05 | 1931.90 | 1960.12 | 1980.59 | 2000.57 |
| Weighted mean | | 696.35 | 848.46 | 985.32 | 1091.31 | 1195.33 | 1263.12 | 1355.48 | 1424.73 | 1504.99 | 1566.75 | 1622.46 | 1671.66 | 1727.71 | 1780.21 | 1826.51 | 1860.72 | 1902.87 | 1938.47 | 1964.29 | 1981.09 | 2000.57 |
| SE | | 39.856 | 32.496 | 28.911 | 32.895 | 26.464 | 36.926 | 23.599 | 28.463 | 18.368 | 15.378 | 14.530 | 12.983 | 10.142 | 11.720 | 10.257 | 16.303 | 5.045 | 3.288 | 0.980 | 0.529 | 0.000 |

rable to the results from MI. This finding indicates that one band is formed per year by bigeye thresher sharks.

Chen et al. (1997) estimated PCL at birth for the bigeye thresher shark to be 73.7 cm, similar to our estimated mean length at the birth mark formation (69.6 cm). Because no growth band was found for embryos, the first band was assumed to be a birth mark.

For comparison with other literature that reported total length (TL), PCL and FL can be converted to TL with the following equations:

female: $TL = 15.3 + 1.81PCL$ ($r^2$=0.90, $n$=177);
$TL = 13.3 + 1.69FL$ ($r^2$=0.89, $n$=177);
male: $TL = 15.1 + 1.76PCL$ ($r^2$=0.88, $n$=68);
$TL = 26.3 + 1.56FL$ ($r^2$=0.81, $n$=68).

The relations between body weight and total length, and body weight and precaudal length are described as follows:

female: $W = 6.87 \times 10^{-5} PCL^{2.769}$ ($r^2$=0.88, $n$=421);
$W = 1.02 \times 10^{-5} TL^{2.78}$ ($r^2$=0.90, $n$=175);

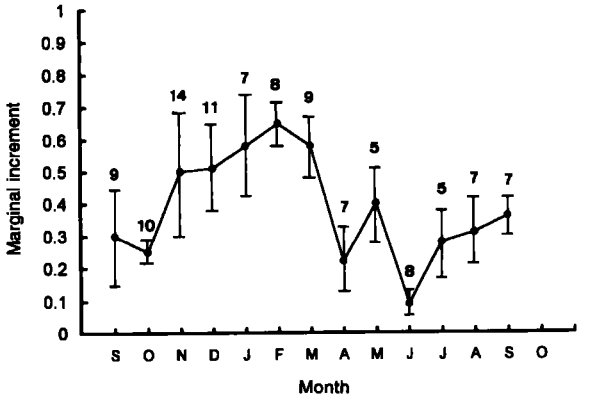


**Figure 4**

Monthly change of marginal increment of male *Alopias superciliosus*. Numbers indicate sample size and vertical bars indicate ±SE.

male: $W = 9.93 \times 10^{-5} PCL^{2.685}$ ($r^2$=0.83, $n$=187);
$W = 3.73 \times 10^{-5} TL^{2.57}$ ($r^2$=0.80, $n$=65).

The parameters of VBGE estimated from band counts for females and males are given in Table 2 and the VBGE in PCL (cm) are

female: $L_t = 224.6 (1 - e^{-0.092(t+4.21)})$;
male: $L_t = 218.8 (1 - e^{-0.088(t+4.24)})$ (Figs. 5, 6).

With the above equations, the asymptotic PCL can be converted to asymptotic TL as 422 cm for female, 385 cm for male. The VBGE in weight (kg) can be expressed as follows:

female: $W_t = 222.8 (1-e^{-0.092(t+4.21)})^{2.769}$;
male: $W_t = 190.5 (1-e^{-0.088(t+4.24)})^{2.685}$.

Female bigeye threshers are estimated to mature between 175 and 180 cm PCL (Chen et al., 1997), 78% and 80% of asymptotic length, and between 12.3 and 13.4 yr old. The largest immature female was 185 cm PCL, 14.6 yr.; the smallest mature female was 154 cm PCL, 8.4 yr. Males mature between 150 and 155 cm PCL (Chen et al., 1997), 69% and 70% of asymptotic length, and between 9 and 10 yr old. The largest immature male was 171 cm PCL, 13 yr; the smallest mature male was 138 PCL, 7 yr (Chen et al., 1997).

The length-frequency histograms for both sexes used in the analysis and results of the best data fits were plotted in Figures 7 and 8, females and males, respectively. In the best fits, age classes 18 and 20 were obtained for females and males, respectively. The estimated modes followed the length-frequency line closely and overlay the peaks well (Figs. 7 and 8). For estimated mean lengths at age of female and males see Table 3. The parameters of VBGE were estimated as $L_\infty$ = 230.5 cm, $K$ = 0.092/yr, $t_0$ = –3.69 for females, and $L_\infty$ = 224.4 cm, $K$ = 0.087/yr, $t_0$ = –4.61 for males; these parameters were similar to those from vertebral band counts (Table 2).

**Table 2**

Comparison of the von Bertalanffy parameters derived from vertebral band count and length-frequency analysis of *Alopias superciliosus*.

| | Male | | | | Female | | | |
|---|---|---|---|---|---|---|---|---|
| Parameters | $L_\infty$ | $K$ | $t_0$ | $n$ | $L_\infty$ | $K$ | $t_0$ | $n$ |
| Vertebral reading | 218.8 | 0.088 | –4.24 | 107 | 224.6 | 0.092 | –4.21 | 214 |
| Length-frequency | 224.4 | 0.087 | –4.61 | 330 | 230.5 | 0.092 | –3.69 | 491 |

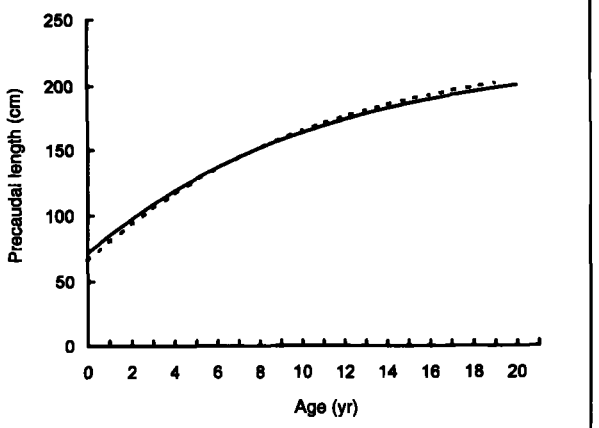


**Figure 5**

The von Bertalanffy growth curve for female *Alopias superciliosus*. (— = vertebral reading, --- = length frequency.

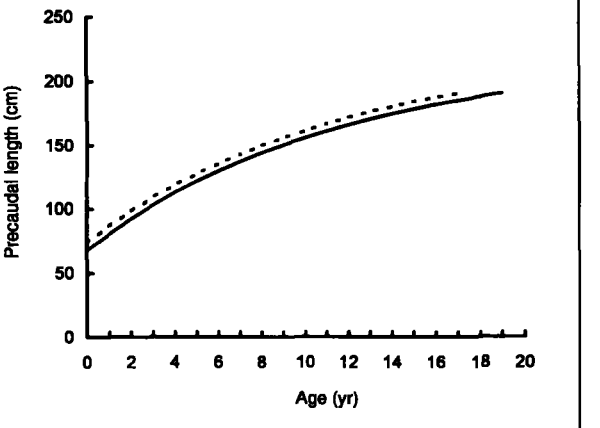


**Figure 6**

The von Bertalanffy growth curve for *male Alopias superciliosus*. (— = vertebral reading, --- = length frequency.

## Discussion

Joung (1993) noted that the ultimate band shown on the x-radiograph was difficult to read with a magnifier. In our study, an image processing system was used to solve this problem.

According to Branstetter (1990), growth coefficients ($K$) in VBGEs falling in the range of 0.05–0.10/yr is a slow-growing species; 0.1–0.2/yr is a moderate-growing species; and 0.2–0.5/yr is a fast-growing species. In this study, $K$ was estimated as 0.092/yr for females, 0.088/yr for males; these are in the slow-growth category. Cailliet et al. (1983) estimated the growth rate of the California common thresher shark (*Alopias vulpinus*) to be 0.108/yr, comparable to our study. Other slow-growing species include the great white shark (*Carcharodon carcharias*) ($K$=0.058/yr, Cailliet et al., 1986), bull shark (*Carcharhinus leucas*)($K$=0.039/yr, Hoenig, 1979), dusky shark (*C. obscurus*) ($K$=0.038–0.039/yr, Natanson et al., 1995), sandbar shark (*C. plumbeus*) ($K$=0.046/yr, Casey and Natanson, 1992, $K$=0.057–0.089/yr, Sminkey and Musick, 1995), scalloped hammerhead (*Sphyrna lewini*) ($K$=0.054/yr, Hoenig, 1979; $K$=0.073/yr, Branstetter, 1987), and *Squalus acanthias* ($K$=0.037/yr, Jones and Geen, 1977).

Most sharks form a vertebral band once each year i.e. *Triakis semifasciata* (Smith, 1984), *Carcharhinus limbatus*, *C. brevipinus* (Branstetter, 1987), *C. plumbeus* (Casey and Natanson, 1992), *C. falciformis*, *Rhizoprionodon terraenovae*, *Galeocerdo cuvieri* (Branstetter and Stiles, 1987), and *Carcharodon carcharias* (Cailliet et al., 1986). Some sharks form two vertebral bands per year, i.e. *Sphyrna lewini* (Chen et al., 1990), *Galeorhinus japonicus* (Tanaka and Mizue, 1978), *Isurus oxyrinchus* (Pratt and Casey, 1983), and *Cetorhinus maximus* (Parker and Stott, 1965). In the present study, although the time of band formation fell within a greater time range, the hypothesis of one band per year was validated by MI and Tanaka and Mizue's (1979) method. Similar results were reported for other species in Alopiidae, i.e. the common thresher sharks (Cailliet et al., 1983) and pelagic thresher sharks (Liao, 1996).

Formation of shark vertebral bands may be related to water temperature, change of prey (Steven, 1975), shark migration, and mating (Pratt and Casey, 1983). Because bigeye thresher sharks have no fixed spawning season, the band formation may not be closely related to mating. Elevated water temperatures in spring and summer are a possible factor in band formation. Jones and Geen (1977) documented that highly calcified bands represent summer growth of vertebral centra. The first vertebral band was assumed to be a birth mark in this study. Similar findings were reported for other species in Alopiidae, i.e. the common thresher sharks, *Alopias vulpinus*, (Cailliet et al., 1983) and pelagic thresher sharks, *A. pelagicus*, (Liao, 1996).

In the present study, ages at maturity were estimated to be 12.3–13.4 yr for females (332–341 cm TL), and 9–10 yr for males (270–288 cm TL). However, Gruber and Compagno (1981) reported younger ages at maturity but similar sizes in the Atlantic Ocean, 4.5 yr (356 cm TL) and 3.5 yr, females and males, respectively. Gruber and Compagno (1981) counted vertebral bands of a 287-cm-TL female and reported 8–11 bands, $2^+$ yr. This length falls in the

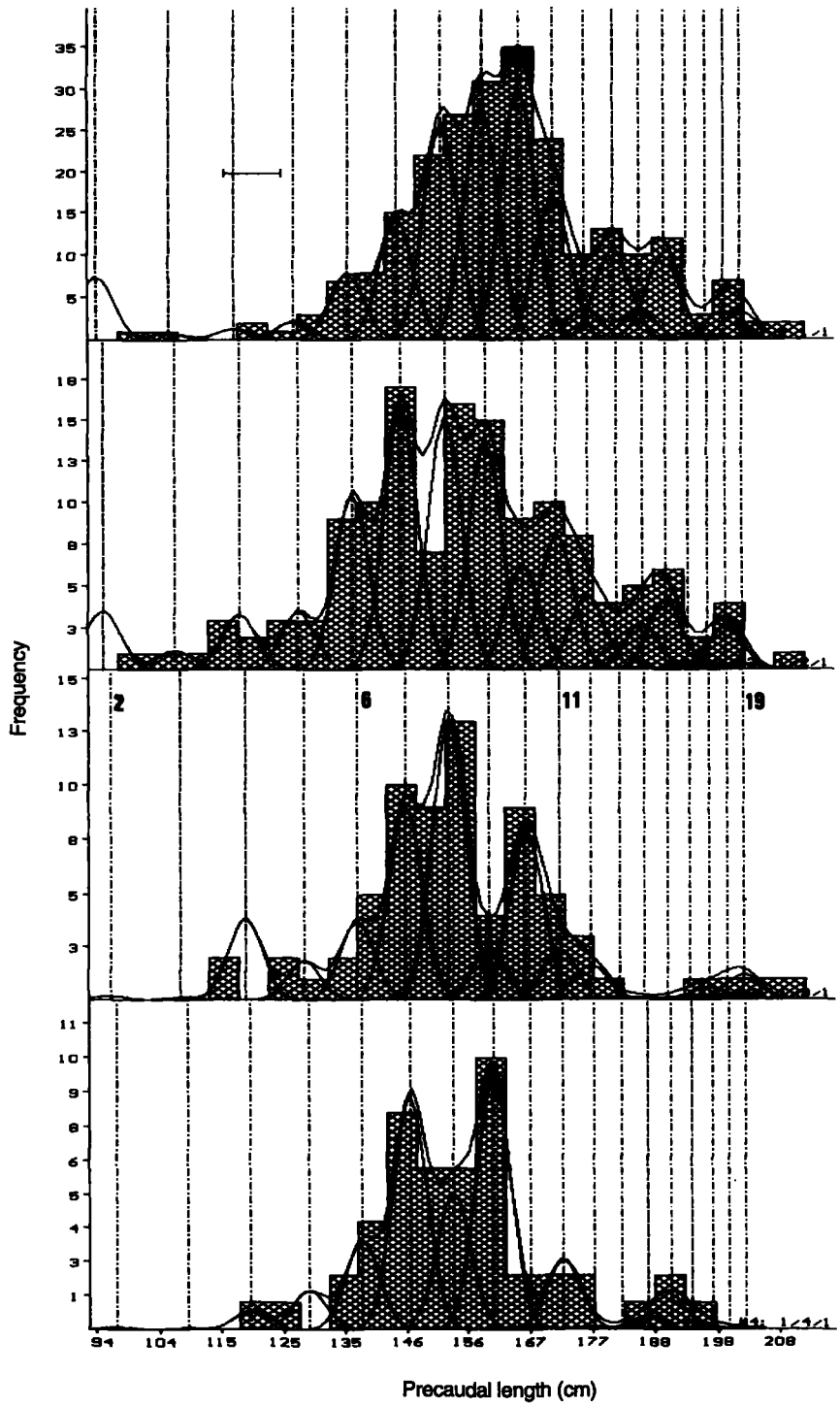


**Figure 7**

Length-frequency histograms for female *Alopias superciliosus* used in the analysis, and results of the best data fits. Horizontal bars indicate the constraints imposed to mean length at age.

**Table 3**

Length (cm) at age estimates (yr) from length-frequency analysis of *Alpias superciliosus*. B = birth.

| Sex | Age (yr) | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | B | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 |
| Female | 66.26 | 80.71 | 93.88 | 105.89 | 116.85 | 126.84 | 135.96 | 144.27 | 151.86 | 158.77 | 165.20 | 170.83 | 176.08 | 180.87 | 185.23 | 198.21 | 192.85 | 196.16 | 199.18 | 201.93 |
| Male | 74.12 | 86.68 | 98.19 | 108.75 | 118.42 | 127.28 | 135.40 | 142.84 | 149.66 | 155.91 | 161.64 | 166.89 | 171.70 | 176.11 | 180.15 | 183.86 | 187.25 | 190.36 | | |

9–10 yr age class according to our estimations. We suggest that the results of Gruber and Compagno (1981), based on Holden's method (1974), may not be an accurate estimate; we believe ours to be more reasonable.

The size at maturity in different areas were similar, i.e. females matured at 332–341 cm TL in this area (Chen et al., 1997), 355 cm TL in the northwestern Atlantic (Stillwell and Casey, 1976), and 340 cm TL in the northeastern Atlantic (Moreno and Moron, 1992). Males matured at 270.1–287.9 cm TL in this area (Chen et al., 1997), 290–300 cm TL in the northwestern Atlantic (Stillwell and Casey, 1976), and 276 cm TL in the northeastern Atlantic (Moreno and Moron, 1992). Thus, size at maturity of the northwestern Pacific populations of *A. superciliosus* was very similar to those of populations elsewhere (Chen et al., 1997).

The maximum TL for female bigeye thresher sharks was 450 cm in Florida waters (Gilmore, 1983), 452 cm in Cuba (Guitart, 1975), 458 cm in New Zealand (Grey, 1928), and 422 cm and 357 cm, female and male, respectively, in this study. Possible reasons why this species is smaller in northeastern Taiwan than in other waters may be due to different environments, genes, gear selection, sampling bias, and fishing mortality.

Age and growth assessment of sharks from hard parts has been verified by length-frequency analysis to increase accuracy (Stevens, 1975; Pratt and Casey, 1983; Natanson et al., 1995). In this study, vertebral and

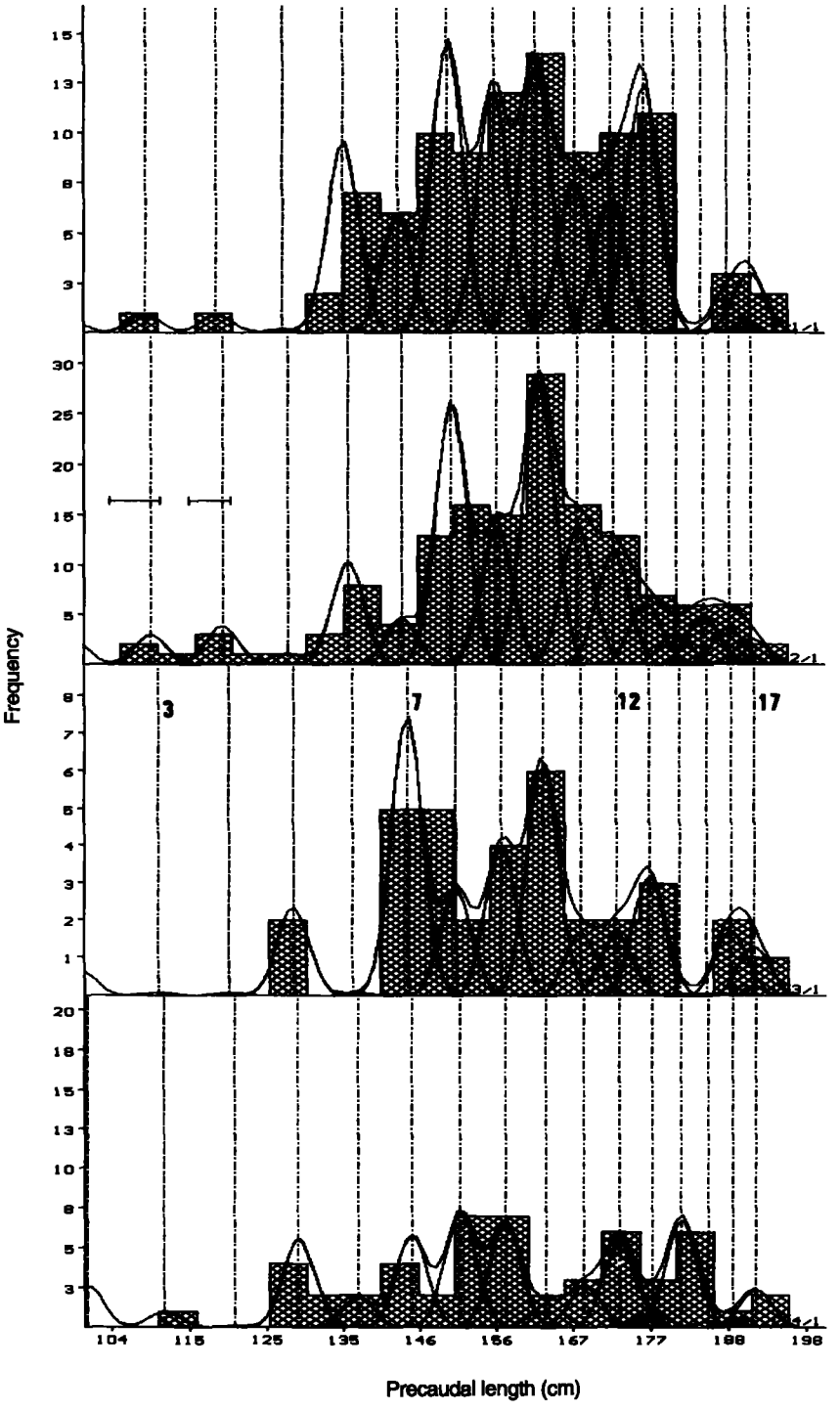


**Figure 8**

Length-frequency histograms for male *Alopias superciliosus* used in the analysis, and results of the best data fits. Horizontal bars indicate the constraints imposed to mean length at age.

length-frequency data were analyzed independently to derive estimates of the von Bertalanffy growth parameters for the bigeye thresher shark. Parameter estimation with MULTIFAN was based on the maximum likelihood method which has been successfully applied to various marine animals (Fournier et al., 1990; Haist and Porter, 1993; Bigelow et al., 1995; Pagavino and Gaertner, 1995). Growth curves derived from MULTIFAN and vertebral band counts are in good agreement for females but the former method yields larger size at age than the latter for males (Figs. 5 and 6). In addition, the similar values of VBGE parameters derived from MULTIFAN and vertebral band counts suggest that the age and growth estimation for bigeye thresher sharks in this study is reliable. The age classes (20 and 18) sliced by MULTIFAN from length-frequency data are less than those from vertebral reading (21 and 20). Small sample size and overlapping lengths at older ages may obscure length modes (Ernizi, 1990), and length-frequency estimates may be somewhat biased because of limitations of data and properties of length-frequency methods (Majkowski et al., 1987; Shepherd et al., 1987; Natanson and Cailliet, 1990). Thus, the vertebral method is considered more robust and the length-frequency analysis is used for verification only.

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# Declines in nearshore rockfish recruitment and populations in the southern California Bight as measured by impingement rates in coastal electrical power generating stations

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**Abstract.**—We used data from fish-impingement studies of the coastal electric generating stations of Southern California Edison Company to examine patterns of nearshore rockfish abundance in the southern California Bight. The impingement data spanned 17 years (1977–93), comprised a minimum of several surveys per month and included power plants from throughout much of the Bight. Sixteen rockfish species were taken and six (olive rockfish, *Sebastes serranoides*; brown rockfish, *S. auriculatus*; bocaccio, *S. paucispinis*; blue rockfish, *S. mystinus*; treefish, *S. serriceps*; and grass rockfish, *S. rastrelliger*) accounted for 99% of all rockfish caught. Most of these fishes were between 0 and 2 years old. Catch rates for all six of these species have dropped substantially since the inception of the survey in 1977. Catch rates peaked in the early 1980s, dropped by a factor of over 100 to a low in 1984, and have generally remained low through 1993. One species, blue rockfish, has not been taken since 1984. We compared our rockfish impingement data from one power station in King Harbor, Redondo Beach, with data from scuba transects conducted during the same period within King Harbor. The results of the two surveys strongly suggest that the catch rates of rockfishes by power plants reflect the abundance of these fishes surrounding the plants. We suggest that the reduction in the abundance of nearshore rockfishes in the southern California Bight is due to both decreased recruitment success, reflecting long-term adverse oceanographic conditions, and to overfishing.

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The oceanographic regime off southern California is extremely dynamic, undergoing decadal changes in temperature, upwelling, and offshore transport (Roemmich and McGowan, 1995; MacCall, 1996). Beginning in 1976, the waters of the southern California Bight (SCB) began to warm and temperatures have generally remained warmer than those of the previous four decades (MacCall, 1996), characterizing part of a process of fluctuating water temperatures that has occurred for thousands of years (Soutar, 1967; Soutar and Isaacs, 1974; Baumgartner et al., 1992).

This warming trend is associated with a decline in upwelling and subsequent decreased zooplankton biomass (Roemmich and McGowan, 1995; Hayward et al., 1996). In addition, several studies in the SCB indicate that this change in the physical regime has led to changes in reef fish population size, community structure, and recruitment (Stephens et al., 1986; Holbrook and Schmitt, 1996). An ongoing 20-year survey at King Harbor, Redondo Beach, as well as one of 13 years duration at Santa Cruz Island, northern Channel Islands, has documented population declines in many fish species (Stephens et al., 1994; Holbrook and Schmitt, 1996). In particular, the King Harbor study shows a severe decline in the abundances of rockfishes (genus *Sebastes*). Some species, such as the blue rockfish, *S. mystinus*, that were very common in the mid-1970s, virtually disappeared by the mid-1980s and have remained absent (Stephens et al., 1986, 1994).

Despite widespread recognition that long-term data are essential for understanding population fluctuations and for correlating changes in population size with environmental events, most studies of reef fishes are limited in both temporal and spatial scales. The few cases where populations have been tracked for many years are limited in spatial scale. Both the Santa Cruz Island and the King Harbor studies, although of relatively long duration, have tracked fish populations at only a single site. A more accurate portrayal of fish abundances would come from multisite surveys, conducted over a number of years. Data from the fish-impingement studies

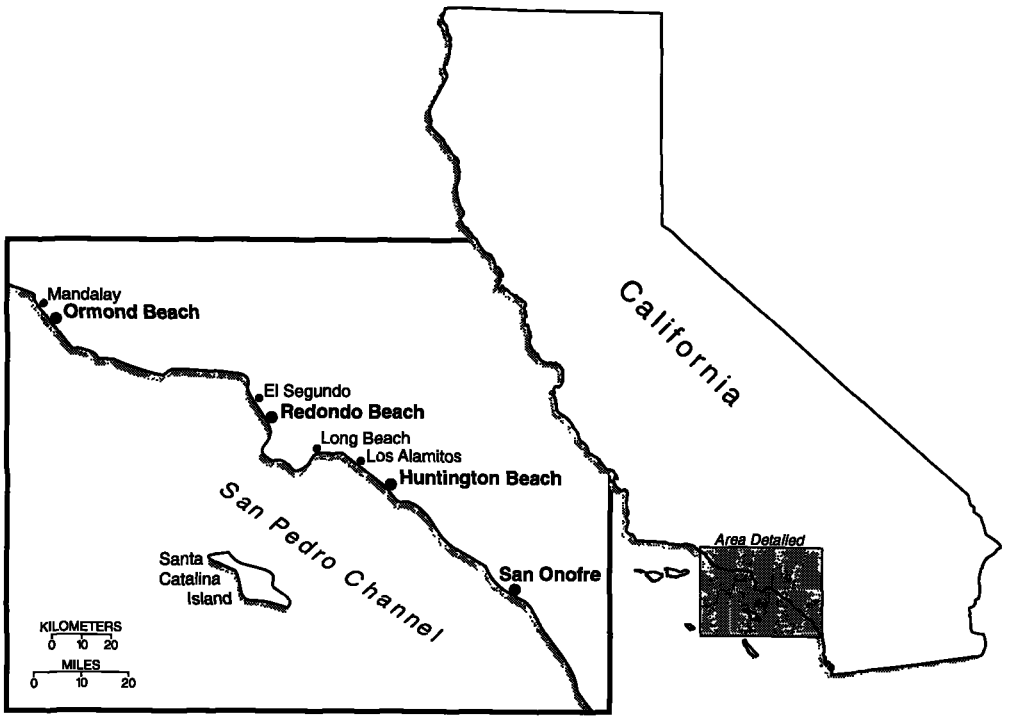


**Figure 1**

Location of the eight Southern California Edison coastal electric generating stations. For this survey, we used fish-impingement data from the four stations indicated in bold.

of the Southern California Edison Company (SCE) provide a unique long-term look at fish populations in the SCB. The impingement data are relatively long-term (17 years), are collected at fine temporal resolution (at minimum several surveys per month), and encompass much of the broad spatial distribution of the SCB.

This paper is the first in a series investigating changes in fish abundances over the past 17 years in the SCB using the extensive data set collected by SCE. Here, we report on patterns of rockfish (genus *Sebastes*) impingement from 1977 to 1993. Although rockfish made up slightly less than 1% of all species impinged in the SCE stations, as a group they are extremely important in both recreational and commercial fisheries in southern California (Wine[1]; Ally et al.[2]; Barsky[3]). In addition to documenting changes in abundance of common species, we discuss patterns of change in abundance in relation to changes in sea surface temperature over the same time period.

## Materials and methods

Data on fish impingement were obtained from the biological monitoring program conducted by Southern California Edison at coastal electric generating stations throughout much of the SCB. Although fish impingement was monitored at all eight stations, we chose to analyze data from the four stations that had the most continuous sampling effort over the period 1977–93 (Fig. 1). Three of the plants, Ormond Beach, Redondo Beach, and Huntington Beach, are fossil fuel fired; San Onofre is a nuclear generating station. Although the timing of sampling among the stations was haphazard, samples were taken at least once and up to 11 days per month. The number of samples taken per year at each station are shown in Table 1.

All power plant intakes are situated on sandy bottom and all are surrounded by varying amounts of rock rubble. Intake openings are at approximately equal depths (8–10 m) with the exception of Redondo Beach station where intakes are situated in slightly deeper water (14 m). The intake openings vary in their distance to the shoreline from 285 m at Redondo Beach to 965 m at San Onofre.

[1] Wine, V. 1979. Southern California independent sport fishing survey. Annual report. 3. Calif. Dep. Fish Game, Mar. Res., Admin. Rep. 79-3.

[2] Ally, J. R. R., D. S. Ono, R. B. Read, and M. Wallace. 1991. Status of major southern California marine sport fish species with management, based on analyses of catch and size composition data collected on board commercial passenger fishing vessels from 1985 through 1987. Calif. Dep. Fish and Game, Mar. Res. Div., Admin. Rep. 90-2, 376 p.

[3] Barsky, K. 1996. California Department of Fish and Game, 530 E. Montecito St., Santa Barbara, CA, 93103. Personal commun.

**Table 1**

Number of fish-impingement samples taken during normal operations at four coastal electrical power generating stations from 1977 to 93.

| Year | Huntington Beach | Ormond | Redondo (units 7–8) | San Onofre 1 | San Onofre 2 | San Onofre 3 |
|---|---|---|---|---|---|---|
| 1977 | 0 | 0 | 87 | 76 | 0 | 0 |
| 1978 | 13 | 13 | 67 | 90 | 0 | 0 |
| 1979 | 55 | 68 | 73 | 93 | 0 | 0 |
| 1980 | 98 | 100 | 103 | 34 | 0 | 0 |
| 1981 | 60 | 58 | 52 | 42 | 0 | 0 |
| 1982 | 47 | 43 | 35 | 19 | 27 | 0 |
| 1983 | 57 | 55 | 48 | 23 | 61 | 8 |
| 1984 | 57 | 50 | 58 | 28 | 65 | 70 |
| 1985 | 56 | 54 | 55 | 63 | 84 | 67 |
| 1986 | 53 | 57 | 49 | 28 | 69 | 101 |
| 1987 | 45 | 57 | 43 | 51 | 57 | 60 |
| 1988 | 41 | 47 | 25 | 42 | 57 | 47 |
| 1989 | 38 | 46 | 47 | 40 | 46 | 58 |
| 1990 | 26 | 37 | 30 | 36 | 55 | 43 |
| 1991 | 16 | 43 | 50 | 48 | 46 | 57 |
| 1992 | 37 | 44 | 38 | 58 | 78 | 68 |
| 1993 | 67 | 40 | 31 | 24 | 65 | 69 |
| Total | 753 | 799 | 737 | 629 | 710 | 648 |

All data presented were obtained during "normal" power plant operations. During normal operation, fishes are entrained in the cooling water and flow through conduits to the station where they are impinged on traveling screens in the forebay of the power plant. "Normal" fish-impingement surveys consist of counting all fishes impinged during a 24-h period of routine plant operations (e.g. on full flow days). Impinged fishes are separated from incidental debris, sorted by species, identified, counted, and measured to standard length (mm).

Because flow rates differed slightly among stations and years, all abundance data are presented as the number of fishes per million gallons of water passing through the intake. Flow rates also varied within each station from month to month but remained constant during any given month. Thus, it was necessary to calculate monthly mean catch rates for each site. Annual mean catch rates are presented in this paper. For most analyses, annual catch is the grand mean of all monthly means across all sites for that year. For one comparison, mean annual catch rates are calculated for the Redondo station only.

**Table 2**

Number of rockfish impinged during normal operations at four coastal electrical power generating stations from 1977 to 93.

| Species | Common name | Number |
|---|---|---|
| *Sebastes serranoides* | Olive rockfish | 14,571 |
| *S. auriculatus* | Brown rockfish | 5586 |
| *S. paucispinis* | Bocaccio | 3262 |
| *S. mystinus* | Blue rockfish | 1640 |
| *S. serriceps* | Treefish | 1124 |
| *S. rastrelliger* | Grass rockfish | 1092 |
| *Sebastes* spp. | Unidentified rockfish | 129 |
| *S. carnatus* | Gopher rockfish | 65 |
| *S. dalli* | Calico rockfish | 44 |
| *S. caurinus* | Copper rockfish | 9 |
| *S. miniatus* | Vermilion rockfish | 8 |
| *S. atrovirens* | Kelp rockfish | 8 |
| *S. goodei* | Chilipepper | 5 |
| *S. melanops* | Black rockfish | 2 |
| *S. ovalis* | Speckled rockfish | 1 |
| *S. maliger* | Quillback rockfish | 1 |
| *S. flavidus* | Yellowtail rockfish | 1 |
| | Total rockfish | 27,546 |

## Results

During this survey, 27,546 rockfishes, representing 16 identifiable species, were caught (Table 2). Olive rockfish (*Sebastes serranoides*) were the most commonly taken, followed by brown rockfish (*S. auriculatus*), bocaccio (*S. paucispinis*), blue rockfish (*S. mystinus*), treefish (*S. serriceps*), and grass rockfish (*S. rastrelliger*). These six most abundant species represented 99% of all rockfish caught. From the lengths of the fishes sampled (Fig. 2), we determined

that most of the rockfishes impinged were between 0 and 2 years old (Love and Westphal, 1981; Love et al., 1990; Love and Johnson, in press).

The life histories of these six species encompass a range of habitat preferences and behaviors. Olive rockfish and blue rockfish are nearshore, midwater fishes. Grass rockfish and treefish are shallow-water benthic species, usually inhabiting high relief. Brown rockfish are found primarily along sand-rock interfaces or over low relief. Bocaccio are midwater fish; the young are found in shallow water and they migrate into deeper water as subadults (Feder et al., 1974).

We analyzed abundance patterns over time for all rockfishes combined and separately for the six most common species. Since the inception of the survey in 1977, mean catch rates for all rockfishes combined have dropped substantially (Fig. 3). Catch rates peaked in the early 1980s, dropped precipitously (by a factor of over 100) to a low in 1984 and have generally remained low through 1993. The exception was a one-year, nearly tenfold rise between 1987 and 1988 which was due primarily to a large influx of young bocaccio, although olive, brown, and grass rockfish catches also increased slightly during this period (Fig. 4).

Despite very different life histories, the six most abundant species showed generally similar impingement patterns over time (Fig. 4). In all six species, peak impingement occurred in the late 1970s or early 1980s. Maximum catches occurred in 1977 (bocaccio), 1980 (grass, blue, and brown rockfish), or 1981 (olive rockfish and treefish). Between 1983 and 1993, with only one exception, impingement of these six species was either extremely low or nonexistent. The exception occurred in 1988, when relatively large numbers of bocaccio were impinged. The 1988 peak in bocaccio abundance was the result of catches at only two stations, Redondo and San Onofre, in May of that year.

Between the late 1970s and early 1990s, there was a sharp drop in the amount of rockfish impingement in the SCE coastal generating stations. We believe that this pattern reflects the abundance of these fishes in nearshore waters at the time. To address this issue, we compared our impingement data for olive rockfish, blue rockfish, and bocaccio with that from visual diving surveys conducted on transects in King Harbor, Redondo Beach (Stephens[4]). The visual surveys primarily record juvenile abundance

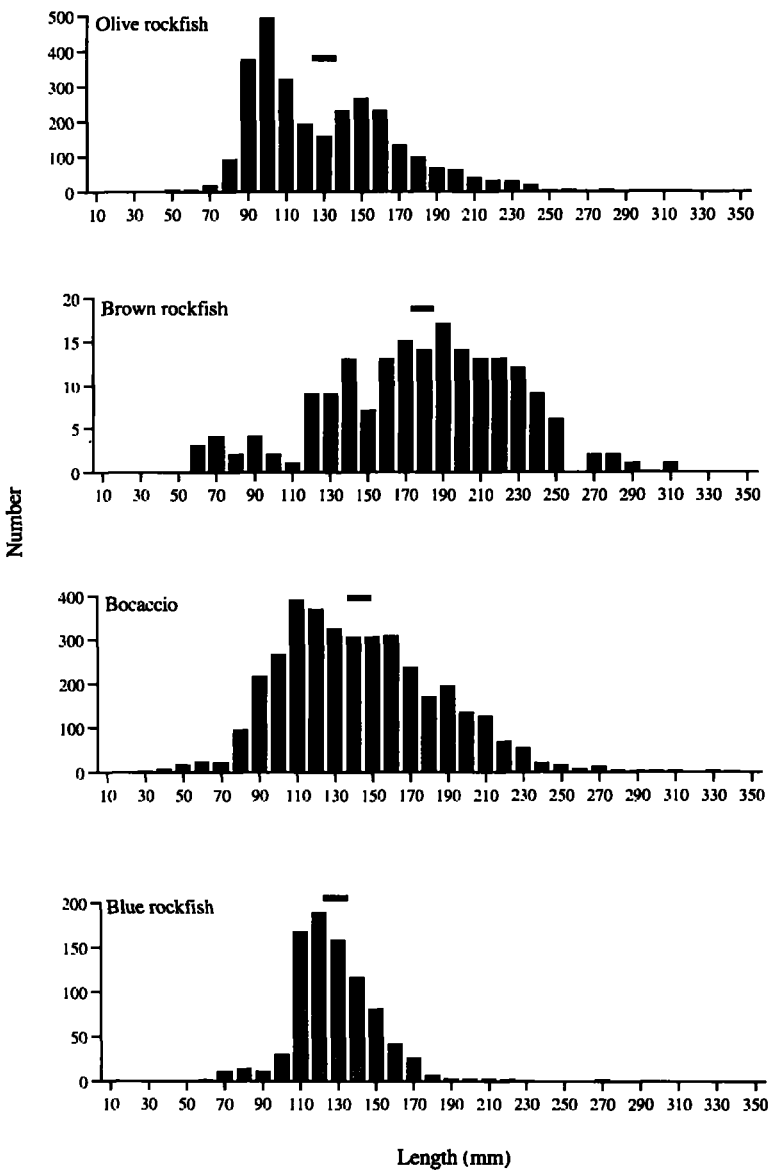


**Figure 2**

Length frequencies (standard length mm) of the four most commonly observed rockfishes in the Southern California Edison impingement studies, 1977–93. Short lines above bars indicate mean length.

[4] Stephens, J. 1997. Department of Biology, Occidental College, 1600 Campus Rd., Los Angeles, CA, 90041. Unpubl. data.

because rockfish of the three target species tend not to remain in King Harbor as adults. For this comparison, we used only the yearly catch rates from the Redondo Beach electrical power generating station that is closest to the King Harbor transects. In the dive survey, all three species were common during the mid- to late-1970s (Fig. 5). However, by 1980, individuals of these species were rarely seen. Blue rockfish and bocaccio have not been observed since that time. Olive rockfish have remained scarce, although small population increases were noted in the late 1980s and early 1990s. The patterns of impingement for these three species at Redondo show similar trends to that from the diver surveys. During the late 1970s, olive rockfish were commonly impinged but catches declined markedly by 1980 (Fig. 5). Two of the slight increases noted in the diver survey in 1985 and 1991 were reflected in the impingement study, although the magnitude of the increase is greater in the SCE data in 1985 and in the diver surveys in 1991. In the impingement survey, blue rockfish catches were relatively high in the late 1970s and declined to zero in 1981 (Fig. 5). This pattern matches precisely the pattern observed in the diver surveys, with one exception. The exception was a one-day pulse of small blue rockfish caught in a single day at the Redondo station in 1982. Regarding blue rockfish, the two data sets are in general agreement; no blue rockfish have either been observed or captured since 1983. Changes in abundance of bocaccio are also similar between the impingement data and the diver surveys (Fig. 5), with the exception of a large pulse of young bocaccio impinged during a single collection in 1988.

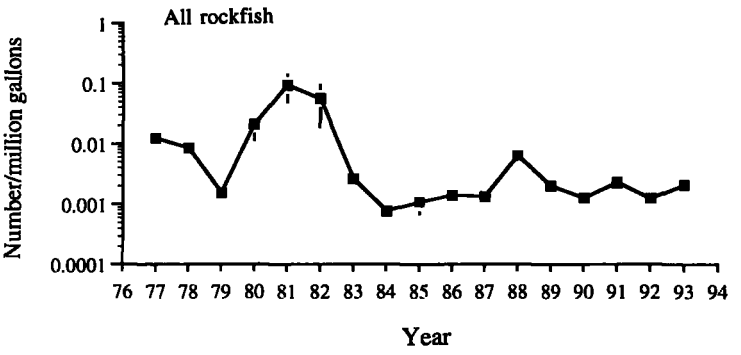


**Figure 3**

Annual number of rockfishes impinged per million gallons of water pumped, for all species of rockfishes combined, 1977–93. Note log scale. See text for description of the calculation of mean. Error bars are ±1 SE.

## Discussion

From at least the 1950s through the late 1970s, black-and-yellow, blue, gopher, and olive rockfishes, as well as young bocaccio, were important components of the inshore rocky reef community of the SCB (Limbaugh, 1955; Ebeling et al., 1980; Larson, 1980; Stephens et al., 1984, 1986; Patton et al., 1985). In particular, blue rockfish and olive rockfish were among the dominant species over many reefs (Carlisle et al., 1964, Ebeling et al., 1980). However, since the early 1980s, most species of rockfishes have nearly disappeared from the nearshore waters of the SCB (Stephens et al., 1994; Larson[5]; Schroeder[6]). On many of the reefs that once held substantial numbers of these species, very few rockfishes remain. Results of the fish-impingement surveys conducted since 1977 support the observation that several species of rockfish are less abundant now than in the late 70s and early 80s. We find it particularly compelling that for at least two species (blue rockfish and grass rockfish), not a single individual was collected in the past ten (blue rockfish) or three (grass rockfish) years.

We feel that the pattern of changing abundance in the impingement study is an accurate reflection of the pattern of change in the nearshore environment. Despite two very different survey methods, the patterns of rockfish abundance derived from the impingement data and the visual survey data from King Harbor were similar. On the gross level, the patterns for three species show amazing similarity; all have declined drastically since the late 70s and have remained low in the 80s and early 90s. On a finer scale, there were several large peaks in the impingement data that were not evident in the visual survey data (Fig. 5: blue rockfish in 1982, bocaccio in 1988). These differences may be due to differences in the ages of some of the fish recorded in the two surveys. Although the visual surveys mainly record juvenile blue rockfish, olive rockfish, and bocaccio, they may occasionally include older individuals, whose population levels may be buffered from the potentially large variations in recruitment by mortality. The impingement collections comprised mainly 0–2 year olds. Both of the large pulses seen in the impingement data were collections taken on a single day.

[5] Larson, R. 1997. Department of Biological Sciences, San Francisco State University, San Francisco, CA 94132. Personal commun.

[6] Schroeder, D. 1997. Marine Science Institute, University of California, Santa Barbara, CA 93106. Personal commun.

It is likely that the decline in rockfish abundance in the southern California Bight was well underway by 1977 when the current impingement surveys started. The King Harbor survey began in 1974 and results showed that the abundance of blue rockfish and bocaccio were at much higher levels from 1974 to 1977 than in later years. For example, blue rockfish were extremely abundant in King Harbor in 1974 but since 1983, not a single blue rockfish has been observed or impinged. There were also occasional impingement collections dating back to 1975 and these also indicate that pre-1977 rockfish catches were as high or higher than 1977 levels. These pre-1977 impingement surveys were too temporally sparse to be included in the complete data set, but they are suggestive. Thus, it appears that, despite larger variation in year to year rockfish impingement during the late 70s and early 80s, there has been an overall decrease since that time which probably reflects a decrease in nearshore populations of these species throughout the southern California Bight (Stephens[4]; Love et al., in press).

Although none of the previously mentioned nearshore studies conducted during the 1950s–1970s were designed to focus on rockfish year-class strength, it appears from these surveys that the widespread abundance of nearshore rockfishes before the early 1980s was generated by a series of strong year classes. During this same period, Southern California trawl studies of two other deeper-dwelling rockfish species implied a similar phenomenon (Mearns et al., 1980). It is likely that recent declines in abundance of these nearshore species were due to a decade-long series of very poor year classes.

What might be responsible for this poor rockfish recruitment? The succession of poor year classes off southern California is likely linked to decade-long changes in oceanographic conditions. Most rockfishes are primatively viviparous (Boehlert et al., 1987) and rockfish larvae are found primarily in the upper mixed layer (Ralston and Howard, 1995). After approximately one month, rockfish larvae metamorphose into pelagic juveniles that spend 3–6 months in the water column as plankton and micronekton

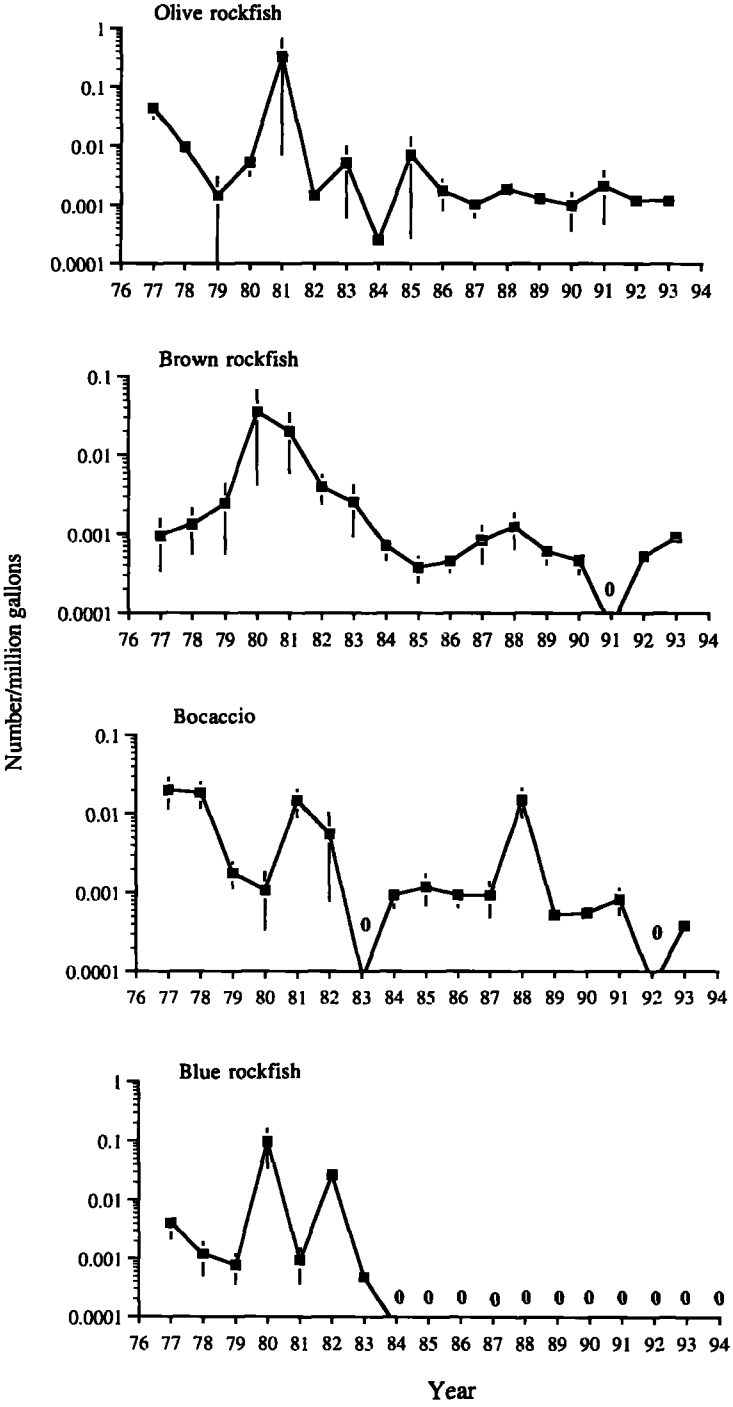


**Figure 4**

Annual number of rockfishes impinged per million gallons of water pumped for the six most commonly impinged species, 1977–93. Note log scale. See text for description of the calculation of mean. Error bars are ±1 SE.

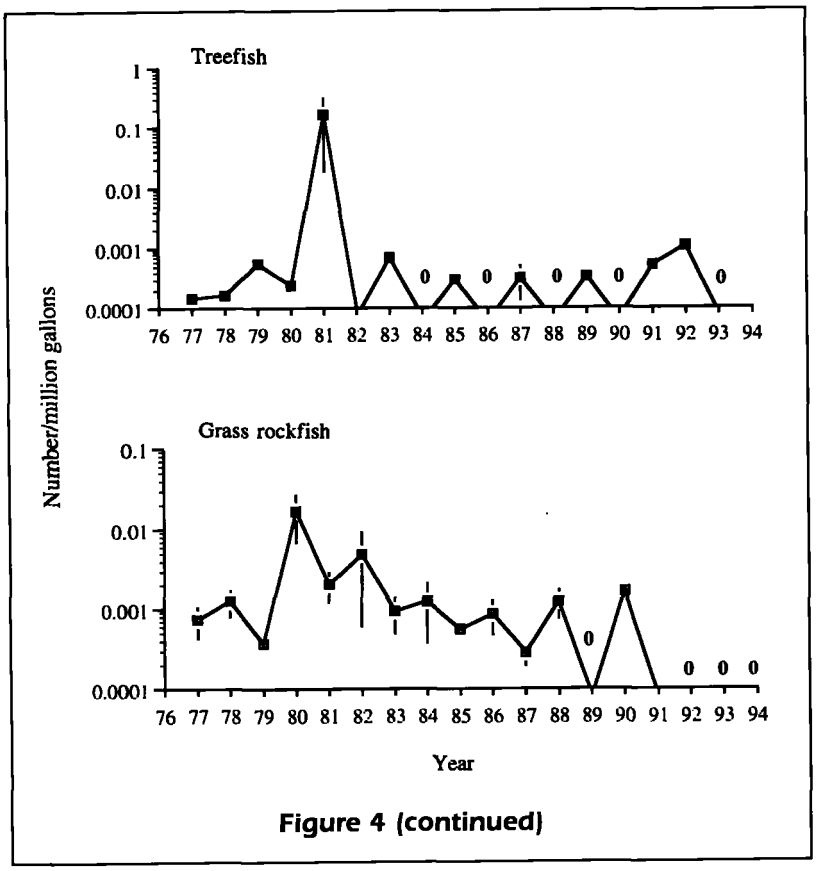


**Figure 4 (continued)**

(Love et al., 1991). It is during the larval and pelagic juvenile stages that rockfish year-class strength is determined (Ralston and Howard, 1995) and upwelling appears to be a particularly important factor affecting survival during these stages. Years with intermediate levels of upwelling seem to correspond with strong year classes (Ainley et al., 1993).

Since the late 1970s, waters in the southern California Bight have warmed approximately 1.5°C and upwelling has declined to approximately one half of the levels observed in the late 70s and early 80s (Norton and Crooke, 1994). In turn, this has led to reduced zooplankton production (Roemmich and McGowan, 1995) and an apparent reduction in the larval and juvenile survivorship of many marine fish species (Holbrook and Schmitt, 1996). The current low-upwelling conditions are probably part of a long-term alternation of warm- and cold-water regimes that extend along much of the northeast Pacific (MacCall, 1996). Poor pelagic juvenile rockfish survivorship of many species also extends at least into central and northern California (Ralston[7]). Juvenile bocaccio recruitment indices for central-northern California (Ralston et al., 1996) show a steady decline similar to the decline we observed for bocaccio in the impingement data.

There has also been a sharp decline in the numbers of both subadult and adult inshore rockfishes in southern California. These reductions are due both to natural mortality and heavy fishery exploitation. Unlike many deeper-water and more northerly species, the inshore rockfishes of California have relatively short life spans, often less than perhaps 25 years (Miller and Geibel, 1973; Love and Westphal, 1981; Love and Johnson, in press). Thus, even without fishing pressure, the number of adults of many of these species would tend to decrease relatively rapidly during extended periods of poor reproduction. In addition, these are also very heavily fished species. Until the early 1990s, most of the catch was made by recreational fishermen (Wine[1]; Ally et al.[2]). Beginning in the early 1990s, a live-fish commercial fishery developed that targets shallow-water species (Barsky[3]).

The sharp decreases in inshore rockfish populations are also mirrored by similar declines in the populations of deeper-water species. Between 1980 and 1996, it appears that there was also a substantial decrease in the numbers of deeper-water rockfishes off southern California. An analysis of the recreational rockfish catch in southern California since 1980 shows steep declines in catches of most of the important species (Love et al., in press). As an example, catches of chilipepper rockfish (*S. goodei*) have declined to 0.5%, bocaccio to 1%, and widow rockfish (*S. entomelas*) to 1.25% of 1980 levels. These declines are almost certainly reflective of lowered abundances of many species rather than a shift in fishing emphasis by recreational vessels.

It is generally held that although reef fish populations exhibit large temporal variations, even undergoing local extinctions, external sources of new young will eventually provide new recruits. Referring specifically to the California coast, MacCall (1996) speculated on the establishment of southern marine species, such as the Pacific seahorse (*Hippocampus ingens*), at the northern ends of their ranges off California. He noted that these animals probably establish themselves during warm-water periods and, in the absence of fishing pressure, may survive colder

[7] Ralston, S. 1996. National Marine Fisheries Service, Tiburon Laboratory, 3150 Paradise Dr., Tiburon, CA, 94920. Personal commun.

periods if the adults suffer low mortality. A similar phenomenon has been described for California sheephead (*Semicossyphus pulcher*) which exhibit episodic recruitment related to anomalous events in current flow (Cowen, 1985).

The reverse of this phenomena has occurred for at least some of the inshore rockfish species, particularly blue rockfish and olive rockfish. In the SCB, both species are near the southern end of their usual geographic ranges and large-scale recruitment may occur only during cold-water cycles, as occurred during the 1960s and early 1970s. During this current warm-water period, recruitment waned and the adult population was expected to decline slowly. However, the continuing fishing pressure on the populations accelerated this process.

On the basis of current flow in the SCB, it is likely that even during periods of successful recruitment, many of the rockfishes in southern California are generated from southern California adults (Reid et al., 1958; Schwartzlose, 1963; Browne, 1993). If true, the sharp drop in the adult populations of many rockfishes is particularly troubling and raises the issue of recruitment overfishing. This is a particularly strong possibility because there is little incentive for recreational anglers to decrease fishing activities on shallow reefs. These rockfishes are caught as part of a species assemblage that includes not only various rockfishes, but also such species as kelp bass (*Paralabrax clathratus*), Pacific barracuda (*Sphyraena argentea*), California sheephead (*Semicossyphus pulcher*), and ocean whitefish (*Caulolatilus princeps*). As long as even moderate numbers of any recreational reef species are taken, recreational vessels will continue to fish on rockfish-depleted reefs and continue to reduce already low numbers of rockfish. Because virtually all inshore reefs in southern California are heavily fished, successful recruitment will likely continue to be hazardous.

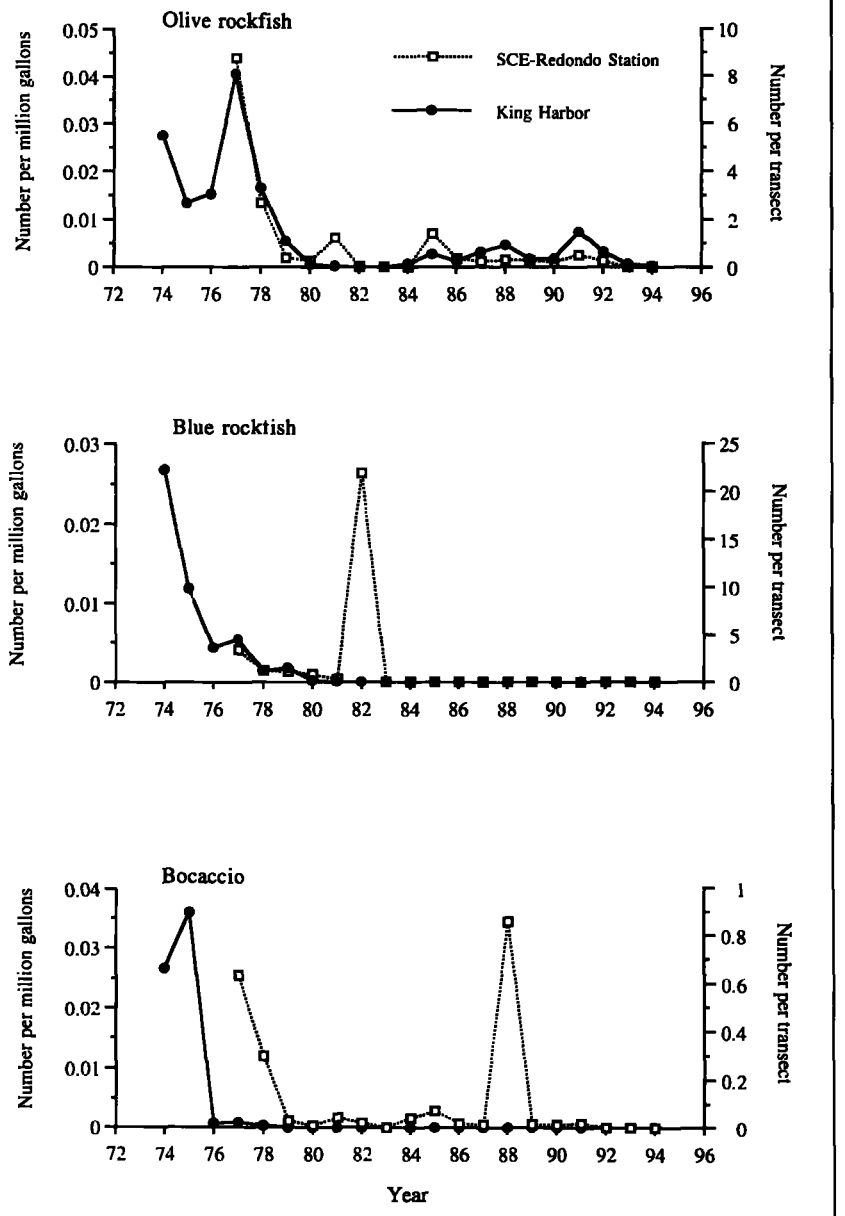


**Figure 5**

A comparison of impingement and diver observations of olive rockfish, blue rockfish and bocaccio from King Harbor, Redondo Beach (1974–94, Stephens[4]) and the SCE Redondo Beach station (1977–94, this study).

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# Geographic variation in genetic and growth patterns of Atka mackerel, *Pleurogrammus monopterygius* (Hexagrammidae), in the Aleutian archipelago

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**Abstract.**—Atka mackerel, *Pleurogrammus monopterygius*, growth data differed significantly by area for length and weight characteristics, suggesting that local aggregations of this species develop differential growth patterns. We analyzed length-at-age and weight-length growth patterns from over 500 fish and 37 protein-coding gene loci to determine the relation among Atka mackerel stocks in the Aleutian Islands. However, the potential stock delineations based on the growth patterns were not supported by the genetic data. Atka mackerel showed a high degree of genetic variability. Variation was detected at 30 of 37 loci; 14 of the 30 loci were variable at the $P_{0.95}$ level. Average heterozygosity for 329 specimens was 0.137, an unusually high value for a marine fish. Between-sample variation among samples was extremely low ($F_{ST}$=0.004), suggesting considerable gene flow throughout the range represented by the samples. On the basis of the genetic data, we cannot reject the null hypothesis that our samples came from a single genetically homogenous population of Atka mackerel. We presume that gene flow occurs throughout the population through the dispersal of pelagic larvae and juveniles. We conclude that despite genetic homogenization, phenotypic variation in Atka mackerel adult life history stages warrants consideration by fishery managers.

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Atka mackerel, *Pleurogrammus monopterygius*, a member of the greenling family Hexagrammidae, is distributed throughout the north Pacific Ocean, the southern Bering Sea, and the Gulf of Alaska. The center of abundance of this semipelagic species is the Aleutian Islands.[1] Greenling larvae and fingerlings (25–30 mm) undergo a pelagic stage and assume an oceanic mode, during which time they reside in the surface layers of the open waters and migrate for considerable distances out to sea (Gorbunova, 1962). Adult (3+ years) Atka mackerel are pelagic during much of the year (in waters <200 m depth) but migrate annually to moderately shallow waters where they become demersal and spawn in areas of strong currents (Gorbunova, 1962). They have specific spawning site preferences and spawning has been observed in island passes in the Aleutian, Shumagin, and Commander Island archipelagoes (Turner, 1886; Rutenberg, 1962).

Historically, large inshore concentrations of spawning Atka mackerel have been the target of subsistence fisheries by native Aleuts (Turner, 1886). The first large-scale commercial catches in the Aleutian Islands and western Gulf of Alaska were taken by Russian fleets beginning in the early 1970s, followed by the Republic of Korea, and to a lesser extent, Japan in the early 1980s (Murai et al., 1981; Berger et al., 1986). Presently, a U.S. trawl fishery harvests Atka mackerel from the eastern Bering Sea and Aleutian Islands regions, with minimal catches from the Gulf of Alaska. From 1992 to 1994, catches averaged about 70,000 metric tons (t) (valued at 17 million U.S. dollars [exvessel] in 1994) and increased to 104,000 t in 1996.[1,2]

[1] Lowe, S. A., and L. W. Fritz. 1996a. Atka mackerel. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands regions as projected for 1997, p. 369–420. North Pacific Fishery Management Council, 605 W. 4th Avenue, Suite 306, Anchorage, AK 99501-2252.

[2] Lowe, S. A., and L. W. Fritz. 1996. Atka mackerel. *In* Stock Assessment and Fishery Evaluation Report for the Groundfish Resources of the Gulf of Alaska as projected for 1997, p. 331–361. North Pacific Fisheries Management Council, 605 W. 4th Avenue, Suite, Anchorage, AK 99501-2252.

An analysis of morphological and meristic data by a Russian scientist indicated separate populations in the Gulf of Alaska and the Aleutian Islands.[3] The meristic study compared the number of dorsal, anal, and pectoral fin rays, total number of vertebrae, and number of gill rakers on the first gill arch from a sample of 100 fish collected off Kodiak Island in the Gulf of Alaska and the Rat Islands in the Aleutian Islands. The morphological study consisted of a statistical comparison of various partial fish body lengths as a percentage of fork length, by area. Lee (1985) also conducted a morphological study analyzing the covariance between four partial fish lengths and fork length by area and sex from samples taken from the Bering Sea, Aleutian Islands, and the Gulf of Alaska. The data showed some differences (although not consistent by area for each characteristic), suggesting a certain degree of reproductive isolation. On the basis of an analysis of variance of Aleutian Islands growth data with year, area, and sex as factors, Kimura and Ronholt (1988) found significant differences in weight and length-at-age of Atka mackerel from six different areas in the Aleutian Islands, indicating potential stock differentiation. Kimura and Ronholt (1988) suggested therefore that Atka mackerel appear to be distributed in localized groups or assemblages once they assume the more demersal phase of their life history. Recent analysis of Aleutian Islands Atka mackerel growth data by current fishery management areas shows a distinctive size cline, with length at age smallest in the western Aleutians and largest in the eastern Aleutians[1,2]

Differential growth by area can be an indication of stock delineations. The presumption for Atka mackerel, based on the morphological and growth analyses, was of at least a discontinuous distribution throughout the Aleutian Archipelago. Genetic tests are necessary to confirm separate stocks and help to further our understanding of the life history and distribution patterns of Atka mackerel. Information about the extent and nature of stock differences is also critical to improve stock assessments for long-term management of the Atka mackerel fisheries in the Gulf of Alaska and Aleutian Islands. To date, there have been no population genetics surveys of this species to determine the existence of discrete stocks.

A preliminary survey of allozymes from 40 individuals indicated a sufficient number of polymorphic loci to conduct a full study of the genetic population structure of this species (Winans et al., 1995). We report here 1) length-at-age and length-weight relations derived from samples taken throughout the Aleutian Archipelago and 2) a genetic survey of Atka mackerel from samples taken from four locations in the Aleutian Islands ranging from 169°W to 172°E (Fig. 1). Our null hypothesis is that there are no differences between samples taken along the Aleutian Archipelago, from Umnak Island in the east to Attu Island in the west.

[3] Levada, T. P. 1979. Comparative morphological study of Atka mackerel. Pac. Sci. Res. Inst. Fish. Oceanogr. 5(TINRO), Vladivostok, U.S.S.R. Unpubl. manuscript, 7 p.

## Materials and methods

### Age, weight, and length data

Biological samples and length and weight information were collected during National Marine Fisheries Service (NMFS) triennial trawl surveys, June to August of 1993 and 1994, from the Gulf of Alaska and Aleutian Islands region, respectively. The sampling coincided with the summer spawning period of Atka mackerel (July to October; McDermott and Lowe, 1997). Random samples of Atka mackerel from the trawl survey catches were sorted by sex, and individual weight and fork-length data were collected. Length was estimated to the nearest one centimeter, and weight was estimated to the nearest gram with a platform scale when weather conditions allowed (Martin and Clausen, 1995). Age structures (sagittal otoliths) were collected by using a length-stratified sampling scheme of five fish per sex, per centimeter length category. An attempt was made to distribute the otolith collections over the entire survey area. Otoliths were placed in vials with 50% ethanol, and age was determined by personnel in the NMFS Age Determination Laboratory.

A total of 510 otoliths were collected and aged (Table 1). Otoliths were prepared by snapping each along the dorsal-ventral plane and passing the broken surface over a flame. The burnt cross-section was examined under a dissecting microscope and illuminated by reflected light (Anderl et. al, 1996).

Growth parameters were estimated by fitting the age-length data to the widely used von Bertalanffy (1938) growth equation:

$$l_t = L_\infty\left(1-e^{-K(t-t_0)}\right),$$

which expresses length at age $t$ ($l_t$) as a function of three parameters: $L_\infty$, $K$, and $t_0$. As age increases, length approaches $L_\infty$, which is the mean asymptotic length. The slope of the von Bertalanffy curve continuously decreases with increasing age as $l_t$ approaches the asymptotic length. This rate of decrease is described by $K$. The parameter $t_0$ is the theoretical time a fish would have been zero length. The

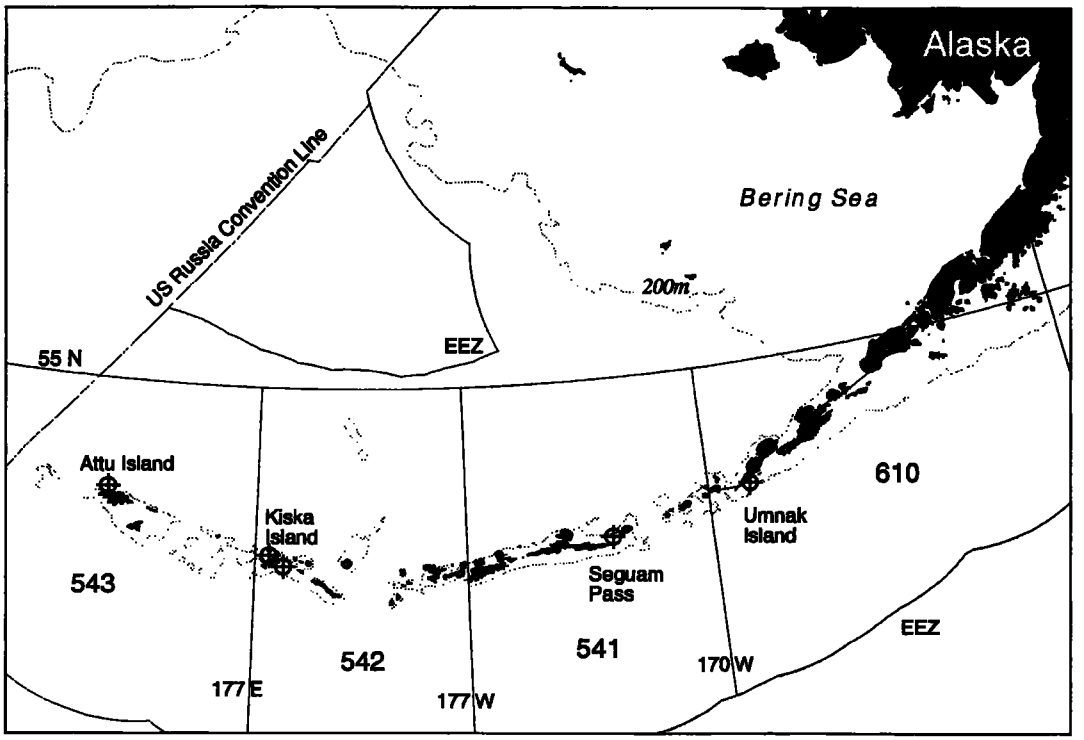


**Figure 1**

Locations of Atka mackerel sample collections in the western Aleutian (543), central Aleutian (542), and eastern Aleutian Islands (541), and western Gulf of Alaska (610) fishery management areas. The U.S. Exclusive Economic Zone (EEZ) is also shown.

growth parameters were determined with a nonlinear least squares procedure (FISHPARM[4]).

Similarly, length-weight relationships were estimated from the following equation:

$$w = al^b,$$

where weight ($w$) varies as a power ($b$) of length ($l$). The coefficients $a$ and $b$ were estimated for each of the four management areas with a nonlinear least squares procedure (FISHPARM[4]). On the basis of the work of Kimura and Ronholt (1988), who found that sex was not an important differentiating variable for growth in Atka mackerel, we present growth curves for the sexes combined.

The age-length and length-weight growth curves for the four management areas were estimated and compared with an $F$-test. To further test for the significance of the differences among areas, regardless of the fit to the von Bertalanffy or length-weight curves, a two-factor analysis of variance (ANOVA) was applied to the age-length and the length-weight data with SPLUS software (Chambers and Hastie, 1992). The age-length ANOVA included age and area as factors and an age × area interaction term, and

**Table 1**

Sample sizes of aged Atka mackerel otoliths from the Gulf of Alaska (area 610), eastern Aleutian Islands (area 541), central Aleutian Islands (area 542), and western Aleutian Islands (area 543) fishery management areas (Fig. 1).

| Age (yr) | Gulf of Alaska (610) | Eastern Aleutian Islands (541) | Central Aleutian Islands (542) | Western Aleutian Islands (543) | Total |
|---|---|---|---|---|---|
| 2 | 22 | 2 | 18 | 19 | 61 |
| 3 | 1 | 7 | 55 | 53 | 116 |
| 4 | 19 | 9 | 22 | 10 | 60 |
| 5 | 43 | 15 | 30 | 25 | 113 |
| 6 | 9 | 44 | 19 | 20 | 92 |
| 7 | 1 | 8 | 7 | 5 | 21 |
| 8 | 0 | 7 | 7 | 8 | 22 |
| 9 | 0 | 1 | 4 | 5 | 10 |
| 10 | 0 | 1 | 1 | 13 | 15 |
| Total | 95 | 94 | 163 | 158 | 510 |

[4] Prager, M. H., C. W. Recksiek, and S. B. Saila. 1987. Nonlinear parameter estimation for fisheries. Michael Prager, Old Dominion University, Dep. of Oceanography, Norfolk, VA 23508. Unpubl. documentation.

**Table 2**

Enzymes examined for allozyme variation. Enzyme commission (EC) numbers follow the IUBMBNC (1992). Tissues examined were muscle (M) and liver (L). Buffers used are described by Aebersold et al. (1987) except for the ACEN7 gel, which is an ACE7 gel with 0.015% beta-nicotinamide adenine dinucleotide added to the gel and which has cathodal electrode buffers.

| Enzyme name | EC Number | Locus | Tissue | Buffer |
|---|---|---|---|---|
| Beta-*N*-Acetylgalactosaminidase | 3.2.1.53 | *bGALA** | L | ACE7 |
| *N*-Acetyl-beta-glucosaminidase | 3.2.1.30 | *bGLUA** | L | ACE7 |
| Aconitate hydratase | 4.2.1.3 | *AH-1** | M | ACE7 |
| | | *AH-2** | L | ACE7 |
| Adenosine deaminase | 3.5.4.4 | *ADA** | M | TBE |
| Adenylate kinase | 2.7.4.3 | *AK** | M | ACE7 |
| Alanine aminotransferase | 2.6.1.2 | *ALAT** | M | TBE |
| Alcohol dehydrogenase | 1.1.1.1 | *ADH** | L | ACE7 |
| Aspartate aminotransferase | 2.6.1.1 | *AAT-1** | M | ACE7 |
| | | *AAT-2** | L | TBCLE, TBE |
| | | *AAT-3** | M | TBCLE, TBE |
| Creatine kinase | 2.7.3.2 | *CK** | M | TBCLE |
| Esterase | 3.1.1.- | *EST** | M | TBCLE |
| Enolase | 4.2.1.11 | *ENO** | M | ACE7 |
| Fumarate hydratase | 4.2.1.2 | *FH** | M | ACEN7 |
| Glucose-6-phosphate isomerase | 5.3.1.9 | *GPI-1** | M | TBCLE |
| | | *GPI-2** | M | TBCLE |
| Glycerol-3-phosphate dehydrogenase (NAD$^+$) | 1.1.1.8 | *G3PDH-1** | M | ACEN7 |
| | | *G3PDH-2** | M | ACEN7 |
| L-Iditol dehydrogenase | 1.1.1.14 | *IDDH** | L | TBCL |
| Isocitrate dehydrogenase (NADP$^+$) | 1.1.1.42 | *IDHP-1** | L | ACE7 |
| | | *IDHP-2** | M | ACE7 |
| L-Lactate dehydrogenase | 1.1.1.27 | *LDH** | M | ACE7 |
| Malate dehydrogenase | 1.1.1.37 | *mMDH** | M | ACEN7 |
| | | *sMDH-1** | ML | ACEN7 |
| | | *sMDH-2** | M | ACEN7 |
| Mannose-6-phosphate isomerase | 5.3.1.8 | *MPI** | M | TBE |
| Peptidase-C | 3.4.-.- | *PEP-C** | M | TBE |
| Phosphoglucomutase | 5.4.2.2 | *PGM** | M | TBCLE, ACE7 |
| Phosphogluconate dehydrogenase (decarboxylating) | 1.1.1.44 | *PGDH** | M | ACE7 |
| Phosphoglycerate kinase | 2.7.2.3 | *PGK** | M | ACE7 |
| Proline dipeptidase | 3.4.13.9 | *PEPD** | M | TBE |
| Pyruvate kinase | 2.7.1.40 | *PK** | M | ACE7 |
| Superoxide dismutase | 1.15.1.1 | *SOD** | L | ACE7 |
| Triose-phosphate isomerase | 5.3.1.1 | *TPI** | M | TBE |
| Tripeptide aminopeptidase | 3.4.11.4 | *PEPB-1** | M | TBE, TC4 |
| | | *PEPB-2** | M | TBE |

the length-weight ANOVA included length and area factors and a length × area interaction term.

## Genetic data

Genetic samples were collected from four locations throughout the Aleutian Archipelago (Fig. 1). Sample sizes were as follows: Attu Island, $n$=74; Kiska Island, $n$=80; Seguam Pass, $n$=100; and Umnak Island, $n$=75. Muscle and liver tissues were collected from each specimen for protein electrophoresis and placed in the onboard freezers until they could be transferred to a freezer set at –80°C.

Genetic variability was examined by using starch gel electrophoresis as described by Aebersold et al. (1987). Initially, we examined 36 enzyme systems, of which 28 were clearly resolved. Those 28 enzyme systems revealed 37 loci. Tissue and buffer combinations for each enzyme are listed in Table 2. Nomenclature for loci and alleles followed Shaklee et al. (1990).

Genetic variability within samples was estimated as average heterozygosity (mean proportion of heterozygous loci per individual), the percentage of polymorphic loci per sample at the $P_{0.95}$ level (frequency of the common allele ≤0.95), and the average num-

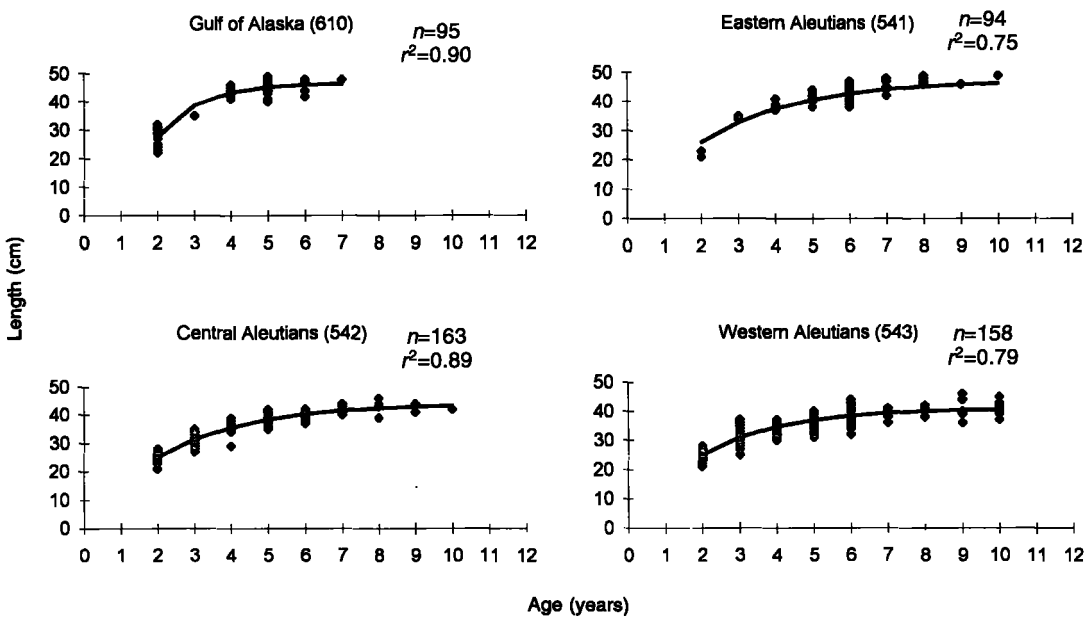


**Figure 2**

Atka mackerel age-length data by fishery management areas, collected from resource assessment surveys of the Gulf of Alaska and Aleutian Islands in 1993 and 1994, respectively. The fitted von Bertalanffy growth curves are plotted. Sample sizes ($n$) and the coefficients of determination ($r^2$) are given.

ber of alleles per locus. Samples were tested individually with chi-square analyses for conformance to expected Hardy-Weinberg proportions and as one pooled sample. The latter method tests the assumption that the samples are not different (i.e. represent one interbreeding population). Differences among samples were examined with Wright's fixation index $F_{ST}$ and Nei's unbiased genetic distance statistic (Nei, 1978) and with standard chi-square contingency table analysis for the $P_{0.95}$ loci. Values of $F_{ST}$ range from zero, indicating no population differentiation, to one, indicating fixation for alternate alleles. Genetic analyses were conducted using the BIOSYS-1 computer program (Swofford and Selander, 1981).

## Results

### Age, weight, and length data

Sample sizes were relatively small when stratified by area, ranging from 95 to 163. Sampled fish lengths ranged from 21 to 49 cm, ages from 2 to 10 years, and weights from 0.084 to 1.9 kg (Figs. 2 and 3). The relatively high coefficients of determination ($r^2$) indicated good fits to the von Bertalanffy and length-weight models (Figs. 2 and 3). An examination of the residuals also indicated no obvious patterns, and the variances of the residuals were homogeneous by age and area for the von Bertalanffy model, and by length and area for the length-weight model. The fitted growth curves for each management are shown together in Figures 4 and 5; Table 3 gives the estimated parameters and standard errors. The $F$-tests revealed that differences in the growth curves among areas were significant ($P<0.0005$) for both the age-length and length-weight data. Because of the low sample sizes for the Gulf of Alaska and eastern Aleutian Islands data, and low numbers of fish in the Gulf of Alaska greater than five years, these data were combined and fit to the von Bertalanffy model. An $F$-test to test for differences between these two specific data sets was highly significant ($P<0.0005$).

The results of the two-way factorial analysis of age-length and length-weight data were highly significant ($P$ of $F \leq 0.0001$, Tables 4 and 5). To account for unequal sample sizes among factors, the ANOVA results in Tables 4 and 5 should be interpreted sequentially. The terms in the tables were added in the order presented, and the $F$-tests were given for each term in sequence. In addition, an ANOVA model was evaluated where the area factor was added first. The result of that $F$-test was also highly significant ($P$ of $F \leq 0.0001$). An examination of the residuals from the age-length and length-weight ANOVA models showed

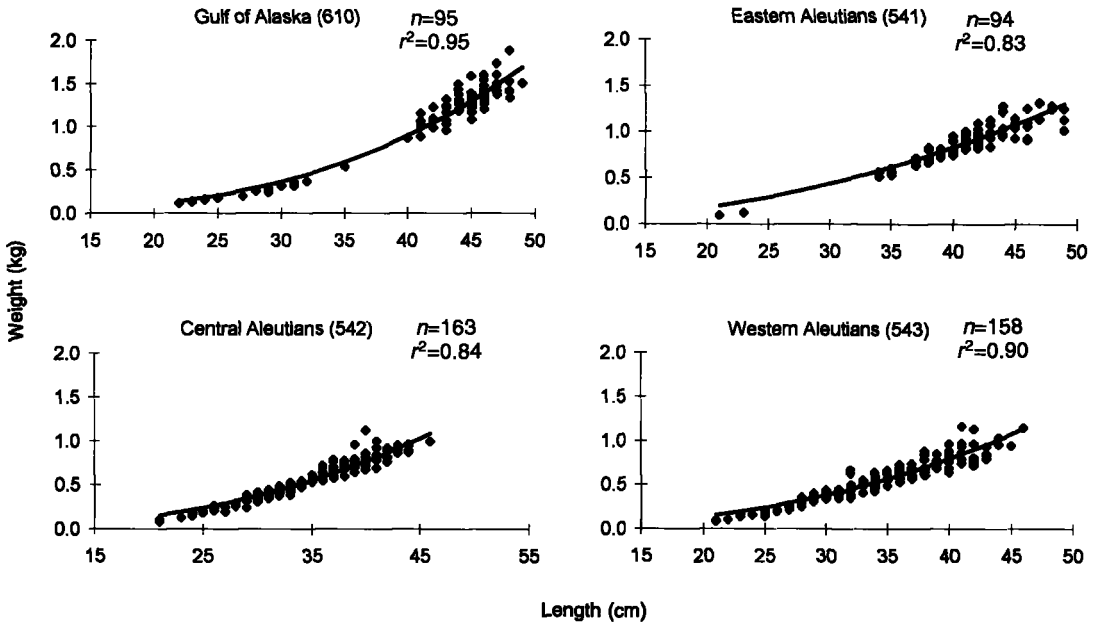


**Figure 3**

Atka mackerel weight-length data by fishery management areas, collected from resource assessment surveys of the Gulf of Alaska and Aleutian Islands in 1993 and 1994, respectively. The fitted weight-length curves are plotted. Sample sizes ($n$) and the coefficients of determination ($r^2$) are given.

no obvious patterns, and the variances of the residuals were homogeneous by age and area, and by length and area, for the age-length and length-weight ANOVA models, respectively.

In order to evaluate the ANOVA model assumption of equality of variances among factors, the distributions of the raw length data by age within each area were examined, and the length distributions at age among areas were compared (Fig. 2), and suggested that the variances do not appear different. Examination of the distributions of the raw weight data by length within each area, and a comparison of the weight distributions at length among areas (Fig. 3), also suggested fairly homogeneous variances. It is noted that the ANOVA model is robust to small departures from the assumption of equal variances (Neter et. al, 1985).

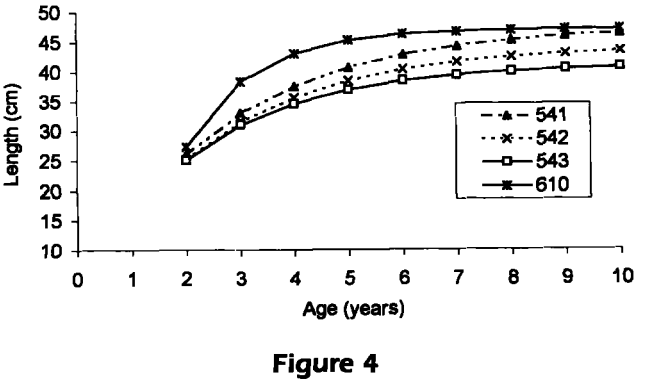


**Figure 4**

Estimated von Bertalanffy growth curves for Atka mackerel by fishery management area (541=eastern Aleutian, 542=central Aleutian, 543=western Aleutian Islands, and 610=western Gulf of Alaska) based on data collected from resource assessment surveys of the Aleutian Islands and Gulf of Alaska during 1993 and 1994, respectively.

## Genetic data

Electrophoretic variation was observed at 30 of the 37 loci (Table 6). A majority of the variable loci (83%) had 2 to 4 alleles per locus. *IDHP-1**, *PEP-C**, and *PGK-1** had 5 alleles each, *AH-2** had 6 alleles, and *ADA** had 9 alleles. There were 14 $P_{0.95}$ loci; the frequency of the common allele at four of these loci (*ADA**, *AH-2**, *ALAT**, and *PEP-C**) was approximately 0.50.

One out of the 120 tests (0.8%) deviated from expected Hardy-Weinberg proportions (at the $P<0.05$ level) in the four samples. The Attu Island sample had an excess of heterozygotes for *ADA** ($P=0.013$).

When the four samples were pooled and tested as one population, none of the 30 tests of polymorphic loci deviated from expected Hardy-Weinberg proportions.

Average heterozygosity ranged from 0.135 to 0.142 (unweighted mean=0.136, Table 7) Percentage of polymorphic loci at the $P_{0.95}$ level ranged from 32.4% to 35.1%, and the mean number of alleles per locus ranged from 2.2 to 2.4. Seventeen unique, rare (frequency ≤0.01) alleles were identified; two each in Umnak Island and Attu Island, four in Kiska Island, and nine in Seguam Pass. Correlation of these alleles with sample size was 0.99.

Allele frequencies were similar for all samples for all polymorphic loci. The largest pair-wise allele frequency difference was 11.7% between Umnak Island ($n$=59) and Seguam Pass ($n$=96) for *ADA**100 (Table 3).[5] Only one of the 14 chi-square contingency tests for the $P_{0.95}$ loci was statistically significant (*AH-2**, $P$=0.004). The total chi-square was not statistically significant ($P$=0.08). Nei's unbiased genetic distance values ranged from 0.0000 to 0.00017 for the four samples. The mean $F_{ST}$ for the 30 polymorphic loci was 0.004.

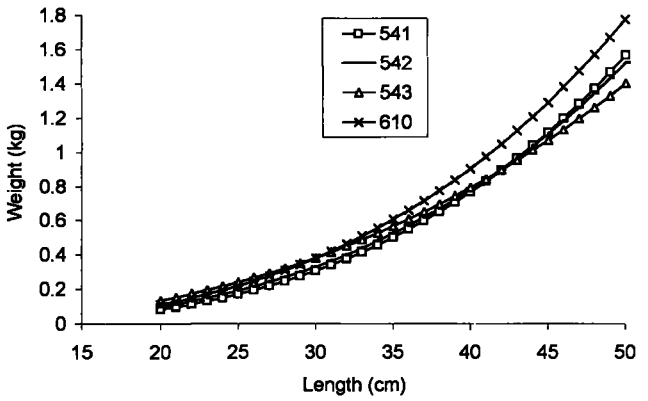


**Figure 5**

Estimated weight-length curves for Atka mackerel by fishery management area (541=eastern Aleutian, 542=central Aleutian, 543=western Aleutian Islands, and 610=western Gulf of Alaska) based on data collected from resource assessment surveys of the Aleutian Islands and Gulf of Alaska during 1993 and 1994, respectively.

## Discussion

### Growth and electrophoretic analyses

Analysis of variance showed that length-at-age and weight-at-age data were statistically different among the four management areas tested. In order to illustrate these differences, the age-length data were fitted to the commonly

[5] The power of this single locus pair-wise comparison is fairly high. For example, the probability of detecting a frequency difference of 0.15 between $P_2$ =0.40 and $P_2$ = 0.55 is 80% for samples consisting of 93 individuals each—similar to these samples sizes (Sokal and Rohlf, 1981). To be 90% certain of detecting such a difference, a sample of 122 individuals is needed.

**Table 3**

Parameter estimates from the von Bertalanffy growth equation ($L_\infty$, $K$, $t_0$), and length-weight relationship ($a$, $b$), standard errors of the parameter estimates, mean square errors (MSE), and sample sizes ($n$) for the western Gulf of Alaska, eastern Aleutian, Central Aleutian, and Western Aleutian Islands.

| | Gulf of Alaska | | Eastern Aleutian Islands | | Central Aleutian Islands | | Western Aleutian Islands | |
|---|---|---|---|---|---|---|---|---|
| | Estimate | Standard error | Estimate | Standard error | Estimate | Standard error | Estimate | Standard Error |
| von Bertalanffy model | | | | | | | | |
| $L_\infty$ | 46.63 | 0.911 | 47.25 | 1.219 | 44.02 | 0.735 | 40.93 | 0.618 |
| $K$ | 0.869 | 0.173 | 0.39 | 0.064 | 0.404 | 0.037 | 0.461 | 0.053 |
| $t_0$ | 0.965 | 0.182 | –0.041 | 0.389 | –0.094 | 0.183 | –0.05 | 0.247 |
| MSE | 5.98 | | 5.36 | | 3.44 | | 6.52 | |
| $n$ | 95 | | 94 | | 163 | | 158 | |
| Length-weight model | | | | | | | | |
| $a$ | 0.859E-05 | 0.452E-05 | 0.237E-03 | 1.103E-04 | 0.878E-04 | 0.316E-04 | 0.652E-04 | 0.190E-04 |
| $b$ | 3.132 | 0.137 | 2.212 | 0.123 | 2.46 | 0.098 | 2.55 | 0.08 |
| MSE | 0.01 | | 0.01 | | 0.01 | | 0.01 | |
| $n$ | 95 | | 94 | | 163 | | 158 | |

**Table 4**

Two-way factorial analysis of variance of Atka mackerel length-at-age data collected from the 1993 and 1994 trawl surveys of the Gulf of Alaska and Aleutian Islands, respectively. The model contains the factors age and area, and an interaction term of age × area. SS = sum of squares.

| Source | df | SS | Mean square | *F*-value | *P*>*F* |
|---|---|---|---|---|---|
| Age | 11 | 14,576.45 | 1325.13 | 275.00 | <0.0001 |
| Area | 3 | 5380.33 | 1793.44 | 372.19 | <0.0001 |
| Age × area | 20 | 260.09 | 13.00 | 2.70 | <0.0001 |
| Error | 477 | 2298.51 | 4.82 | | |

**Table 5**

Two-way factorial analysis of variance of Atka mackerel length-weight data collected from the 1993 and 1994 trawl surveys of the Gulf of Alaska and Aleutian Islands, respectively. The model contains the factors length and area, and an interaction term of length × area. SS = sum of squares.

| Source | df | SS | Mean square | *F*-value | *P*>*F* |
|---|---|---|---|---|---|
| Length | 28 | 59.73 | 2.13 | 278.13 | <0.0001 |
| Area | 3 | 1.21 | 0.40 | 52.77 | <0.0001 |
| Length × area | 56 | 1.65 | 0.10 | 3.85 | <0.0001 |
| Error | 425 | 3.26 | 0.01 | | |

**Table 6**

Allele frequencies for 22 loci in Atka mackerel. "No." represents the number of successfully screened fish. Rare variation is described for 7 alleles[1] and 8 additional loci.[2] Seven loci were monomorphic: *AK**, *CK**, *bGALA**, *bGLUA**, *mMDH-2**, *sMDH-2**, and *PEPB-2**.

| Locus, sample size and alleles | Sample location: Umnak Island | Seguam Pass | Kiska Island | Attu Island |
|---|---|---|---|---|
| *AAT-1** | | | | |
| No. | 39 | 100 | 73 | 74 |
| *-100 | 1.000 | 0.995 | 0.993 | 0.993 |
| *-63 | 0.000 | 0.005 | 0.007 | 0.007 |
| *AAT-2** | | | | |
| No. | 62 | 100 | 80 | 73 |
| *100 | 0.815 | 0.860 | 0.875 | 0.829 |
| *60 | 0.185 | 0.135 | 0.112 | 0.164 |
| *115 | 0.000 | 0.000 | 0.006 | 0.007 |
| *82 | 0.000 | 0.005 | 0.006 | 0.000 |
| *AAT-3** | | | | |
| No. | 70 | 89 | 76 | 73 |
| *100 | 0.900 | 0.916 | 0.888 | 0.925 |
| *110 | 0.100 | 0.084 | 0.112 | 0.075 |
| *ADA** | | | | |
| No. | 59 | 96 | 78 | 72 |
| *100 | 0.534 | 0.417 | 0.449 | 0.444 |
| *75 | 0.280 | 0.292 | 0.269 | 0.285 |
| *89 | 0.025 | 0.036 | 0.026 | 0.021 |
| *110 | 0.008 | 0.031 | 0.064 | 0.049 |
| *115 | 0.000 | 0.010 | 0.026 | 0.000 |
| *120 | 0.110 | 0.172 | 0.135 | 0.174 |
| *130 | 0.034 | 0.016 | 0.032 | 0.014 |
| *140 | 0.000 | 0.010 | 0.000 | 0.000 |
| *155 | 0.008 | 0.016 | 0.000 | 0.014 |
| *ADH** | | | | |
| No. | 69 | 100 | 76 | 67 |
| *-100 | 0.870 | 0.875 | 0.908 | 0.836 |
| *-183 | 0.094 | 0.100 | 0.086 | 0.149 |
| *-250 | 0.022 | 0.025 | 0.007 | 0.015 |
| *-25 | 0.014 | 0.000 | 0.000 | 0.000 |

| Locus, sample size and alleles | Sample location: Umnak Island | Seguam Pass | Kiska Island | Attu Island |
|---|---|---|---|---|
| *AH-2**[3] | | | | |
| No. | 56 | 96 | 80 | 71 |
| *100 | 0.536 | 0.521 | 0.613 | 0.514 |
| *115[a] | 0.384 | 0.354 | 0.300 | 0.366 |
| *120 | 0.054 | 0.063 | 0.044 | 0.070 |
| *117 | 0.009 | 0.000 | 0.019 | 0.014 |
| *94 | 0.009 | 0.005 | 0.000 | 0.014 |
| *84 | 0.009 | 0.057 | 0.025 | 0.021 |
| *ALAT** | | | | |
| No. | 63 | 92 | 78 | 73 |
| *100 | 0.563 | 0.533 | 0.564 | 0.555 |
| *70 | 0.413 | 0.457 | 0.436 | 0.425 |
| *120 | 0.024 | 0.011 | 0.000 | 0.021 |
| *EST** | | | | |
| No. | 62 | 74 | 73 | 61 |
| *100 | 0.645 | 0.608 | 0.541 | 0.648 |
| *90 | 0.290 | 0.345 | 0.390 | 0.303 |
| *110 | 0.040 | 0.041 | 0.062 | 0.033 |
| *85 | 0.024 | 0.007 | 0.007 | 0.016 |
| *G3PDH-1** | | | | |
| No. | 74 | 94 | 80 | 74 |
| *-100 | 0.993 | 0.995 | 0.981 | 1.000 |
| *-70 | 0.007 | 0.005 | 0.019 | 0.000 |
| *G3PDH-2**[1] | | | | |
| No. | 72 | 98 | 67 | 74 |
| *100 | 0.993 | 0.964 | 0.985 | 1.000 |
| *125 | 0.007 | 0.031 | 0.015 | 0.000 |
| *GPI-1** | | | | |
| No. | 73 | 100 | 80 | 74 |
| *100 | 0.904 | 0.880 | 0.881 | 0.926 |
| *25 | 0.096 | 0.120 | 0.119 | 0.074 |

*continued*

**Table 6 (continued)**

| Locus, sample size and alleles | Sample location: Umnak Island | Seguam Pass | Kiska Island | Attu Island |
|---|---|---|---|---|
| *IDDH*[1]* | | | | |
| No. | 63 | 86 | 76 | 74 |
| *100 | 0.984 | 0.948 | 0.954 | 0.973 |
| *165 | 0.016 | 0.006 | 0.007 | 0.007 |
| *25 | 0.000 | 0.041 | 0.039 | 0.020 |
| *IDHP-1** | | | | |
| No. | 100 | 80 | 74 | |
| *100 | 1.000 | 1.000 | 0.988 | 0.980 |
| *65 | 0.000 | 0.000 | 0.000 | 0.007 |
| *140 | 0.000 | 0.000 | 0.000 | 0.014 |
| *MPI** | | | | |
| *100 | 0.971 | 0.969 | 0.994 | 0.993 |
| *110 | 0.014 | 0.020 | 0.006 | 0.007 |
| *116 | 0.014 | 0.000 | 0.000 | 0.000 |
| *90 | 0.000 | 0.010 | 0.000 | 0.000 |
| *PEPB-1*[1]* | | | | |
| *n* | 74 | 90 | 80 | 74 |
| *100 | 0.993 | 0.994 | 1.000 | 0.993 |
| *90 | 0.007 | 0.000 | 0.000 | 0.007 |
| No. | 73 | 99 | 80 | 74 |
| *100 | 0.562 | 0.576 | 0.544 | 0.500 |
| *110 | 0.397 | 0.394 | 0.387 | 0.439 |
| *118 | 0.007 | 0.005 | 0.019 | 0.034 |
| *90 | 0.000 | 0.005 | 0.000 | 0.007 |
| *113 | 0.034 | 0.020 | 0.050 | 0.020 |
| *PEPD** | | | | |
| No. | 63 | 93 | 80 | 74 |
| *100 | 0.738 | 0.742 | 0.794 | 0.804 |
| *110 | 0.222 | 0.226 | 0.175 | 0.182 |
| *120 | 0.024 | 0.011 | 0.025 | 0.014 |
| *92 | 0.016 | 0.022 | 0.006 | 0.000 |
| *PGDH*[1]* | | | | |
| No. | 69 | 99 | 79 | 72 |
| *100 | 0.819 | 0.818 | 0.816 | 0.771 |
| *80 | 0.152 | 0.152 | 0.152 | 0.153 |
| *115 | 0.022 | 0.030 | 0.032 | 0.076 |
| *PGK-1*[1]* | | | | |
| No. | 72 | 100 | 79 | 74 |
| *100 | 0.785 | 0.765 | 0.829 | 0.770 |
| *71 | 0.097 | 0.115 | 0.082 | 0.122 |
| *45 | 0.097 | 0.090 | 0.082 | 0.101 |
| *15 | 0.014 | 0.030 | 0.006 | 0.007 |
| *PGM*[1]* | | | | |
| No. | 74 | 99 | 80 | 74 |
| *100 | 0.926 | 0.960 | 0.944 | 0.953 |
| *80 | 0.074 | 0.040 | 0.050 | 0.047 |
| *SOD** | | | | |
| No. | 75 | 96 | 80 | 74 |
| *100 | 0.993 | 0.964 | 0.981 | 0.993 |
| *190 | 0.007 | 0.036 | 0.019 | 0.007 |
| *TPI** | | | | |
| No. | 74 | 100 | 80 | 74 |
| *-100 | 1.000 | 1.000 | 0.994 | 0.986 |
| *-500 | 0.000 | 0.000 | 0.006 | 0.014 |

[1] Variation at alleles not listed above where the frequency of the allele is < 0.010: *G3PDH-2*90* and *IDDH*40* in Seguam Pass; *IDHP-1*90* and **50* in Kiska Island; *PEPB1*115* in Seguam Pass; *PGDH*70* and *PGK-1*55* in Gulf of Alaska; and *PGM*115* in Kiska Island.

[2] Variation at 8 loci not listed above where the frequency of the alternate allele is < 0.010: *AH-1*118* in Attu Island; *ENO*-180* in Seguam Pass; *FH*77*, and *GPI-2*93* , and **105* in Kiska Island; *IDHP-2*73* in Seguam Pass; *LDH*155* in Attu Island; *MDH-1*150* (*n*=100) and *PK*-350* in Seguam Pass.

[3] A seventh allele (**110*) could not be reliably distinguished from the **115* allele and therefore was pooled with the latter allele.

used von Bertalanffy curve, and the length-weight data were fitted to an allometric length-weight relationship. The *F*-tests on the growth curves determined that there was significant variability in the data among areas that was explained by separate growth curves rather than a single growth curve for all areas combined. Although the Gulf of Alaska and eastern Aleutian Islands data sets were small, data fits to the separate von Bertalanffy models were good, and an *F*-test indicated that separate growth curves were appropriate. There were low numbers of fish greater than five years in the Gulf of Alaska; however, the data set still allowed for fairly precise estimation of the asymptotic length (CV=0.02), the parameter most likely to be affected by the lack of older ages.

Morphological and meristic evidence and growth patterns suggest that Atka mackerel may have some degree of stock separation, at least by broad geographic areas (the eastern Bering Sea, Aleutian Islands, and Gulf of Alaska[1,2,3]; Lee, 1985; Kimura and Ronholt, 1988). The present study is the first genetic

**Table 7**

Within-sample genetic variability over 37 loci.

| Location | Average heterozygosity | Percent of loci $P_{0.95}$ | Average number of alleles/locus |
|---|---|---|---|
| Umnak Island | 0.135 | 35.1 | 2.2 |
| Seguam Pass | 0.142 | 32.4 | 2.4 |
| Kiska Island | 0.135 | 35.1 | 2.3 |
| Attu Island | 0.137 | 32.4 | 2.2 |

survey of Atka mackerel intended to help understand the level and pattern of reproductive isolation among areas thought to be reflected in the areal growth differences. Samples of Atka mackerel were collected during the spawning season when groups of this species are locally aggregated, presumably providing the best separation of potentially reproductively isolated groups.

Our results show that Atka mackerel have above-average levels of genetic variation for a marine fish. The average heterozygosity per locus for Atka mackerel is 0.137, well above the average reported by Ward et al. (1994) for 57 species of marine fish (0.064 ± 0.004). Assuming that the majority of the allozyme variation is selectively neutral (Kimura, 1968), we believe that large levels of genetic variation are most parsimoniously explained by large, historically stable populations. An alternative explanation is that large levels of variability reflect a response to inhabiting a heterogeneous habitat (Avise, 1994). Nonetheless, 30 polymorphic loci provide substantial statistical power to assess the level of between-sample differentiation.

Between-sample variation was extremely low among the four samples of Atka mackerel. In a study where electrophoretic data for marine, freshwater, and anadromous fishes were compared, Ward et al. (1994) calculated an average $G_{ST}$ ( roughly equivalent to $F_{ST}$) of 0.062 for 57 species of marine fish (compared with 0.22 for freshwater species of fish). The $F_{ST}$ for Atka mackerel (0.004) is far smaller than this average, providing evidence that a large amount of gene flow is occurring throughout the range represented by these samples. Very low genetic distance values between samples were observed; the largest distance value between two samples was 0.00017, indicating little or no stock differentiation. Furthermore, the nonsignificant Hardy-Weinberg test of the four samples pooled together did not indicate any between-sample heterogeneity. In light of these two genetic results, we can not reject the null hypothesis that our samples came from a single genetically homogenous population of Atka mackerel. There was also no apparent gradual differentiation throughout the Aleutian Archipelago corresponding to the clinal geographic variation seen in the growth data. Stock delineations based on the age-length and weight-length relationships were not supported by the allozyme data.

## Concordance of electrophoretic and growth data sets

A lack of congruence between genetic and life history characteristics was also found for Pacific ocean perch by Seeb and Gunderson (1988). They analyzed data from the Washington coast to the Bering Sea. Stock delineations based on age structure, age-length relationships, and ages at maturity were not supported by the allozyme data. Although they did not find clear genetic stock differentiation, they did find a cline of gene frequencies within the Gulf of Alaska and significant allele frequency differences between the extremes of the geographic range for some loci.

There are at least three possible explanations for the lack of genetic stock differentiation for Atka mackerel in the Aleutian Islands. First, the genetic technique surveyed invariant gene loci when in fact genetic differences may exist among the sampled stocks. As in any genetic study, the absence of genetic differentiation does not preclude the possibility that true genetic differences exist, and other genetic techniques may be employed to further examine this possibility (Avise, 1994). Second, the species could perform a major spawning migration encompassing the entire population, with mixing and spawning in one area. Third, separate spawning locations are used but gene flow occurs among locations through the dispersal of pelagic larvae and juveniles. We consider the third explanation most likely given the growth differences seen in adult Atka mackerel.

The Aleutian Archipelago encompasses several wide and deep straits that could form barriers to significant movement across the island chain for adult demersal fish residing over the continental shelf. The pelagic behavior of larval and juvenile fish and their presumed distribution in the open ocean habitat, however, would make them susceptible to wide dispersal by currents, thus accounting for the genetic homogeneity among samples. A schematic diagram of the basic surface currents in the north Pacific is shown in Figure 6 (McAlister and Favorite, 1977). The Alaska stream flows westward throughout the Aleutian Archipelago, with significant northward flow to the Bering Sea through Amukta, Amchitka, and Buldir passes. The North Aleutian current flows eastward to Umnak Island providing a thorough mixing mechanism across the Aleutian Island chain. The currents could thus provide the mechanism for sufficient gene flow through the Aleutian chain to actually prevent genetic differentiation. It is presumed that adults do not undertake large-scale migrations and assume a fairly localized existence, which might thus account for the differences in length, age, and weight comparisons of the adults. Observed spawning areas in the Aleutian, Shumagin, and Commander Islands, which have been historically referenced in the literature (Turner, 1886; Rutenberg, 1962), are thus presumed to attract nearby resident schools that migrate inshore.

Although there are no major currents flowing eastward from the Aleutian Islands to the Gulf of Alaska,

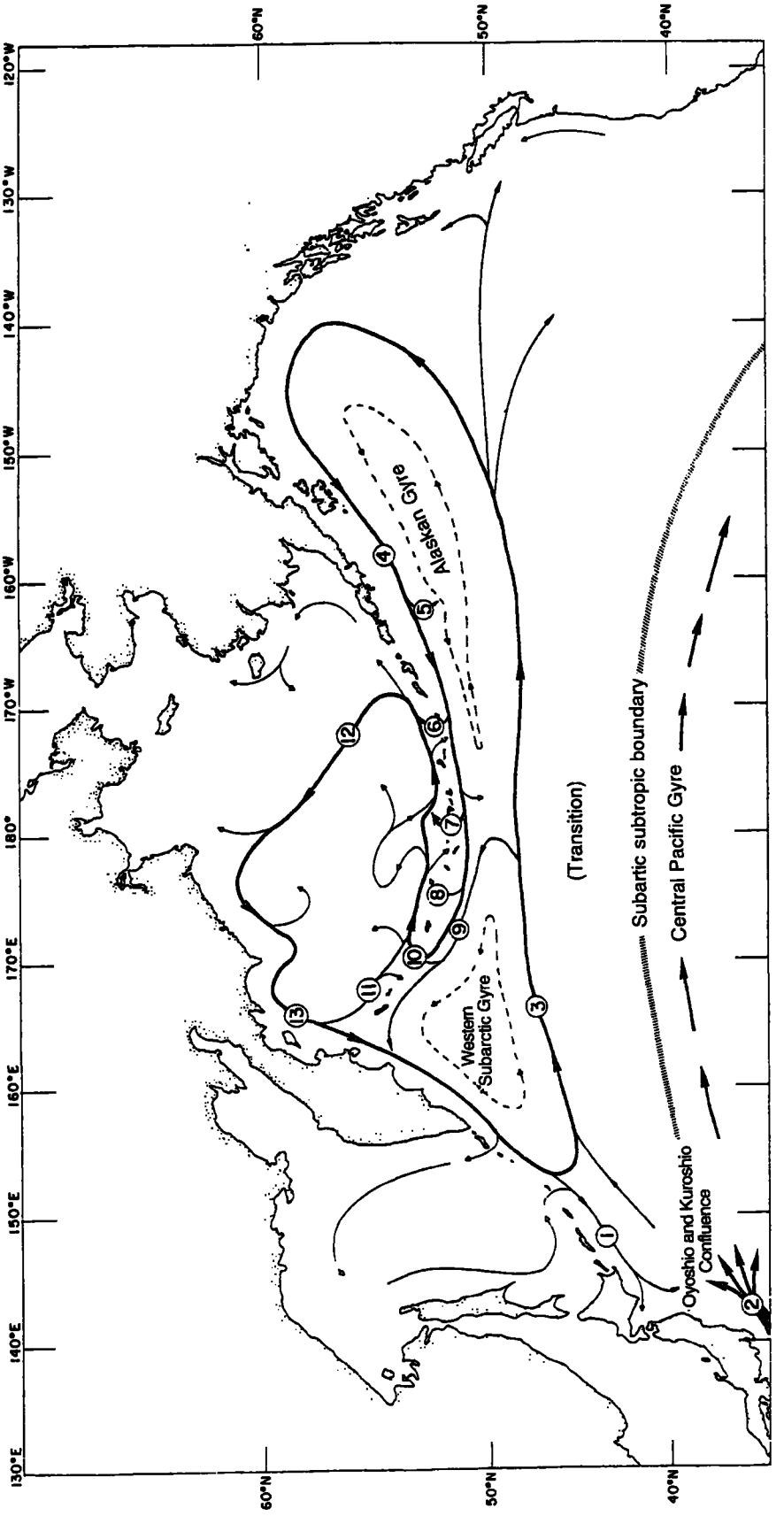


**Figure 6**

Subarctic Pacific region showing the western subarctic gyre and the Alaskan gyre within the subarctic gyre and associated currents. Numbers refer to currents: 1 = Oyashio; 2 = Kuroshio; 3 = subarctic; 4 = Alaskan Stream; 5 = Aleutian; 6 = Amukta; 7 = Amchitka; 8 = Buldir; 9 = west subarctic; 10 = Near; 11 = Commander; 12 = Transverse; and 13 = East Kamchatka (as presented by McAlister and Favorite, 1977).

the western Gulf of Alaska portion of the population may be the result of juvenile or adult migration (or both) or habitat expansion. Kimura and Ronholt (1988) postulated that Gulf of Alaska Atka mackerel are at the extreme limit of their geographic range (the extreme limit of which is populated only during periods of favorable environmental conditions).

Zolotov (1984) found that Atka mackerel spawning habitat in Russian waters extended from the Kamchatka Peninisula through the Kurile Islands almost without breaks. Continuous distribution of Atka mackerel spawning habitat and dispersal of larvae into the open ocean pointed to an absence of mechanisms that would result in reproductively isolated stocks in Russian waters. Zolotov (1984) thus concluded that Atka mackerel did not form ecological groupings along the Kamchatka Peninsula and Kurile Islands but made up a single population. Although we cannot rule out that there are unknown mechanisms or processes which might result in reproductive isolation of groupings of Aleutian Island Atka mackerel, life history information suggests that a process for extensive mixing occurs during the early life stages. We currently do not have any observations to support the necessary processes (e.g. larval retention, natal homing, genetic imprinting), that would result in reproductive isolated populations in the Aleutian Islands.

We interpret the areal growth differences exhibited by Atka mackerel as indications of localized assemblages made up of groupings from a single mixing stock that aggregates during the adult portion of its life history. We suggest that the local specific growth variability seen in adults is a reflection of environmental effects. It is unknown which environmental characteristics might be most influential on growth of Atka mackerel; however, temperature and salinity are noted to be the most important hydrological factors affecting the distribution of hexagrammids, and food, predators, and parasites the most important biological factors (Rutenberg, 1962). Seeb and Gunderson (1988) noted that local growth and age-at-maturity differences could also reflect historical influences and fishing pressure. A large and sustained Atka mackerel fishery has been conducted throughout the Aleutian Islands since the early 1970s. Catches have fluctuated with the demise of the foreign fishery and the development of the domestic fishery, and in recent years the fishery has been concentrated in the eastern Aleutian Islands where the largest fish reside. The fish in the western Aleutian Islands were not heavily exploited from 1980 to 1994, but they have historically been the smallest fish. The geographic size cline noted in the growth data seems to run counter to what we might expect given the differential fishing pressure.

## Stock assessment and management implications

The stock structure of Atka mackerel has stock assessment and fishery management implications. From a stock assessment perspective, we are interested in elucidating the underlying population processes that would result in stock separation, or lack of, and in evaluating the impacts of the fishery on the genetic stock(s), particularly on the spawning concentrations. From a fishery management perspective, the practical recognition of fishery-targeted assemblages (not necessarily genetically distinct) and the spatial and temporal affects of harvesting these assemblages are of interest.

Historically, small-scale Alaskan subsistence fisheries targeted spawning concentrations of Atka mackerel, but the very shallow and presumably rough habitat of the spawning grounds are not accessible to the current large-scale commercial fisheries. Analysis of commercial fishery data indicates that bottom trawling is probably not disturbing the nesting sites.[6] Thus, the unique reproductive life history features of Atka mackerel may provide for some protection of the spawning stock.

Booke (1981) distinguished between inherited (genetic) versus "acquired" or "environmentally induced" characters; the latter including morphological and phenotypic characteristics. Because acquired phenotypic markers by definition are appropriated through contact with the environment, they may not reflect the population genetic characteristics (Avise, 1994). However, acquired markers can serve an important role in population analysis because they can reveal where individuals have spent various portions of their lives (Avise, 1994). From both a stock assessment and fishery management perspective, the localized aggregations of adult Atka mackerel, although not genetically distinct, are important to our understanding of the population dynamics of this species and the impact of the fishery.

Indications of localized populations of Atka mackerel raise the issue of potential localized depletion by the fishery. Another fundamental fishery management and assessment question has been the relation of Gulf of Alaska Atka mackerel to Aleutian Islands Atka mackerel. Atka mackerel are currently managed by two major areas, the Gulf of Alaska and the Aleutian Islands, and by three subareas within the Aleutian Islands. For management purposes, there are at least two catch quotas that must be set given the management area boundary at 170°W which divides the Gulf of Alaska and the Aleutian Islands. Any further subdivisions of the quota are generally based on stock separation rationale or the desire to spread out fishing effort over large geographic areas (or both). The Gulf of Alaska Atka mackerel are assessed separately from Aleutian Islands Atka mackerel, mainly because of the different sources of data (two different survey time series), and to a lesser extent on the presumption that Gulf of Alaska Atka mackerel showed some level of separation from Aleutian Islands Atka mackerel. The results of this study show no evidence of Atka mackerel genetic stock separation between the western Gulf of Alaska and throughout the Aleutian Islands chain. However, because adults show evidence of localized aggregations, it seems appropriate to set at least two separate quotas in Alaskan waters (Gulf of Alaska and Aleutian Islands), with further subdivisions to distribute fishing effort.

The North Pacific Fishery Management Council (NPFMC) implemented Amendment 28 to the "Fishery Management Plan for the Groundfish of the Bering Sea and Aleutian Islands," creating three subareas within the large Aleutian Islands management area (Fig. 1). The impetus for the implementa-

[6] Fritz, L. W., and S. A. Lowe. 1997. Seasonal distributions of Atka mackerel (*Pleurogrammus monopterygius*) in commercially-fished areas of the Aleutian Islands and Gulf of Alaska. NMFS. Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115-0070. Unpubl. manuscript.

tion of additional management areas was the possibility of localized depletion of Atka mackerel by the fishery given the presumed localized distribution of this species and the localized, highly concentrated fishery effort. This study shows that genetically distinct populations of Atka mackerel do not exist in this area, and therefore a significant amount of gene flow may occur among locales within this species. However, gene flow is presumably occurring during the early life stages (larval, juvenile) and is dependent on dispersal by currents. The potential for localized depletion by the fishery at the adult stage is still a concern. Until we have a better understanding of the dispersal and distribution mechanisms affecting Atka mackerel early life stages, management strategies should strive to spread out fishing effort to help reduce the potential for localized depletion. We conclude that despite the genetic homogenization, the phenotypic variation in adult Atka mackerel warrants consideration by fishery managers.

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**Abstract.**—The species *Myxine glutinosa* has long been recognized as encompassing both eastern and western North Atlantic populations. Wisner and McMillan (1995) have proposed splitting the species into *M. limosa* (Girard, 1858; western North Atlantic) and *M. glutinosa* (Linnaeus, 1758; eastern North Atlantic). We examined a variety of morphological characteristics, including cusp counts, slime pore counts (total, prebranchial, trunk, and tail), total length, and body proportions (prebranchial, trunk, and tail length, maximum width and depth, and depth at cloaca). Several western Atlantic populations of varying size were compared with one large sample from the waters between Sweden and Denmark. The results indicate that although specimens from the Gulf of Maine differ significantly from those collected in the eastern North Atlantic, specimens collected from the mid-Atlantic coastal region of the United States and from northern Canadian waters are less distinctive. In addition, there are significant morphological differences among the populations sampled in the western North Atlantic. It is therefore suggested that until and unless molecular data indicate otherwise, the species name *M. glutinosa* be retained as encompassing both eastern and western North Atlantic populations.

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# A population profile for hagfish, *Myxine glutinosa*, in the Gulf of Maine. Part 2: Morphological variation in populations of *Myxine* in the North Atlantic Ocean

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Only one hagfish, *Myxine glutinosa* (Linnaeus, 1758), has been found on both sides of the North Atlantic Ocean; this is the only hagfish reported from within the Gulf of Maine. *Myxine glutinosa* are an important species in the Gulf of Maine because 1) they are present in substantial numbers (densities may reach 500,000/km$^2$), and they may have a considerable impact on the benthic community (Lesser et al., 1996; Martini et al., 1997b), 2) they have direct and indirect effects on commercial fisheries in the Gulf of Maine, through predation on groundfish in fixed gear fisheries and through competition for shrimp, and 3) they have commercial value as the basis for a leather fishery that provided Gulf of Maine fishermen with $1.2 million in 1996.

The first part of this study (Martini et al., 1997a) presents morphological data and a population profile for hagfish in the inner Gulf of Maine. In this report we compare the morphological characteristics of this population with those of *M. glutinosa* populations in other geographical regions. Wisner and McMillan (1995) proposed splitting *M. glutinosa* into *M. glutinosa* (Linnaeus, 1758) for the eastern North Atlantic (ENA) and *Myxine limosa* (Girard, 1858) for the western North Atlantic (WNA). The proposed separation was based on differences in size at sexual maturity, maximum size, and the color of preserved specimens. We undertook this analysis initially to see if there were significant morphometric differences that would support the separation of species. This ultimately led us to perform statistical comparisons among our morphological data, collected in the inner portion of the Gulf of Maine, and the data of other researchers working with eastern and western North Atlantic populations of *M. glutinosa*.

## Materials and methods

Wisner and McMillan included morphometric data for *Myxine* collected over a very broad area. The latitudinal limits were 33°46'N to 66°39'N, and the longitudes ranged from 79°42'W to 52°13'W. Of the 138 specimens cited in their report, only 28 (20%) were collected within the boundaries of the Gulf of Maine. Their study provided detailed data

on the numbers of slime pores (prebranchial, trunk, tail, and total) and total cusp counts for *Myxine* in the eastern and western North Atlantic. Through correspondence with Robert L. Wisner,[1] we obtained data and collection information for 73 western North Atlantic (WNA) and 179 eastern North Atlantic (ENA) specimens. These data sets permitted extensive comparisons with our morphological data for 1478 specimens from the inner Gulf of Maine (WNA).

Methods of measuring and counting followed those of Fernholm and Hubbs (1981) and McMillan and Wisner (1984). The body axis was divided into prebranchial, trunk, and tail regions. The prebranchial measurement extends from the tip of the snout to the anterior margin of the pharyngocutaneous duct (pcd), the trunk continues to the anterior margin of the cloaca, and the tail region extends from that point to the tip of the tail. The sum of these measurements is equal to the total length (TL). The proportional measurements were recorded in millimeters and converted to percentages of total length. Additional data included body depth, body width, cloacal depth, and tail depth (in mm and %TL); total slime pore count (TP) with prebranchial, trunk, and tail counts (as values and %TP), and total cusp counts.

Morphological data were collected from 306 hagfish from the inner Gulf of Maine during five years of trap surveys at depths of 120–150 m by staff and students of the Shoals Marine Laboratory. Samples were collected from late June to early September. The traps used in this study were comparable to those set by the commercial hagfishing fleet. The trap used on most trips consisted of a weighted garbage can with 5–7.5 cm holes in the side and an inner, baited trap of wire screening. After collection, the animals were transferred to tanks of chilled seawater (2–6°C) at 32–35 ppt salinity for transport to the marine laboratory. All measurements were taken on fresh specimens. Total length data from these samples were combined with length data provided by the New England Fisheries Development Association for 1172 hagfish collected by fishermen within 80 km of the shoreline in the southern Gulf of Maine over the period of June–July 1995. All specimens were collected at depths of 120–180 m.

Samples from elsewhere in the North Atlantic were collected by either trawling or trapping at depths of 30–600 m between 1965 and 1987 (Wisner[1]). Collections in the eastern North Atlantic were from midsummer (August); those from the western North Atlantic were from all seasons. The morphological data from these collections were recorded from preserved specimens by Robert L. Wisner and Charmion McMillan. An analysis of variance was performed on the data with the fixed effect of collection site by using Statview 4.5 (Abacus Concepts Inc., 1995). This analysis consisted of post-hoc multiple comparison tests (Scheffe *F*-test) at the 5% level of significance.

## Results

When plotted out on regional charts (Fig. 1), the data

[1] Wisner, R. L. 1996. Marine Biology Research Division, Univ. California, San Diego, La Jolla, CA 92093-0202. Unpubl. data.

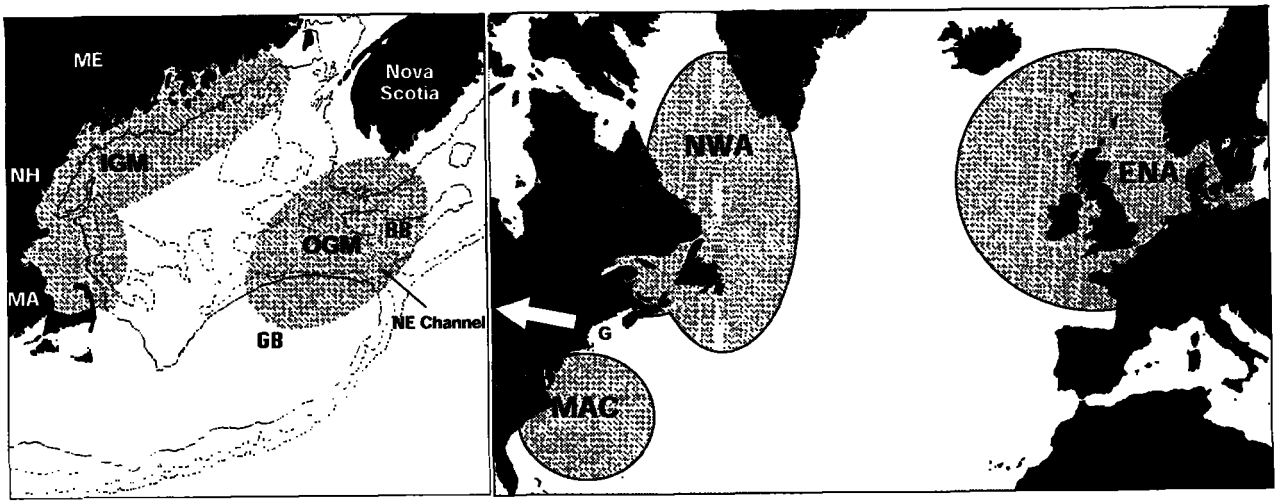


**Figure 1**

Sampled populations of *M. glutinosa* in the eastern and western North Atlantic. The shaded areas indicate the approximate range of collection sites for each data set. (**Left**) Collection sites within the Gulf of Maine. The 100-m, 200-m, and 300-m depth contour lines are indicated. OGM = outer Gulf of Maine; IGM = inner Gulf of Maine; BB = Brown's Bank; GB = George's Bank (**Right**) Other collection sites in the North Atlantic. ENA = eastern North Atlantic; NWA = Northwest Atlantic; G = Gulf of Maine (see [left]); and MAC = mid-Atlantic coast.

**Table 1**

Morphological measurements for *Myxine glutinosa* in the eastern and western North Atlantic. Asterisks indicate values significantly different ($P<0.0001$) from the Eastern Atlantic population.

| Character | Mean | SD | Range | %TL[1] | SD | Range | *n* |
|---|---|---|---|---|---|---|---|
| Eastern North Atlantic group (ENA) | | | | | | | |
| Total length (mm) | 299 | 31 | 227–387 | 100 | | | 179 |
| Prebranchial (snout:pcd) | 82 | 8 | 61–101 | 27.4 | 1.1 | 24–31 | 179 |
| Trunk | 174 | 20 | 133–227 | 58.2 | 1.5 | 54–62 | 179 |
| Tail | 44 | 5 | 33–59 | 14.9 | 0.9 | 12–18 | 179 |
| Width | 14 | 2 | 10–21 | 4.9 | 0.5 | 3–6 | 179 |
| Depth (trunk) | 18 | 3 | 13–26 | 6.1 | 0.6 | 5–8 | 179 |
| Depth (cloaca) | 14 | 2 | 10–20 | 4.7 | 0.5 | 4–7 | 179 |
| Depth (tail) | 15 | 2 | 12–20 | 5.1 | 0.4 | 4–6 | 179 |
| Inner Gulf of Maine group (IGM) | | | | | | | |
| Total length (mm)[2] | 524* | 102 | 170–950 | 100 | | | 1478 |
| Prebranchial (snout:pcd) | 135 | 27 | 54–200 | 26.7* | 1.6 | 24–37 | 143 |
| Trunk | 311 | 72 | 28–459 | 61.4 | 5.9 | 42–83 | 143 |
| Tail | 64 | 14 | 25–106 | 12.6* | 1.2 | 9–17 | 143 |
| Width | 14 | 7 | 4–35 | 2.7* | 1.1 | 2–6 | 91 |
| Depth (trunk) | 22 | 7 | 8–35 | 4.2* | 0.7 | 2–7 | 87 |
| Depth (cloaca) | 19 | 5 | 6–28 | 3.7* | 0.5 | 2–5 | 198 |
| Depth (tail) | 20 | 5 | 8–30 | 4.0* | 0.5 | 2–5 | 97 |

[1] %TL = Percentage of total length. Values were log-transformed before comparison.
[2] Combined data, from Martini et al., 1997a, and Kuenstner, 1996.

collection sites fell into four groups: 1) mid-Atlantic coast (MAC), from the latitude of Charleston, South Carolina, to the southern coast of New England ($n$=51, with data on total length, slime pore counts, and cusp counts), 2) the outer Gulf of Maine (OGM), from the area of Brown's Bank ($n$=13, with data on total length, slime pore counts, and cusp counts), 3) the northwestern Atlantic (NWA) off Labrador, including Davis Strait ($n$=9, with data on total length, slime pore counts, and cusp counts), and 4) the eastern North Atlantic (ENA), from the Skaggerrack, between Sweden and Denmark ($n$=179, data on total length, proportional lengths, slime pore counts, and cusp counts). Our data set comprised a separate group, 5) the inner Gulf of Maine (IGM), represented by samples from within 80 km of the shoreline ($n$=1478 for total lengths, $n$=143 for proportional measurements, $n$=94–97 for slime pore counts and cusp counts).

Comparisons of morphometric data for the ENA and IGM populations, the two groups for which the greatest number of measurements were available, showed differences in total length and proportional measurements (Table 1). Table 2 presents data on cusp counts and slime pore counts for all groups (NWA, IGM, OGM, MAC, and ENA). The proportional measurements expressed as %TL and %TP were log-transformed before analysis and retransformed for presentation in the tables. Figure 2 illustrates the results of the post-hoc multiple comparison tests (Scheffe $F$-test) at the 5% level of significance. Table 3 details these results. Table 4 compares the data on total length for the sampled populations.

These results can be briefly summarized as follows:

1 The NWA sample, closest geographically to the ENA population, can be distinguished from the ENA only in terms of the trunk slime pores as a percentage of the total slime pore count. The total length data for the NWA and ENA groups are not significantly different.
2 The NWA sample is distinct from the OGM sample in terms of the total slime pore count and differs from the IGM sample with regard to prebranchial, trunk, and total slime pore counts as well as the total cusp count. The differences in regional slime pore count between the NWA and IGM samples were not significant when compared as percentages of the total slime pore count.
3 The OGM sample differs from the ENA sample in terms of the total slime pore count, and from the IGM sample in terms of the trunk slime pore count (as a value, not as a percentage of total slime pores) and in the total slime pore count. The total length data for the OGM and ENA groups were not significantly different, but the OGM animals were significantly smaller than those of the IGM.
4 The mid-Atlantic coastal group (MAC) has characters that overlap those of other groups. The MAC

**Table 2**

Tooth cusp counts and slime pore counts for populations of *Myxine glutinosa* L. in the eastern and western North Atlantic. Parenthetical values refer to the data expressed as a percentage of the total number of slime pores.

| Character | Population | Mean | SD | Range | *n* |
|---|---|---|---|---|---|
| Total cusp count | NWA | 32 | 1 | 31–34 | 9 |
| | OGM | 35 | 2 | 33–39 | 7 |
| | IGM | 35 | 2 | 28–40 | 97 |
| | MAC | 35 | 2 | 30–38 | 51 |
| | ENA | 34 | 1 | 29–38 | 101 |
| Total slime pore count | NWA | 95 | 2 | 91–101 | 9 |
| | OGM | 106 | 4 | 100–113 | 13 |
| | IGM | 114 | 7 | 91–128 | 94 |
| | MAC | 100 | 4 | 91–108 | 51 |
| | ENA | 96 | 5 | 85–108 | 143 |
| Prebranchial slime pores (%) | NWA | 26 (27) | 3 (2) | 23–32 (25–29) | 9 |
| | OGM | 31 (29) | 1 (1) | 28–32 (28–30) | 13 |
| | IGM | 33 (29) | 4 (3) | 20–45 (21–40) | 94 |
| | MAC | 28 (28) | 2 (2) | 25–33 (25–33) | 51 |
| | ENA | 27 (28) | 3 (2) | 20–36 (24–33) | 143 |
| Trunk slime pores (%) | NWA | 58 (61) | 3 (1) | 56–66 (59–62) | 9 |
| | OGM | 63 (59) | 2 (1) | 59–67 (57–61) | 13 |
| | IGM | 67 (59) | 4 (3) | 51–77 (51–69) | 94 |
| | MAC | 59 (59) | 2 (2) | 54–65 (55–64) | 51 |
| | ENA | 56 (58) | 3 (<0.5) | 50–63 (57–60) | 143 |
| Tail slime pores (%) | NWA | 11 (12) | 1 (2) | 8–13 (8–14) | 9 |
| | OGM | 13 (12) | 1 (1) | 11–15 (10–14) | 13 |
| | IGM | 13 (11) | 2 (1) | 8–19 (9–15) | 94 |
| | MAC | 12 (12) | 1 (1) | 10–14 (10–14) | 51 |
| | ENA | 12 (13) | 1 (1) | 8–15 (9–14) | 143 |

data and the NWA sample differ significantly in the total cusp count. The MAC sample differs from the OGM sample in terms of the total slime pore count; it differs from the IGM sample in terms of prebranchial, trunk, tail, and total slime pore counts; the regional differences are not significant when compared as percentages of the total slime pore count. The MAC sample differs from the ENA sample in the trunk slime pore count (as a value, not as a percentage of total slime pores) and total cusp count. The total length data for the MAC, OGM, and ENA groups are not significantly different; all are significantly smaller than the IGM animals.

5 The IGM data is distinct from the ENA group for trunk, tail, and total slime pore and cusp count data. The IGM and ENA groups also differ significantly in prebranchial, trunk, and tail lengths, body width, body depth, tail depth, and cloacal depth (as percentages of total body length).

6 Hagfish from the inner Gulf of Maine were significantly larger than hagfish collected in any other location ($P<0.0001$). The average lengths of the OGM and MAC samples (315 mm and 280 mm respectively) were not significantly different from that of the ENA population (290 mm; see Tables 4 and 5). Further, we are unaware of any records for *M. glutinosa* larger than 450 mm outside of the Gulf of Maine or the adjacent continental slopes. Wisner and McMillan (1995) reported total lengths of 117–501 mm for their WNA sample ($n$=78). With deletion of the 13 animals known to be from the outer Gulf of Maine, the size range becomes 117–446 mm. This range, which still includes 15 animals from the outer Gulf of Maine,[2] is within the size range reported for eastern North Atlantic *M. glutinosa* (maximum size of 450 mm. It may also be significant that one of the OGM specimens, 350 mm in total length, contained fully mature eggs (SI075-689, from 42°40.5' N, 66°37'W; Wisner[1]). This is above the size of sexual maturity for eastern North Atlantic *M. glutinosa* (200 mm) but below the apparent length at maturity for specimens in the IGM sample (400 mm; Martini et al., 1997a). The large maximum size and large size at maturity

[2] Data forms did not permit determination of individual sizes, only ranges for these collection sites.

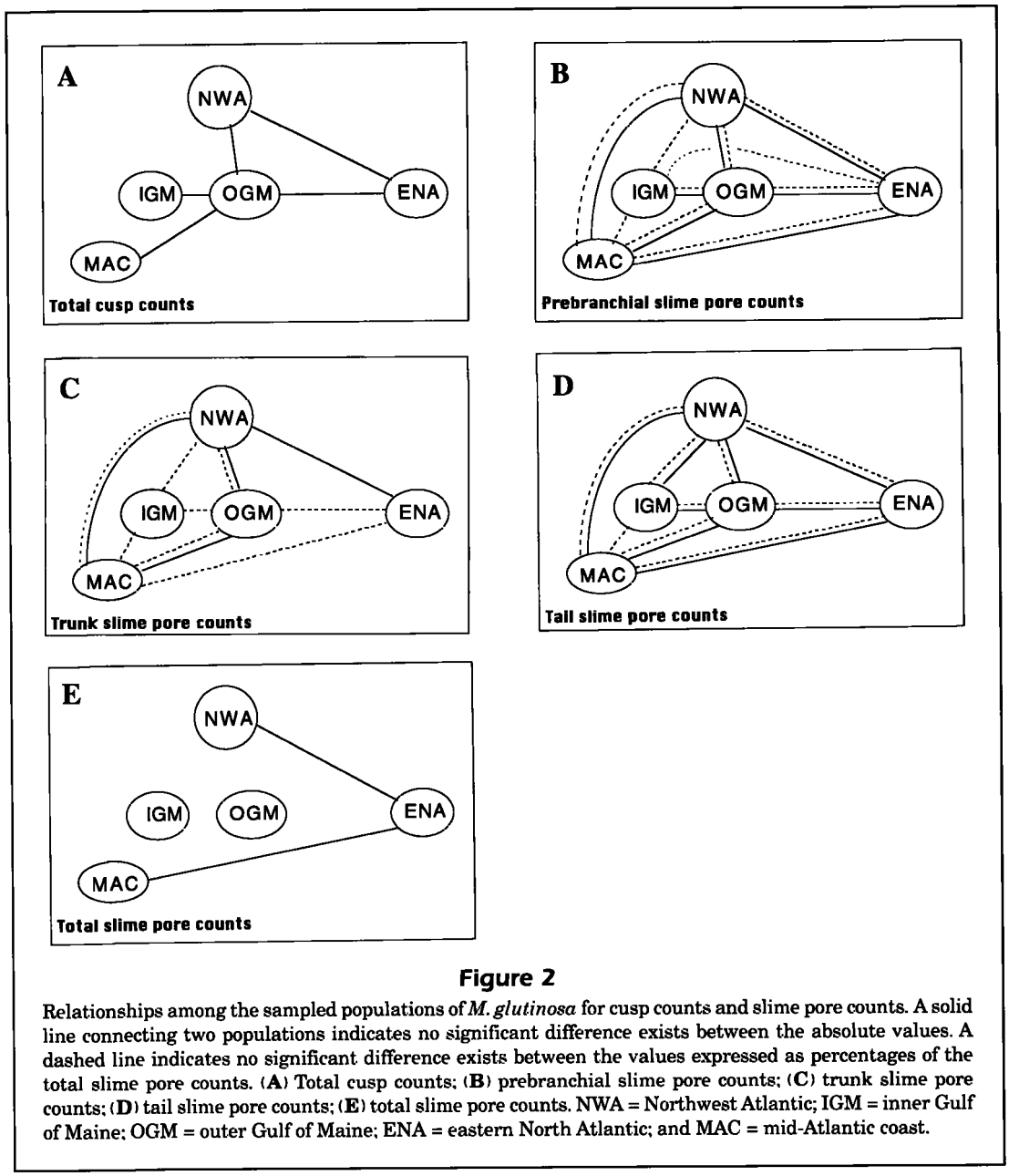


**Figure 2**

Relationships among the sampled populations of *M. glutinosa* for cusp counts and slime pore counts. A solid line connecting two populations indicates no significant difference exists between the absolute values. A dashed line indicates no significant difference exists between the values expressed as percentages of the total slime pore counts. (**A**) Total cusp counts; (**B**) prebranchial slime pore counts; (**C**) trunk slime pore counts; (**D**) tail slime pore counts; (**E**) total slime pore counts. NWA = Northwest Atlantic; IGM = inner Gulf of Maine; OGM = outer Gulf of Maine; ENA = eastern North Atlantic; and MAC = mid-Atlantic coast.

that has been widely attributed to *M. glutinosa* in the western North Atlantic thus appears to be valid only for the inner Gulf of Maine.

In summary, the IGM group is significantly larger in total length than any other population sampled. Proportional measurements could be compared only between the IGM and ENA samples. In addition to having much greater total length, hagfish from the IGM sample are more slender (both in width and depth) and have shorter prebranchial segments and shorter, narrower tails than ENA specimens. Allometric effects are probably not responsible for these differences, which remain significant even when the IGM data set is restricted to animals of the same size range as that in the ENA sample (<400 mm). Total length, slime pore counts, and total cusp counts could be compared among all groups. The highest variability observed was in the total slime pore count. Specimens from the Gulf of Maine (IGM and OGM) differed from one another and from all other sample groups. In terms of the regional distribution of slime pores, there were significant differences between the IGM and ENA samples when compared as absolute values or as percentages of the total slime pore count. Differences in the regional distribution of slime pores

**Table 3**

Results of post-hoc multiple comparison tests (Scheffe *F*-test) at the 5% level of significance. For counts, means, and standard deviations, refer to Table 2. The asterisks (*) indicate values significant at the 5% level (Scheffe *F*-test).

| Groups compared | Mean diff. | | *P*-value | |
|---|---|---|---|---|
| Prebranchial slime pore counts, as value and percentage of total (in parentheses) | | | | |
| IGM vs. MAC | 5.216 | (0.020) | <0.0001* | (0.4127) |
| IGM vs. NWA | 7.517 | (0.033) | <0.0001* | (0.1905) |
| IGM vs. OGM | 2.756 | (0.005) | 0.2380 | (0.9979) |
| IGM vs. ENA | 6.045 | (0.014) | <0.0001* | (0.0915) |
| MAC vs. NWA | 2.301 | (0.019) | 0.7105 | (0.8340) |
| MAC vs. OGM | −2.46 | (0.009) | 0.4471 | (0.9913) |
| MAC vs. ENA | .828 | (−0.010) | 0.8798 | (>0.9999) |
| NWA vs. ENA | −1.472 | (−0.019) | 0.9448 | (0.8091) |
| OGM vs. NWA | 4.761 | (0.028) | 0.0865 | (0.6534) |
| OGM vs. ENA | 3.288 | (0.009) | 0.0661 | (0.9849) |
| Trunk slime pore counts as value and percentage of total (in parentheses) | | | | |
| IGM vs. MAC | 8.550 | (0.002) | <0.0001* | (0.9985) |
| IGM vs. NWA | 9.197 | (−0.017) | <0.0001* | (0.2559) |
| IGM vs. OGM | 4.838 | (0.004) | 0.0022* | (0.9985) |
| IGM vs. ENA | 11.170 | (0.010) | <0.0001* | (0.0212)* |
| MAC vs. NWA | 0.647 | (−0.019) | 0.9997 | (0.2076) |
| MAC vs. OGM | −3.712 | (0.002) | 0.0861 | (>0.9999) |
| MAC vs. ENA | 2.619 | (0.008) | 0.0030* | (0.3125) |
| NWA vs. ENA | 1.972 | (0.027) | 0.8591 | (0.0054)* |
| NWA vs. OGM | −4.359 | (0.022) | 0.2478 | (0.2986) |
| OGM vs. ENA | 6.331 | (0.006) | <0.0001* | (0.9760) |
| Tail slime pore counts as value and percentage of total (in parentheses) | | | | |
| IGM vs. MAC | 0.995 | (−0.006) | 0.0166* | (0.0694) |
| IGM vs. NWA | 1.655 | (−0.005) | 0.1012 | (0.9683) |
| IGM vs. ENA | 0.794 | (−0.012) | 0.0088* | (<.0001)* |
| IGM vs. OGM | −0.276 | (−0.010) | 0.9987 | (0.0694) |
| MAC vs. NWA | 0.660 | (0.001) | 0.9538 | (0.9995) |
| MAC vs. OGM | −1.271 | (−0.004) | 0.2460 | (0.9376) |
| MAC vs. ENA | −0.201 | (−0.006) | 0.9940 | (0.1040) |
| NWA vs. ENA | −0.861 | (−0.007) | 0.8116 | (0.6125) |
| NWA vs. OGM | −1.932 | (−0.006) | 0.1156 | (0.9204) |
| OGM vs. ENA | 1.075 | (−0.001) | 0.3745 | (>0.9999) |
| Total slime pore counts | | | | |
| IGM vs. MAC | 14.227 | | <0.0001* | |
| IGM vs. NWA | 18.429 | | <0.0001* | |
| IGM vs. OGM | 7.566 | | 0.0039* | |
| IGM vs. ENA | 17.38 | | <0.0001* | |
| MAC vs. NWA | 4.203 | | 0.6730 | |
| MAC vs. OGM | −6.661 | | 0.0353* | |
| MAC vs. ENA | 3.154 | | 0.0922 | |
| NWA vs. OGM | −10.863 | | 0.0054* | |
| NWA vs. ENA | −1.076 | | 0.9995 | |
| OGM vs. ENA | 9.787 | | <0.0001* | |
| Total cusp counts | | | | |
| IGM vs. MAC | 0.432 | | 0.9625 | |
| IGM vs. NWA | 3.409 | | 0.0006* | |
| IGM vs. OGM | 0.235 | | >0.9999 | |
| IGM vs. ENA | 1.883 | | <0.0001* | |
| MAC vs. NWA | 2.978 | | 0.0109* | |
| MAC vs. ENA | 1.667 | | 0.0003* | |
| MAC vs. OGM | −0.197 | | >0.9999 | |
| NWA vs. ENA | −1.310 | | 0.7119 | |
| NWA vs. OGM | −3.175 | | 0.1263 | |
| OGM vs. ENA | 1.864 | | 0.4313 | |

between the groups IGM-MAC, IGM-NWA, IGM-OGM, and MAC-ENA were not significant when compared as percentages of the total slime pore count. Total cusp counts differed significantly between NWA-IGM, NWA-MAC, IGM-ENA, and MAC-ENA.

## Discussion

The primary goal of this analysis was to assess the validity of the proposed splitting of *M. glutinosa* L. into two species. With the exception of the IGM data, the proposal by Wisner and McMillan (1995) was based on a general morphological comparison of animals collected from the eastern and western North Atlantic. This study used their data, assigned to the NWA, OGM, MAC, and ENA groups. As is often the case when working with fishes whose lifestyles, habits, and population dynamics are poorly understood, there are a number of potential complicating factors that could bias these data. For example, both the Wisner and McMillan study and our own have compared specimens collected by 1) different methods, 2) at different times, and 3) at different depths. This is not unusual; the majority of the 59 currently recognized species of hagfishes are known from small numbers of animals (often just one) caught accidentally in mobile fisheries gear. The limitations of our data sets are therefore shared not just with Wisner and McMillan (1995) but with many other studies of hagfish systematics. Our goal was to determine if—given the limitations of the available data—the proposed split could be justified on the basis of the available morphological data.

We will now discuss each of these complicating factors as they influence hagfish collections in general, and the data in this study in particular.

### The collection method might affect the size range of animals captured

Comparative data on trawl versus trap collection of *Myxine* are unavailable, but it is known that trawl-

**Table 4**

Size distribution in populations of *Myxine glutinosa* in the eastern and western North Atlantic. Total length measurements (in mm) reported for eastern and western Atlantic populations (all groups). See text for explanation of abbreviations.

| | NWA | OGM | IGM | MAC | ENA |
|---|---|---|---|---|---|
| | | 315 | 509 | 280 | 299 |
| Average | 190–405 | 215–510 | 195–724 | 220–380 | 227–392 |
| range | ($n$=11)[1] | ($n$=13)[1] | ($n$=306)[3] | ($n$=13)[1] | ($n$=179)[1] |
| | | | 529 | | 312 |
| | | 103–405 | 170–950 | 220–420 | 253–362 |
| | | ($n$=8)[2] | ($n$=1172)[4] | ($n$=37)[2] | ($n$=8)[5] |
| | | | | | <450[6] |

[1] From Wisner and McMillan (1995).
[2] From raw data provided by R. Wisner (see Footnote 1 in main text).
[3] From Martini et al. (1997a).
[4] From Kuenstner (1996).
[5] From Fernholm (1981).
[6] From Adams and Strahan (1963).

**Table 5**

Results of post-hoc multiple comparison tests of total lengths; asterisks (*) indicate values significant at the 5% level (Scheffe $F$-test). See text for explanation of abbreviations.

| Groups compared | Mean difference | $P$-value |
|---|---|---|
| IGM vs. MAC | 231.490 | <0.0001* |
| IGM vs. NWA | 213.798 | <0.0001* |
| IGM vs. OGM | 196.381 | <0.0001* |
| IGM vs. ENA | 213.099 | <0.0001* |
| MAC vs. NWA | −17.692 | 0.9996 |
| MAC vs. OGM | 35.109 | 0.9698 |
| MAC vs. ENA | −18.391 | 0.9943 |
| NWA vs. ENA | −1.217 | >0.9999 |
| NWA vs. OGM | −17.417 | 0.9996 |
| OGM vs. ENA | 16.718 | 0.9904 |

ing estimates of hagfish population density produce gross underestimates (Wakefield, 1990). Given the maximum swimming rate of adult *Myxine* (<1 m/sec, Foss, 1968), hagfish of any size are probably unable to outrun a trawl. We would predict that trapping would collect smaller individuals that might slip through the trawl mesh, whereas trawling could collect mature animals that might not be attracted to traps (breeding hagfish may not feed; Walvig, 1963). However, because we have no indication of allometric effects of body size on any morphometric character for *M. glutinosa*, the statistical comparisons of slime pore counts, cusp counts, or proportional measurements should be unaffected by variations in total length among the sample populations. Neither traps with large-bore entrances or trawl nets, the collection methods used for these data, should bias the maximum recorded size.

### Collections made at different times of the year may produce biased samples owing to seasonal migrations or breeding activities

Although no large-scale tagging studies have been performed, field observations and their relatively inefficient and slow swimming speed suggest that *M. glutinosa* are relatively sedentary animals with small home ranges. Among hagfishes, only *Eptatretus burgeri* is known to have seasonal migrations (Fernholm, 1974), and their migration is related to a specific breeding cycle that is unique among hagfishes. *Myxine glutinosa* has no particular breeding period, and adults at all stages of gonadal development are present throughout the year (Walvig, 1963; Martini et al., 1997b). There were no significant differences in the population profiles for animals collected at our primary study site in June–September from one year to the next, and although weather and sea-state conditions prohibited collection in midwinter, no population differences, in terms of size range or abundance, were apparent in ROV surveys performed in December–January as compared to July–August (Martini, personal obs.).

### Collections made at different depths may yield different sex ratios and population profiles

The reported depth range of *M. glutinosa* is extensive (50–1100 m). There are no reports of depth stratification by size or sex for any species of *Myxine*, and only suggestions of unequal depth distribution (by size and sex) for two species of *Eptatretus* (*E. stouti* and *E. deani*) (Johnson, 1994; Wakefield, 1990). All known *M. glutinosa* populations have sex ratios that are highly skewed in favor of females, but above the size at sexual maturity there are males and females of all sizes. Any variations in the sex ratios would not affect the morphological parameters we compared because no sexual dimorphism has been reported for these characters in *M. glutinosa* or any other hagfish species.

### The IGM data were collected from fresh, rather than preserved, specimens

Fixation shrinkage of 10–15% may occur in preserved specimens (Wisner[1]). This shrinkage would not affect parameters such as cusp counts or slime pore counts, but it would potentially affect total length. Shrinkage alone, however, could not account for the magnitude of the observed differences in maximum total length (950 mm for IGM, versus a maximum of

510 mm elsewhere in the WNA, and 450 mm in the ENA) or the minimum size at sexual maturity (400 mm for the IGM vs. 200 mm for the ENA). Shrinkage may have affected some of the proportional comparisons between the IGM and ENA samples, but the effect is not straightforward. The IGM hagfish (fresh measurement) have proportionately shorter prebranchial segments and tails than the ENA specimens (preserved measurement), and the IGM specimens are more slender (both in width and depth).

### The morphological measurements were made by different groups

We do not believe that the differences observed among these populations reflect variation in protocol between the research groups because differences in slime pore counts and cusp counts among the sampled populations remain if the IGM data are set aside, and a single team (Wisner and McMillan) collected the NWA, OGM, ENA, and MAC data sets.

## Conclusions

Our analyses of the available data do not support a clean division between eastern and western North Atlantic populations of *M. glutinosa*. We therefore support retention of the species name *M. glutinosa* for both eastern and western populations pending the results of mtDNA analysis or other molecular comparisons.

Specific arguments against species or subspecies division include the following: 1) Considerable variability exists in the total slime pore count among the WNA groups examined; 2) Although there were significant regional differences in slime pore count between the IGM and ENA samples, when compared as absolute values or as percentages of the total slime pore count, this was not the case for the other WNA groups; 3) Total cusp counts were also variable, with significant differences noted between NWA-IGM, NWA-MAC, IGM-ENA, and MAC-ENA; and 4) The degree of differentiation versus the ENA group, in increasing order, would be NWA (trunk slime pore percentage) → OGM (total slime pore count) → MAC (trunk slime pore count and cusp count) → IGM (total, trunk, and tail slime pore counts and cusp count).

This pattern suggests, but does not prove, the existence of clinal variations that may reflect the degree of relative isolation of the populations. Although on a map the Gulf of Maine appears continuous with the western North Atlantic, in fact it is almost completely isolated from the offshore waters by extensive banks and shoals (Fig. 1A). There is only one deepwater connection (260–270 m) between the Gulf of Maine and the North Atlantic. This narrow connection, the Northeast Channel, extends between Brown's Bank (BB), where the majority of the OGM samples were collected, and a shallow ridge that extends northeast from George's Bank (GB). Oceanographically the Gulf of Maine resembles a landlocked sea, like the Mediterranean, rather than a contiguous portion of the North Atlantic. For example, the salinity, temperature, tides, and current dynamics of the Gulf of Maine are distinct from those of the North Atlantic. This combination of factors could isolate hagfish populations within the Gulf of Maine from those elsewhere in the western North Atlantic. The distinct characteristics of the Gulf of Maine environment may also be linked to physiological differences between *M. glutinosa* in the Gulf of Maine versus the eastern North Atlantic. For example, *M. glutinosa* in the eastern North Atlantic have been maintained at water temperatures as high as 15°C (Palmgren, 1927; Gustafson, 1935), whereas specimens at the Shoals Marine Laboratory (Gulf of Maine) quickly become moribund as temperatures approach 10°C (Martini, personal obs.).

The size difference between the IGM and other sampled populations could be a function of age, with members of the IGM population having longer lifespans. However, this is impossible to evaluate without growth rate or longevity data—which does not presently exist for this or any other species of hagfish. Alternatively, the large total size and large size at maturity for hagfish within the Gulf of Maine may reflect the relative availability of food. It is interesting to note that Kendall described winter flounder (*Pleuronectes americanus* [formerly *Pseudopleuronectes americanus*]) of the George's Bank region as a separate species from those found elsewhere in the western North Atlantic, on the basis of its unusually large size; this proposal was ultimately rejected because there were no other morphological differences. It is not clear, however, that the ecosystem in the inner Gulf of Maine is significantly more productive than that of the Skaggerack in the eastern North Atlantic; both areas support substantial commercial fisheries.

Wisner and McMillan (1995) proposed species separation based on maximum size, size at maturity, and differences in the color of preserved specimens. As indicated above, the large maximum size and large size at maturity appear to be characteristic of the IGM population only, rather than a general characteristic of WNA populations of *Myxine*. We remain unable to evaluate the significance of the color differences in preserved specimens noted by Wisner and McMillan (1995) for eastern versus western North

Atlantic *Myxine*. The patterns they described as typical for the WNA are not found in our preserved specimens from the IGM. Further, our field data, which included ROV and submersible observations and trap collections, indicate that the described color patterns are not characteristic of living members of the inner Gulf of Maine populations. Whether they are characteristic of other WNA populations, or typical of only a few subpopulations, remains to be determined.

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**Abstract.**—We used allozyme analyses to investigate genetic variation among commercially exploited populations of *Chionoecetes bairdi* (Tanner) and *C. opilio* (snow) crabs in Alaskan waters. Data were collected from 34 presumptive loci in 1002 *C. bairdi* and 539 *C. opilio* sampled throughout the commercially important range of each species in Alaska. Average observed heterozygosities were 0.027 for *C. bairdi* and 0.013 for *C. opilio*. Low levels of geographic differentiation were detected among populations of *C. bairdi* and *C. opilio*, and our data suggest that subpopulations of *C. bairdi* exist within the Bering Sea. Further, evidence of gene introgression was found between *C. bairdi* and *C. opilio* in the Bering Sea. We also included a geographic isolate, North Atlantic *C. opilio*, in the analyses. Little differentiation was found, and no private alleles were detected in North Atlantic *C. opilio* despite significant geographic separation from Alaskan *C. opilio*.

# Low levels of genetic diversity in highly exploited populations of Alaskan Tanner crabs, *Chionoecetes bairdi*, and Alaskan and Atlantic snow crabs, *C. opilio**

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Five species of the genus *Chionoecetes*, Majidae, are described from the North Pacific region (Rathbun, 1925; Garth, 1958). The nearly circumpolar range of *C. opilio* (snow crab) includes the Bering Sea, the Arctic Ocean, the western North Pacific coast of Asia, and the northern Atlantic Ocean. *Chionoecetes bairdi*, *C. angulatus*, and *C. tanneri* are widespread in the eastern North Pacific (Garth, 1958). *Chionoecetes japonicus* is found only in the western North Pacific along the coast of Asia. In the Alaskan waters of the Bering Sea, the distribution of *C. bairdi* is strongly associated with the continental slope areas along the coast of the Alaska Peninsula, and the Pribilof Islands (Otto, 1982), and there is considerable overlap in the distribution of *C. bairdi* and *C. opilio* (Karinen, 1974).

Commercial fisheries for male *C. bairdi* and *C. opilio* in Alaska, along with king crabs (*Paralithodes* and *Lithodes*) have long been the world's most abundant sources of crabs and have considerable current and historical commercial importance in Alaska (Otto, 1990). *Chionoecetes bairdi* are faster growing, larger, and more valuable than *C. opilio*. Commercial harvests of *C. bairdi* in the Bering Sea and Gulf of Alaska fisheries peaked in the late 1970s, declined throughout the 1980s, and although some populations of *C. bairdi* have recently rebounded, many fisheries remain closed owing to low abundance (Kruse, 1993). Rapid development of the Bering Sea *C. opilio* fishery coincided with the decline of *C. bairdi* fisheries, and although *C. opilio* have dominated landings of Bering Sea crabs since the mid-1980s, catches have also declined dramatically in recent years (ADF&G, 1994).

Declining abundances of Bering Sea and Gulf of Alaska crab populations have intensified competition for the remaining resources and have lead to re-evaluation of crab fishery management practices. Gen-

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erally when a population or stock is modeled, the assumption is made that the individuals within the population are uniform, but it is important that this assumption be verified (Cobb and Caddy, 1989). In practice, a stock is often defined as 1) a production or management unit about which conclusions can be made without regard for differences within the group and exchanges with other groups, or as 2) biologically, a genetically discrete population (reviewed in Cobb and Caddy, 1989). However, stock identity of decapod populations has been largely ignored or problematic (Cobb and Caddy, 1989; Kruse, 1993).

Existing shellfish management units in Alaska were originally established according to historical fishing grounds of red king crab. Current area lines for *C. bairdi* and *C. opilio* were based on mark-and-recapture data, natural geographic barriers, and areas of stock abundance grouped by major fishing grounds. Although genetic surveys were not conducted on unexploited *Chionoecetes* populations in Alaska, the establishment of a genetic baseline is critical for verifying current fishery management units and for monitoring potential fishery-induced genetic changes. Additionally, the genetics of *C. bairdi* and *C. opilio* populations in the Bering Sea is complicated by the presence of hybrids of these two species. *Chionoecetes bairdi* and *C. opilio* appear to have many similar morphological, physiological, and reproductive features (Watson, 1970; Slizkin, 1990) that allow them to hybridize in areas of range overlap (Karinen and Hoopes, 1971; Somerton, 1981; Hoopes et al.[1]).

Many studies suggest that commercial fishing activities may have significant genetic effects on fish stocks without reducing them to near extinction (for example, see reviews in Allendorf et al., 1987; Thorpe, 1993), and genetic selection against fast growth may result from intense fishing pressure (Kruse, 1993; Stevens et al., 1993); however, these effects can be assessed only if there are comparative baseline data.

In 1990 we began genetic investigations of *C. bairdi* and *C. opilio* populations in Alaska using allozyme electrophoresis. Our objectives were 1) to assess genetic variation in exploited populations of *C. bairdi* and *C. opilio* in Alaska and 2) to determine if significant differentiation exists to warrant re-examination of current management units.

## Materials and methods

### Population sample collections

Samples of *C. bairdi* and *C. opilio* were obtained between 1989 and 1993 from population assessment trawl and pot survey catches, test fishery pot catches, and dockside commercial pot catches. Crabs caught in pots set in adjacent areas were pooled into a single collection (Table 1). *Chionoecetes bairdi* were collected from sites ranging from Seymour Canal in Southeast Alaska to northwest of the Pribilof Islands in the Bering Sea (Table 1; Fig. 1). *Chionoecetes opilio* were collected from sites in the Bering Sea. In addition, we obtained a collection of *C. opilio* from the North Atlantic for comparison with Bering Sea samples. Eighteen collections of *C. bairdi* and nine collections of *C. opilio* were analyzed in this study.

**Table 1**
Collection information for *Chionoecetes* specimens.

| Location number | Location[1] | Date | *n* |
|---|---|---|---|
| *Chionoecetes bairdi* | | | |
| 1[2] | Bristol Bay | Jun 90 | 50 |
| | Bristol Bay | Jun 91 | 50 |
| 2[2] | Bering Sea and Pribilof Islands | Jul 90 | 50 |
| | Bering Sea and Pribilof Islands | Apr 91 | 75 |
| | Bering Sea and Pribilof Islands | Jul 92 | 30 |
| | Bering Sea and Pribilof Islands | Mar 93 | 50 |
| | Bering Sea and Pribilof Islands | Jul 93 | 80 |
| 3 | Port Moller | Jun 90 | 42 |
| 4 | Sand Point and Pavlof Bay | Aug 90 | 50 |
| 5 | Kodiak N. Mainland | Feb 90 | 50 |
| 6 | Kodiak S. Sitkalidak Strait | Feb 90 | 50 |
| 7 | Kamishak Bay | Jun 90 | 50 |
| 8 | Montague Strait | Jul 90 | 50 |
| 9 | Kachemak Bay | Jun 90 | 50 |
| 10 | Prince William Sound | Aug 90 | 50 |
| 11 | Sullivan Island | Jul 93 | 100 |
| 12 | Seymour Canal | Sep 89 | 50 |
| | Seymour Canal | Jul 93 | 75 |
| *Chionoecetes opilio* | | | |
| *I*[2] | Bering Sea | Apr 91 | 75 |
| | Bering Sea | Mar 93 | 50 |
| *II*[2] | St. Matthew Island | Jul 90–Aug 90 | 100 |
| | St. Matthew Island | Jul 92–Aug 92 | 100 |
| *III*[2] | Pribilof Island | Jul 90 | 44 |
| | Pribilof Island | Aug 90 | 50 |
| | Pribilof Island | Jul 92 | 40 |
| | Pribilof Island | Jun 93–Jul 93 | 80 |
| | Nova Scotia, North Atlantic | Sep 91 | 97 |

[1] Latitude and longitude locations available from authors.
[2] Collections within geographic location pooled for analyses; *C. bairdi* collection sites in the Bering Sea and Pribilof Islands were overlapping.

[1] Hoopes, D. T., J. F. Karinen, and M. J. Pelto. 1970. King and Tanner crab research. International North Pacific Fisheries Commission Annual Rep. 1970:110–120.

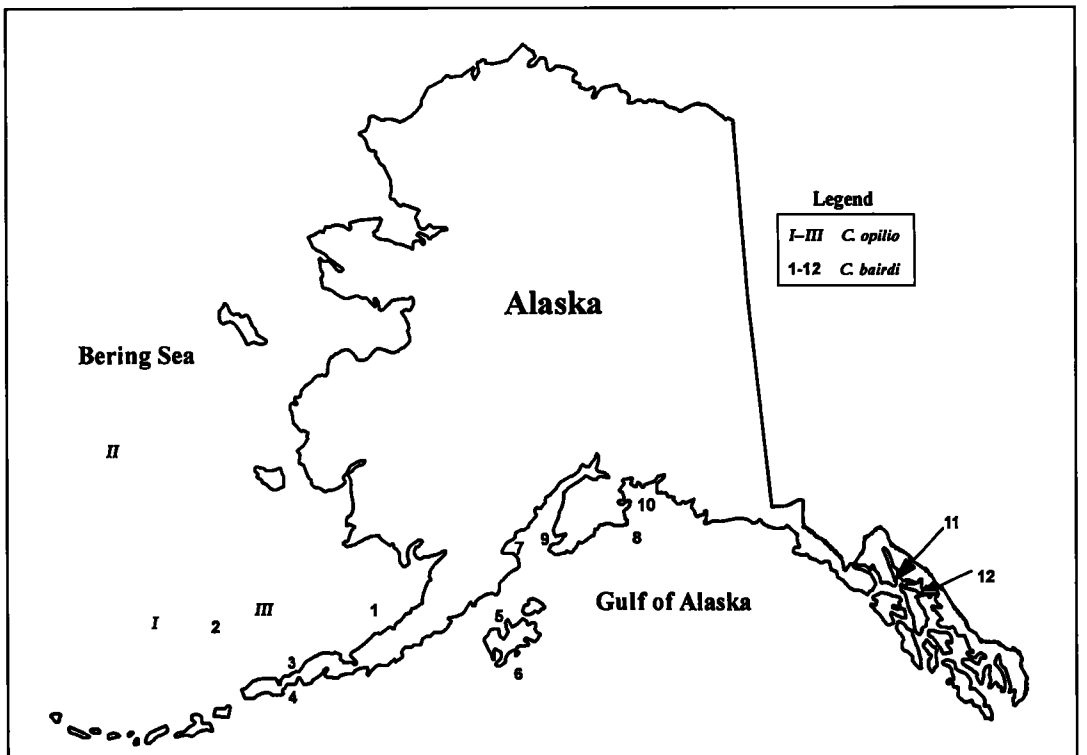


**Figure 1**

Locations of samples of *C. bairdi* and *C. opilio* in Alaska analyzed for genetic variation. Numbers correspond to populations described in Table 1. *C. bairdi* sample locations are labelled 1–12. *C. opilio* sample locations are labelled *I–III*.

Tissues (muscle, gill, hepatopancreas, and heart) were dissected from each individual, placed in a labelled tube, which was chilled on wet ice, capped, and frozen at –15°C (1989–90 collections) or in liquid nitrogen (1991–93 collections). Freezing generally occurred within 20 minutes after dissection but in some cases was as long as 1 hour. Tissues were transported to the laboratory on dry ice or liquid nitrogen and stored at –80°C until analysis. Several locations were sampled in multiple years.

## Allozyme electrophoresis

Procedures for horizontal starch gel electrophoresis followed those of Harris and Hopkinson (1976) and Aebersold et al. (1987). Activity reflecting 34 presumed loci were resolved with the following buffers (Table 2): 1) N-(3-aminopropyl)-morpholine, citrate (AC, pH 6.1, 6.9) (Clayton and Tretiak, 1972); 2) Tris, borate, citrate, lithium hydroxide (TBCL, pH 8.7) (Ridgway et al., 1970); 3) Tris, citrate (TC, pH 7.0) (Shaw and Prasad, 1970); 4) Tris, citrate (TC, pH 8.0) (Selander et al., 1971); and 5) Tris, borate, EDTA (TBE, pH 8.5) (Boyer et al., 1963). Gene nomenclature followed Shaklee et al. (1990). Allelic standards were used to compare relative mobilities between species.

## Genetic differentiation

We estimated allele frequencies, calculated average observed heterozygosities, and tested conformation of genotype frequencies to Hardy-Weinberg expected frequencies with log-likelihood ratios (modified from Weir, 1990) for each collection ($\alpha$=0.05, adjusted for multiple tests [Rice, 1989]). Samples of *C. bairdi* collected from the Bering Sea and Pribilof Island areas were pooled because sample sites were overlapping. Interannual heterogeneity of multiple-year collections in Bristol Bay, Bering Sea, St. Matthew Island, Pribilof Islands, and Seymour Canal was tested by using log-likelihood statistics (Sokal and Rohlf, 1995). Multiple-year collections within a site were pooled for further analyses if no significant heterogeneity existed ($P$<0.01). We estimated degree of population subdivision by using Wright's (1978) nonhierarchical $F$ statistics and a hierarchical log-likelihood analysis. We used FSTAT (version 1.2)(Goudet, 1995) to

**Table 2**

Allozyme protocols to resolve enzyme coding loci in *Chionoecetes* samples. Enzyme nomenclature follows Shaklee et al. (1990), and locus abbreviations are given. Tissue abbreviations are: (M) muscle, (H) heart, (G) gill, and (P) hepatopancreas. Buffers are described in the text.

| Enzyme or protein | Enzyme number | Locus | Tissue | Buffer |
|---|---|---|---|---|
| Aspartate aminotransferase | 2.6.1.1 | *AAT-1*, AAT-2** | M | TBE |
| Aconitate hydratase | 4.2.1.3 | *AH-2**[2] | M | TC7.0 |
| | | *AH-3** | M | TC7.0 |
| Adenosine deaminase | 3.5.4.4 | *ADA-1*, ADA-3** | G,M,H | TBCL |
| | | *ADA-2** | P | TBCL |
| Alanine aminotransferase | 2.6.1.2 | *ALAT** | M | TBCL |
| Cytochrome-b5[1] | 1.8.1.4 | *CBYR** | M | TBCL |
| β-N-Acetylgalactosaminidase | 3.2.1.53 | *βGALA** | G,P | TBCL, TBE |
| Glyceraldehyde-3-phosphate dehydrogenase | 1.2.1.12 | *GAPDH** | M | AC6.1 |
| N-Acetyl-β-glucosaminidase | 3.2.1.30 | *βGLUA** | G,P | TBCL |
| Glycerol-3-phosphate dehydrogenase | 1.1.1.8 | *G3PDH-1** | M | TC7.0 |
| | | *G3PDH-2** | H,M | TC7.0 |
| Glucose-6-phosphate isomerase | 5.3.1.9 | *GPI-A1** | M | TBCL |
| Isocitrate dehydrogenase (NADP+) | 1.1.1.42 | *IDHP-1** | H | TC7.0 |
| Malate dehydrogenase | 1.1.1.37 | *MDH-A1*, MDH-A2** | M | AC6.1 |
| Malic enzyme (NADP+) | 1.1.1.40 | *MEP-1** | H | TC7.0 |
| Mannose-6-phosphate isomerase | 5.3.1.8 | *MPI** | M | TBE |
| Dipeptidase | 3.4.-.- | *PEPA** | H,P | TBE |
| Proline dipeptiase | 3.4.13.9 | *PEPD-2** | G,P | TBCL |
| Phosphogluconate dehydrogenase | 1.1.1.44 | *PGDH** | H | TC7.0 |
| Phosphoglucomutase | 5.4.2.2 | *PGM-1** | M,H | TC7.0 |
| General (unidentified) protein | | *PROT-1*, PROT-2*, PROT-3** | M | TBCL |
| Superoxide dismutase | 1.15.1.1 | *SOD-1**[2] | M | TBCL |
| Triose-phosphate isomerase | 5.3.1.1 | *TPI-1** | M | TBE |

[1] This locus expressed with both CBYR* and GR*; preferential stain is CBYR*.
[2] Used in *C. opilio* statistical analysis only.

test significance of $F_{ST}$ values (2000 permutations). Allele frequencies were used to generate distance matrices of Cavalli-Sforza and Edwards chord distances (Cavalli-Sforza and Edwards, 1967). Computations were made with *S-Plus* analytical software (MathSoft Inc., 1997).

## Results

### *Chionoecetes bairdi*

Twenty-seven loci were scored consistently in *C. bairdi* populations and were used in the data analyses. Temporal variation was examined for multiple-year collections of *C. bairdi* from Bristol Bay, the Bering Sea and Pribilof Islands area, and Seymour Canal (Table 1). No significant interannual differences ($P<0.01$) were found within each geographic location; therefore these collections were pooled for subsequent analyses.

Fifteen loci, *AAT-1**, *AAT-2**, *AH-3**, *ALAT**, *CBYR**, *G3PDH-1**, *G3PDH-2**, *GPI-A1**, *IDHP-1**, *MDH-A1**, *PEPA**, *PGDH**, *PGM-1**, *PROT-3**, and *TPI-1** were polymorphic (Table 3). At four loci, *G3PDH-1**, *GPI-A1**, *IDHP-1**, and *PEPA**, the most common allele had a frequency of ≤0.95 in at least one population. Twelve monomorphic loci, *ADA-1**, *ADA-2**, *ADA-3**, *βGALA**, *GAPDH**, *βGLUA**, *MDH-A2**, *MEP-1**, *MPI**, *PEPD-2**, *PROT-1**, and *PROT-2** were included in the 27-locus analyses. Seven monomorphic loci, *AH-2**, *mMDH-1**, *PEPD-1**, *SOD-1**, *SOD-2**, *TPI-2**, and *XO** were not scorable in all populations and were not included in our analyses. We could not interpret the genetic basis for the variation we observed in two consistently resolved zones of esterase activity; therefore those data were excluded.

Three collections of *C. bairdi*, Sand Point and Pavlof, Port Moller, and Prince William Sound, with sample sizes of <25 at informative loci, *AH-3** and *IDHP-1**, were not included in the population data analyses; however, we report allele frequencies in Table 3.

Genotype frequencies at all loci conformed to Hardy-Weinberg expectations; therefore we assumed all sam-

**Table 3**

Allele frequency estimates for *Chionoecetes bairdi* and *C. opilio* collections. ND indicates no data. Dashed lines indicate frequency of 0.000.

| | *AAT-1** | | | | | *AAT-2** | | | | *AH-2** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Population[1] | *n* | *100 | *64 | *210 | *120 | *n* | *100 | *131 | *69 | *n* | *100 | *110 | *83 |
| *Chionoecetes bairdi* | | | | | | | | | | | | | |
| Bristol Bay pooled | 100 | 0.995 | — | — | 0.005 | 100 | 1.000 | — | — | ND | | | |
| Bering Sea pooled | 283 | 1.000 | — | — | — | 274 | 0.998 | — | 0.002 | 280 | 1.000 | — | — |
| Port Moller 1990 | 42 | 1.000 | — | — | — | 42 | 1.000 | — | — | 42 | 1.000 | — | — |
| Sand Pt/Pavlof 1990 | 37 | 1.000 | — | — | — | 47 | 1.000 | — | — | ND | | | |
| Kodiak N. 1990 | 48 | 1.000 | — | — | — | 48 | 0.990 | 0.010 | — | 38 | 1.000 | — | — |
| Kodiak S. 1990 | 43 | 0.988 | — | — | 0.012 | 43 | 0.988 | 0.012 | — | 36 | 1.000 | — | — |
| Kamishak 1990 | 50 | 0.990 | 0.010 | — | — | 50 | 1.000 | — | — | 50 | 1.000 | — | — |
| Montague St. 1990 | 42 | 1.000 | — | — | — | 49 | 1.000 | — | — | 50 | 1.000 | — | — |
| Kachemak Bay 1990 | 50 | 1.000 | — | — | — | 50 | 0.990 | 0.010 | — | 50 | 1.000 | — | — |
| Prince Wm. Sd. 1990 | 50 | 1.000 | — | — | — | 50 | 1.000 | — | — | 50 | 1.000 | — | — |
| Sullivan Is. 1993 | 100 | 1.000 | — | — | — | 100 | 0.995 | 0.005 | — | 100 | 1.000 | — | — |
| Seymour C. pooled | 125 | 1.000 | — | — | — | 123 | 1.000 | — | — | 125 | 1.000 | — | — |
| *Chionoecetes opilio* | | | | | | | | | | | | | |
| Bering Sea pooled | 124 | 0.992 | — | 0.004 | 0.004 | 123 | 1.000 | — | — | 115 | 0.991 | 0.009 | — |
| St. Matt. Is. pooled | 192 | 0.992 | — | — | 0.008 | 193 | 0.987 | 0.005 | 0.008 | 200 | 1.000 | — | — |
| Pribilof Is. pooled | 211 | 0.991 | 0.005 | — | 0.005 | 193 | 0.995 | 0.003 | 0.003 | 214 | 0.993 | 0.002 | 0.005 |
| Atlantic O. 1991 | 97 | 1.000 | — | — | — | 97 | 0.995 | 0.005 | — | 97 | 1.000 | — | — |

| | *AH-3** | | | | | *ALAT** | | | *CBYR** | | | *G3PDH-1** | | | *G3PDH-2*[2] | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Population[1] | *n* | *100 | *94 | *91 | *106 | *n* | *100 | *87 | *n* | *100 | *117 | *n* | *100 | *117 | *n* | *100 | *86 | *111 |
| *Chionoecetes bairdi* | | | | | | | | | | | | | | | | | | |
| Bristol Bay pooled | 100 | 0.005 | 0.995 | — | — | 100 | 1.000 | — | 100 | 1.000 | — | 96 | 0.974 | 0.026 | 100 | 1.000 | — | — |
| Bering Sea pooled | 279 | 0.014 | 0.982 | 0.004 | — | 283 | 0.998 | 0.002 | 285 | 0.998 | 0.002 | 265 | 0.958 | 0.042 | 196 | 0.949 | 0.008 | 0.043 |
| Port Moller 1990 | 42 | — | 1.000 | — | — | 42 | 1.000 | — | 42 | 1.000 | — | 41 | 0.976 | 0.024 | 20 | 0.950 | 0.025 | 0.025 |
| Sand Pt/Pavlof 1990 | 3 | — | 1.000 | — | — | ND | | | 50 | 1.000 | — | 1 | 1.000 | — | ND | | | |
| Kodiak N. 1990 | 38 | 0.013 | 0.987 | — | — | 50 | 1.000 | — | 50 | 1.000 | — | 46 | 0.967 | 0.033 | 50 | 0.990 | — | 0.010 |
| Kodiak S. 1990 | 33 | 0.015 | 0.985 | — | — | 50 | 1.000 | — | 50 | 1.000 | — | 37 | 0.946 | 0.054 | 42 | 1.000 | — | — |
| Kamishak 1990 | 50 | — | 1.000 | — | — | 50 | 1.000 | — | 50 | 1.000 | — | 49 | 0.990 | 0.010 | 50 | 1.000 | — | — |
| Montague St. 1990 | 49 | — | 1.000 | — | — | 49 | 1.000 | — | 50 | 1.000 | — | 50 | 0.970 | 0.030 | 31 | 1.000 | — | — |
| Kachemak Bay 1990 | 50 | — | 1.000 | — | — | 50 | 1.000 | — | 50 | 1.000 | — | 50 | 0.950 | 0.050 | 50 | 0.970 | — | 0.030 |
| Prince Wm. Sd. 1990 | 50 | — | 0.990 | 0.010 | — | 50 | 1.000 | — | 50 | 1.000 | — | 50 | 0.970 | 0.030 | 47 | 1.000 | — | — |
| Sullivan Is. 1993 | 95 | 0.011 | 0.979 | 0.011 | — | 97 | 1.000 | — | 50 | 1.000 | — | 89 | 0.933 | 0.067 | 49 | 0.980 | — | 0.020 |
| Seymour C. pooled | 122 | 0.004 | 0.992 | 0.004 | — | 125 | 1.000 | — | 100 | 1.000 | — | 122 | 0.959 | 0.041 | 109 | 1.000 | — | — |
| *Chionoecetes opilio* | | | | | | | | | | | | | | | | | | |
| Bering Sea pooled | 124 | 0.923 | 0.077 | — | — | 123 | 1.000 | — | 125 | 0.996 | 0.004 | 125 | 0.988 | 0.012 | 96 | 0.995 | — | 0.005 |
| St. Matt. Is. pooled | 197 | 0.939 | 0.058 | — | 0.003 | 195 | 1.000 | — | 200 | 1.000 | — | 198 | 0.990 | 0.010 | 174 | 0.994 | — | 0.006 |
| Pribilof Is. pooled | 213 | 0.937 | 0.063 | — | — | 214 | 1.000 | — | 214 | 1.000 | — | 214 | 0.998 | 0.002 | 183 | 0.992 | 0.003 | 0.005 |
| Atlantic O. 1991 | 95 | 0.937 | 0.063 | — | — | 97 | 1.000 | — | 97 | 1.000 | — | 97 | 1.000 | — | 94 | 1.000 | — | — |

*continued*

ples were from single panmictic populations. Average observed heterozygosities ranged from 0.016 to 0.035.

## Among-population variation

Various measures indicated a low level of population differentiation. $F_{ST}$ values were low, however two loci, *G3PDH-2** and *PEPA** with respective $F_{ST}$ values of 0.0137 ($P$=0.0005) and 0.0154 ($P$=0.0020), and the overall $F_{ST}$ value of 0.0046 for 15 polymorphic loci ($P$=0.0295) differed significantly from zero. A comparison of all *C. bairdi* populations with a hierarchical log-likelihood analysis, indicated significant heterogeneity at four loci, *G3PDH-2**, *IDHP-1**, *PEPA**, and PROT-3*; however the overall statistic was not significant (Table 4). In contrast, when populations

## Table 3 (continued)

| Population[1] | *GPI-A1** | | | | | | | | *IDHP-1** | | | | | *MDH-A1** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *n* | *100 | *142 | *60 | *158 | *9 | *55 | *19 | *n* | *100 | *81 | *119 | *90 | *n* | *100 | *79 | *128 |
| *Chionoecetes bairdi* | | | | | | | | | | | | | | | | | |
| Bristol Bay pooled | 100 | 0.970 | — | 0.020 | — | 0.005 | — | 0.005 | 79 | 0.633 | 0.278 | 0.082 | 0.006 | 100 | 1.000 | — | — |
| Bering Sea pooled | 283 | 0.971 | 0.005 | 0.018 | — | 0.002 | 0.002 | 0.002 | 275 | 0.562 | 0.358 | 0.074 | 0.006 | 283 | 0.995 | 0.005 | — |
| Port Moller 1990 | 42 | 0.988 | — | 0.012 | — | — | — | — | 9 | 0.611 | 0.389 | — | — | 42 | 1.000 | — | — |
| Sand Pt/Pavlof 1990 | 50 | 0.980 | — | 0.010 | — | 0.010 | — | — | 34 | 0.691 | 0.162 | 0.147 | — | 8 | 1.000 | — | — |
| Kodiak N. 1990 | 49 | 0.959 | 0.010 | 0.031 | — | — | — | — | 49 | 0.592 | 0.357 | 0.051 | — | 49 | 1.000 | — | — |
| Kodiak S. 1990 | 50 | 0.930 | 0.020 | 0.030 | — | 0.010 | — | 0.010 | 36 | 0.722 | 0.264 | 0.014 | — | 39 | 1.000 | — | — |
| Kamishak 1990 | 50 | 0.990 | — | — | — | 0.010 | — | — | 30 | 0.683 | 0.267 | 0.050 | — | 50 | 1.000 | — | — |
| Montague St. 1990 | 50 | 1.000 | — | — | — | — | — | — | 50 | 0.510 | 0.430 | 0.060 | — | 50 | 1.000 | — | — |
| Kachemak Bay 1990 | 50 | 0.980 | — | 0.010 | — | 0.010 | — | — | 28 | 0.571 | 0.286 | 0.107 | 0.036 | 50 | 1.000 | — | — |
| Prince Wm. Sd. 1990 | 49 | 0.990 | — | — | — | 0.010 | — | — | 7 | 0.643 | 0.214 | 0.143 | — | 50 | 1.000 | — | — |
| Sullivan Is. 1993 | 100 | 0.985 | — | 0.015 | — | — | — | — | 82 | 0.634 | 0.341 | 0.024 | — | 99 | 1.000 | — | — |
| Seymour C. pooled | 124 | 0.992 | — | 0.004 | — | 0.004 | — | — | 122 | 0.574 | 0.348 | 0.078 | — | 125 | 0.996 | — | 0.004 |
| *Chionoecetes opilio* | | | | | | | | | | | | | | | | | |
| Bering Sea pooled | 125 | 0.984 | 0.004 | 0.004 | 0.004 | — | 0.004 | — | 125 | 1.000 | — | — | — | 125 | 0.992 | 0.008 | — |
| St. Matt. Is. pooled | 200 | 0.988 | 0.013 | — | — | — | — | — | 196 | 1.000 | — | — | — | 200 | 0.973 | 0.027 | — |
| Pribilof Is. pooled | 214 | 0.986 | 0.012 | 0.002 | — | — | — | — | 207 | 0.990 | 0.005 | 0.005 | — | 213 | 0.986 | 0.014 | — |
| Atlantic O. 1991 | 97 | 0.974 | 0.026 | — | — | — | — | — | 97 | 1.000 | — | — | — | 97 | 0.990 | 0.010 | — |

| Population[1] | *MDH-A2** | | | *PEPA** | | | | *PGDH** | | | | | *PGM-1** | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *n* | *100 | *65 | *n* | *100 | *138 | *64 | *n* | *100 | *112 | *124 | *91 | *n* | *100 | *82 | *114 | *103 | *88 | *75 |
| *Chionoecetes bairdi* | | | | | | | | | | | | | | | | | | | |
| Bristol Bay pooled | 100 | 1.000 | — | 92 | 0.940 | 0.022 | 0.038 | 92 | 0.995 | 0.005 | — | — | 100 | 0.995 | — | — | 0.005 | — | — |
| Bering Sea pooled | 283 | 1.000 | — | 279 | 0.991 | 0.004 | 0.005 | 269 | 0.996 | — | 0.004 | — | 268 | 0.996 | 0.004 | — | — | — | — |
| Port Moller 1990 | 42 | 1.000 | — | 39 | 0.987 | — | 0.013 | 18 | 1.000 | — | — | — | 42 | 1.000 | — | — | — | — | — |
| Sand Pt/Pavlof 1990 | 8 | 1.000 | — | 40 | 0.975 | — | 0.025 | 47 | 1.000 | — | — | — | 13 | 1.000 | — | — | — | — | — |
| Kodiak N. 1990 | 49 | 1.000 | — | 48 | 0.990 | 0.010 | — | 40 | 1.000 | — | — | — | 47 | 0.989 | — | — | — | — | 0.011 |
| Kodiak S. 1990 | 40 | 1.000 | — | 43 | 0.977 | 0.012 | 0.012 | 34 | 1.000 | — | — | — | 38 | 0.987 | 0.013 | — | — | — | — |
| Kamishak 1990 | 50 | 1.000 | — | 49 | 1.000 | — | — | 45 | 1.000 | — | — | — | 50 | 0.980 | 0.010 | — | — | — | 0.010 |
| Montague St. 1990 | 50 | 1.000 | — | 50 | 1.000 | — | — | 49 | 1.000 | — | — | — | 42 | 1.000 | — | — | — | — | — |
| Kachemak Bay 1990 | 50 | 1.000 | — | 50 | 1.000 | — | — | 46 | 0.989 | — | — | 0.011 | 50 | 1.000 | — | — | — | — | — |
| Prince Wm. Sd. 1990 | 50 | 1.000 | — | 47 | 0.989 | — | 0.011 | 49 | 1.000 | — | — | — | 50 | 1.000 | — | — | — | — | — |
| Sullivan Is. 1993 | 99 | 1.000 | — | 92 | 0.995 | — | 0.005 | 84 | 0.994 | — | 0.006 | — | 99 | 0.995 | 0.005 | — | — | — | — |
| Seymour C. pooled | 125 | 1.000 | — | 118 | 0.983 | 0.004 | 0.013 | 119 | 0.992 | — | 0.008 | — | 125 | 0.992 | — | — | — | 0.008 | — |
| *C. opilio* | | | | | | | | | | | | | | | | | | | |
| Bering Sea pooled | 125 | 1.000 | — | 125 | 0.992 | 0.008 | — | 123 | 0.980 | — | 0.020 | — | 125 | 0.992 | 0.008 | — | — | — | — |
| St. Matt. Is. pooled | 200 | 0.998 | 0.002 | 187 | 1.000 | — | — | 183 | 0.970 | — | 0.030 | — | 198 | 0.982 | 0.005 | 0.003 | 0.003 | 0.008 | — |
| Pribilof Is. pooled | 214 | 1.000 | — | 199 | 0.997 | 0.003 | — | 196 | 0.967 | 0.008 | 0.025 | — | 214 | 0.993 | 0.002 | — | — | 0.005 | — |
| Atlantic O. 1991 | 97 | 1.000 | — | 97 | 0.995 | 0.005 | — | 97 | 0.985 | 0.005 | 0.010 | — | 97 | 0.964 | — | — | — | 0.036 | — |

| Population[1] | *PROT-3** | | | *SOD-1** | | | *TPI-1** | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | *n* | *100 | *88 | *n* | *100 | *109 | *n* | *-100 | *100 | *-41 |
| *Chionoecetes bairdi* | | | | | | | | | | |
| Bristol Bay pooled | 100 | 0.010 | 0.990 | 125 | 1.000 | — | 100 | 1.000 | — | — |
| Bering Sea pooled | 283 | 0.016 | 0.984 | 273 | 1.000 | — | 284 | 0.996 | — | 0.004 |
| Port Moller 1990 | 42 | — | 1.000 | 39 | 1.000 | — | 42 | 1.000 | — | — |
| Sand Pt/Pavlof 1990 | 50 | — | 1.000 | 50 | 1.000 | — | 47 | 0.979 | — | 0.021 |
| Kodiak N. 1990 | 50 | — | 1.000 | 50 | 1.000 | — | 50 | 0.990 | — | 0.010 |
| Kodiak S. 1990 | 50 | — | 1.000 | 50 | 1.000 | — | 47 | 1.000 | — | — |
| Kamishak 1990 | 50 | — | 1.000 | 50 | 1.000 | — | 49 | 1.000 | — | — |
| Montague St. 1990 | 50 | — | 1.000 | 50 | 1.000 | — | 50 | 1.000 | — | — |

*continued*

**Table 3 (continued)**

| Population[1] | *PROT-3** | | | *SOD-1** | | | *TPI-1** | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | *n* | *100 | *88 | *n* | *100 | *109 | *n* | *-100 | *100 | *-41 |
| *Chionoecetes bairdi*, continued | | | | | | | | | | |
| Kachemak Bay 1990 | 50 | — | 1.000 | 50 | 1.000 | — | 50 | 1.000 | — | — |
| Prince Wm. Sd. 1990 | 50 | — | 1.000 | 50 | 1.000 | — | 50 | 1.000 | — | — |
| Sullivan Is. 1993 | 100 | — | 1.000 | ND | | | 100 | 1.000 | — | — |
| Seymour C. pooled | 125 | — | 1.000 | 125 | 1.000 | — | 125 | 1.000 | — | — |
| *Chionoecetes opilio* | | | | | | | | | | |
| Bering Sea pooled | 124 | 0.992 | 0.008 | 122 | 1.000 | — | 125 | 0.992 | 0.004 | 0.004 |
| St. Matt. Is. pooled | 196 | 0.997 | 0.003 | 198 | 0.997 | 0.003 | 198 | 0.995 | 0.002 | 0.002 |
| Pribilof Is. pooled | 214 | 0.986 | 0.014 | 211 | 0.998 | 0.002 | 214 | 1.000 | — | — |
| Atlantic O. 1991 | 97 | 1.000 | — | 97 | 1.000 | — | 97 | 0.990 | 0.010 | — |

[1] Port Moller, Sand Point/Pavlof Bay, and Prince William Sound *C. bairdi* populations not included in analyses.
[2] *G3PDH-1*87* was pooled with **100*.

were grouped by major geographic regions (Bering Sea, Gulf of Alaska, and Southeast Alaska) for comparison, the overall log-likelihood statistic was highly significant ($P<0.01$, Table 4). *G3PDH-2** and *PROT-3** contributed most to the observed among-region heterogeneity. Within the Bering Sea, pooled samples collected from Bristol Bay (east of approximately 162°45'W long.) were significantly different from pooled samples from the Bering Sea and Pribilof Island areas (west of approximately 167°00'W long.). In this comparison, *G3PDH-2**, *IDHP-1**, and *PEPA** allelic frequencies differed significantly.

The following were the low-frequency alleles detected according to their respective major geographic regions: 1) Bering Sea, *AAT-2*69*, *ALAT*87*, *CBYR*117*, *G3PDH-2*86*, *GPI-A1*55*, *MDH-A1*79*, *PGDH*112*, *PGM-1*103*, and *PROT-3*100*; 2) Gulf of Alaska, *AAT-1*64*, *PGDH*91*, and *PGM-1*75*; and 3) Southeast Alaska, *MDH-A1*128* and *PGM-1*88*. The *PROT-3*100* allele, likely an introgressed *C. opilio* allele, contributed significantly to the overall heterogeneity observed among the major geographic regions of Bering Sea, Gulf of Alaska, and Southeast Alaska. Genetic distance measurements (Cavalli-Sforza and Edwards, 1967) within *C. bairdi* populations ranged from 0.031 to 0.059.

### *Chionoecetes opilio*

Twenty-nine loci were scored consistently in all collections and were used in the data analyses. No significant temporal variation ($P<0.01$) was found within multiple-year collections in the Bering Sea, St. Matthew Island, and the Pribilof Islands. We pooled these collections for further analyses.

Seventeen loci, *AAT-1**, *AAT-2**, *AH-2**, *AH-3**, *CBYR**, *G3PDH-1**, *G3PDH-2**, *GPI-A1**, *IDHP-1**, *MDH-A1**, *MDH-A2**, *PEPA**, *PGDH**, *PGM-1**, *PROT-3**, *SOD-1**, and *TPI-1**, were polymorphic in at least one population (Table 3). Twelve monomorphic loci were *ADA-1**, *ADA-2**, *ADA-3**, *ALAT**, *βGALA**, *GAPDH**, *βGLUA**, *MEP-1**, *MPI**, *PEPD-2**, *PROT-1**, and *PROT-2**. One polymorphic locus, *AH-3**, was variable at a frequency of ≥0.05 in at least one population.

Genotype frequencies at all loci conformed to Hardy-Weinberg expectations; therefore we assumed all samples were from single panmictic populations. Average observed heterozygosities were lower than those for *C. bairdi* and ranged from 0.012 to 0.013 in Alaskan populations; the average heterozygosity was 0.010 in Atlantic Ocean *C. opilio*.

### Among-population variation

$F_{ST}$ of 17 polymorphic loci was not significantly different from zero for Alaskan populations ($P=0.4270$) or when the Atlantic Ocean collection was included ($P=0.7130$). However, the $F_{ST}$ value for *PGM-1** was highly significant ($P=0.0050$) in comparisons of Atlantic Ocean and Alaskan *C. opilio*. A hierarchical log-likelihood analysis of these loci revealed very low levels of heterogeneity among all *C. opilio* (Table 5). In this analysis, *PGM-1** was also highly significant ($P=0.0071$) in comparisons of Atlantic Ocean and Alaskan *C. opilio*. Among all *C. opilio*, *PGM-1** was significant ($P=0.0361$). The overall log-likelihood statistic for all loci among all *C. opilio* was significant ($P=0.0382$)(Table 5). Low-frequency alleles detected in Alaskan collections were *AAT-1*64*, **210*, and **120*, *AAT-2*69*, *AH-2*110* and **83*, *AH-3*106*, *CBYR*117*, *G3PDH-1*117*, *G3PDH-2*86* and **111*, *GPI-A1*60*,

*158, and *55, IDHP-1*81 and *119, MDH-A2*65, PGM-1*82, *114, and *103, PROT-3*88, SOD-1*109, and TPI-1*-41. Differing PGM-1* alleles and allele frequencies contributed most to the overall levels of differentiation observed between Alaskan and Atlantic Ocean *C. opilio* populations. Multilocus between-population chord distance measures ranged from 0.029 to 0.033 in Alaskan collections and increased to 0.043 when we added the Atlantic Ocean population.

## Comparison of *C. bairdi* and *C. opilio* from Alaska

A total of 27 loci, *AAT-1*, AAT-2*, AH-3*, ADA-1*, ADA-

**Table 4**

Hierarchical log-likelihood analysis for *Chionoecetes bairdi*.

| | df | *AAT-1** | df | *AAT-2** | df | *AH-3** | df | *ALAT** |
|---|---|---|---|---|---|---|---|---|
| Total | 16 | 13.10 | 16 | 12.70 | 16 | 14.72 | 8 | 2.21 |
| Among | 2 | 1.23 | 2 | 6.35* | 2 | 1.90 | 1 | 1.60 |
| Within | 14 | 11.87 | 14 | 6.35 | 14 | 12.82 | 7 | 0.61 |
| Bering Sea | 2 | 2.69 | 2 | 0.62 | 2 | 2.54 | 1 | 0.61 |
| Gulf of Alaska | 12 | 9.18 | 12 | 5.73 | 12 | 10.28 | 6 | 0.00 |
| Among | 2 | 1.49 | 2 | 0.10 | 2 | 1.54 | 1 | 0.00 |
| Within | 10 | 7.69 | 10 | 5.63 | 10 | 8.74 | 5 | 0.00 |
| Northern Gulf | 8 | 7.69 | 8 | 4.83 | 8 | 5.38 | 4 | 0.00 |
| Southeast | 2 | 0.00 | 2 | 0.80 | 2 | 3.36 | 1 | 0.00 |
| | df | *CBYR** | df | *G3PDH-1** | df | *G3PDH-2** | df | *GPI-A1** |
| Total | 8 | 2.21 | 8 | 8.25 | 16 | 43.07** | 40 | 37.66 |
| Among | 1 | 1.61 | 1 | 0.31 | 2 | 13.82** | 5 | 3.89 |
| Within | 7 | 0.60 | 7 | 7.94 | 14 | 29.25** | 35 | 33.77 |
| Bering Sea | 1 | 0.60 | 1 | 1.01 | 2 | 16.84** | 5 | 3.50 |
| Gulf of Alaska | 6 | 0.00 | 6 | 6.93 | 12 | 12.41 | 30 | 30.27 |
| Among | 1 | 0.00 | 1 | 1.16 | 2 | 0.49 | 5 | 6.25 |
| Within | 5 | 0.00 | 5 | 5.77 | 10 | 11.92 | 25 | 24.02 |
| Northern Gulf | 4 | 0.00 | 4 | 3.85 | 8 | 9.94 | 20 | 21.57 |
| Southeast | 1 | 0.00 | 1 | 1.92 | 2 | 1.98 | 5 | 2.45 |
| | df | *IDHP-1** | df | *MDH-A1** | df | *PEPA** | df | *PGDH** |
| Total | 24 | 38.63* | 16 | 10.40 | 16 | 30.30* | 24 | 15.60 |
| Among | 3 | 3.79 | 2 | 5.96 | 2 | 4.55 | 3 | 2.87 |
| Within | 21 | 34.84* | 14 | 4.44 | 14 | 25.75* | 21 | 12.73 |
| Bering Sea | 3 | 3.56 | 2 | 1.82 | 2 | 14.04 | 3 | 3.91 |
| Gulf of Alaska | 18 | 31.28 | 12 | 2.62 | 12 | 11.71 | 18 | 8.82 |
| Among | 3 | 5.51 | 2 | 0.78 | 2 | 2.62 | 3 | 0.77 |
| Within | 15 | 25.77 | 10 | 1.84 | 10 | 9.09 | 15 | 8.05 |
| Northern Gulf | 12 | 20.83 | 8 | 1.84 | 8 | 8.22 | 12 | 7.13 |
| Southeast | 3 | 4.94 | 2 | 0.00 | 2 | 0.87 | 3 | 0.92 |
| | df | *PGM-1** | df | *PROT-3** | df | *TPI-1** | df | Overall |
| Total | 32 | 27.40 | 8 | 18.22* | 8 | 6.29 | 256 | 280.75 |
| Among | 4 | 6.43 | 1 | 17.83** | 1 | 0.58 | 32 | 72.71** |
| Within | 28 | 20.97 | 7 | 0.39 | 7 | 5.71 | 224 | 208.04 |
| Bering Sea | 4 | 3.87 | 1 | 0.39 | 1 | 1.21 | 32 | 57.22 |
| Gulf of Alaska | 24 | 17.10 | 6 | 0.00 | 6 | 4.50 | 192 | 150.82 |
| Among | 4 | 3.01 | 1 | 0.00 | 1 | 0.77 | 32 | 24.49 |
| Within | 20 | 14.09 | 5 | 0.00 | 5 | 3.73 | 160 | 126.33 |
| Northern Gulf | 16 | 13.38 | 4 | 0.00 | 4 | 3.73 | 128 | 108.40 |
| Southeast | 4 | 0.71 | 1 | 0.00 | 1 | 0.00 | 32 | 17.93 |

* Test is significant at $\alpha = 0.05$.
** Test is significant at $\alpha = 0.01$.

*2*, ADA-3*, ALAT*, CBYR*, βGALA*, GAPDH*, βGLUA*, G3PDH-1*, G3PDH-2*, GPI-A1*, IDHP-1*, MDH-A1*, MDH-A2*, MEP-1*, MPI*, PEPA*, PEPD-2*, PGDH*, PGM-1*, PROT-1*, PROT-2*, PROT-3**, and *TPI-1**, were scored in all *C. bairdi* and *C. opilio* populations analyzed; 16 loci, *AAT-1*, AAT-2*, AH-3*, ALAT*, CBYR*, G3PDH-1*, G3PDH-2*, GPI-A1*, IDHP-1*, MDH-A1*, MDH-A2*, PEPA*, PGDH*, PGM-1*, PROT-3**, and *TPI-1**, were polymorphic in at least one population of either species. Eleven loci, *ADA-1*, ADA-2*, ADA-3*, βGALA*, GAPDH*, βGLUA*, MEP-1*, MPI*, PEPD-2*, PROT-1**, and *PROT-2**, were monomorphic for the identical allele. Significant differences ($P<0.01$) between the two species were detected at eight loci, *AH-3*, G3PDH-1*, GPI-A1*, IDHP-1*, MDH-A1*, PEPA*, PGDH**, and *PROT-3**. Two loci, *AH-3** and *PROT-3**, were particularly informative with nearly fixed differences for alternate alleles (Table 3). In addition, with the exception of *C. opilio* from the Pribilof Island area collections, *C. opilio* expressed only the *IDHP-1*100* allele, whereas *C. bairdi* were highly variable. Several low-frequency variants ($P<0.05$) also contributed to the overall differences between the species. Numerous low-frequency alleles detected in only Bering Sea collections of *C. bairdi* were also detected in Alaskan *C. opilio* collections, including the following: *AAT-2*69, CBYR*117, G3PDH-2*86, GPI-A1*55, MDH-A1*79, PGM-1*103*, and *PROT-3*88*. Also, a rare allele, *PGDH*112*, was detected only in Bristol Bay *C. bairdi* and in Pribilof Island and Atlantic Ocean *C. opilio*.

Multilocus variation between species was estimated by genetic-distance measures. Between-species genetic-distance measures ranged from 0.222 to 0.251. The largest genetic distance was between Atlantic *C. opilio* and two northern Gulf of Alaska *C. bairdi* populations, those of Kachemak Bay and Montague Strait. The smallest between-species genetic distance was that for Pribilof Island and Bering Sea *C. opilio* compared with that for Bering Sea and Pribilof Island *C. bairdi*.

**Table 5**

Hierarchical log-likelihood analysis for *Chionoecetes opilio*.

| Source | df | Overall |
|---|---|---|
| Total | 96 | 121.93* |
| Among | 32 | 41.63 |
| Within | 64 | 80.30 |
| Bering Sea | 64 | 80.30 |
| Atlantic Ocean | 0 | 0.00 |

* Significant value ($P<0.05$)

### *Chiocoetes bairdi* × *C. opilio* hybrids

Hybrids between *C. bairdi* and *C. opilio* crabs in the Bering Sea have been identified morphologically and genetically (Karinen and Hoopes, 1971; Johnson, 1976; Grant et al., 1978; Hoopes et al.[1]). Several collections in our study had allele frequencies suggesting either low levels of introgression between the species or the inclusion of hybrid or backcross individuals in the collection. For example, low frequencies of *PROT-3*100* were observed in *C. bairdi* crabs from Bristol Bay, the Bering Sea, and the Pribilof Islands. *PROT-3*100* was not observed in *C. bairdi* from non-Bering Sea collections. Similarly, *PROT-3*88* was observed in *C. opilio* collections from the Bering Sea, St. Matthew Island, and the Pribilof Islands, and low frequencies of *IDHP-1*81* and **119* were observed in Pribilof Island *C. opilio* collections; these alleles were not observed in *C. opilio* collected from the Atlantic Ocean.

## Discussion

Allozyme electrophoresis techniques have been used extensively to describe evolutionary relationships within genera of decapod crustaceans (Bert, 1986; Bert and Harrison, 1988; Busack, 1989; Abdullah and Shukor, 1993); however, these techniques have generally revealed very low levels of intraspecific genetic variation (Nelson and Hedgecock, 1980; Smith et al., 1980; Busack, 1988; Seeb et al., 1990b). Exceptions to this generalization are found in species that occur over broad geographic areas or in widely different environments (Nelson and Hedgecock, 1980; Mulley and Latter, 1981; Kartavtsev et al., 1991). Significant population heterogeneity has been found in species that exhibit highly specialized life history attributes (Stevens, 1991) and in some freshwater species (Macaranas et al., 1995; Fetzner et al., 1997). Within a marine species, Seeb et al. (1990a) discriminated populations of red king crab from major geographic areas of the Gulf of Alaska and Bering Sea. Allozyme techniques have also been used to examine seasonal variability of decapod larval, megalopal, and adult allelic frequencies (Kordos and Burton, 1993).

Davidson et al. (1985) examined population structure in North Atlantic *C. opilio* using allozymes and interpreted their observed esterase polymorphisms as phenotypic expressions of probable genotypic differences. However, we feel caution should be used in interpreting their data until genetic transmission of these markers can be shown by inheritance studies because we were unable to interpret the genetic basis of observed esterase activity.

The importance of tissue quality for allozyme studies is well documented (e.g. Utter et al., 1987) but is particularly critical for crustacean tissue, which degrades more rapidly than finfish tissue. Laboratory analysis revealed obvious differences in enzyme resolution for several loci that resulted in conservative allele pooling and loss of some population data. Optimal sample handling may have increased detectable variation.

## Population diversity of *C. bairdi*

We detected differences among *C. bairdi* populations of the three major geographic regions: Bering Sea, Gulf of Alaska, and Southeast Alaska. Most notably, we detected population subdivision within the Bering Sea. Samples collected in Bristol Bay (east of approximately 162°45'W long.) were statistically different from samples collected near the Pribilof Islands (west of approximately 167°00'W long.).

Other biological data support our inference that subpopulations of *C. bairdi* occur within the Bering Sea. Using trawl survey data from 1974 onward, Otto (1982) reported size-frequency distributions of *C. bairdi* in the Pribilof Islands that were different from those in the area north of the Alaska Peninsula, including Bristol Bay. Further, as National Marine Fisheries Service (NMFS) trawl assessment surveys expanded westward, it became evident that crabs in the Pribilof area were larger in size compared with those along the continental slope north and west of the Pribilof Islands. Somerton (1981) found size differences among large females from the eastern Bering Sea seemed to partition into two subareas along 167°15'W long. The mean size of adult females was quite constant in the eastern subarea (east of 167°15'W long.) but decreased steadily in the western subarea. Although both investigators speculated upon the possibility of genetic or environmental factors causing these differences, the species has been considered a single Bering Sea stock for management purposes (Otto, 1982). In our study, we lacked *C. bairdi* specimens from west of approximately 173°W long. and thus were unable to test whether crabs collected from near the Pribilof Islands differed from crabs collected near the continental slope. Although there does not appear to be a precise correlation between our findings and the observations of Otto (1982) and Somerton (1981), all data seem to suggest that *C. bairdi* in the Bering Sea may not be composed of a single panmictic population.

However, any conclusions we may draw from biochemical data should be confirmed by other types of data. The American lobster (*Homarus americanus*) is a case in point. Tracey et al. (1975) noted genetic and morphological differences between inshore and offshore populations. In tagging studies, Fogarty et al. (1980) demonstrated limited movement of lobsters released at inshore stations, in contrast with extensive seasonal migrations by lobsters tagged at offshore locations. These studies indicated that despite the potential for genetic exchange during seasonal mixing, the inshore and offshore populations retained their genetic identity.

The planktotrophic larvae of *Chionoecetes* may spend up to two months in surface waters (Slizkin, 1990), raising the possibility that larvae released in one area may become recruits in another. Further, most of what is known or hypothesized about migration of Bering Sea *C. bairdi* is based upon abundance and distribution estimates from annual NMFS trawl surveys and subsequent fishery captures.[2] Migration studies of *Chionoecetes* in Alaska have been hindered by tag losses after molting. Development of a permanent tag for *Chionoecetes* would provide a valuable tool for examining population migration and further for evaluating the null hypothesis of panmixia. Our findings of regional and within-Bering Sea heterogeneity among *C. bairdi* populations merit further investigation.

## Population diversity of *C. opilio*

We detected only small differences between Bering Sea and North Atlantic *C. opilio*, primarily in *PGM-1** allele frequencies. The low-frequency alleles of other loci observed in Alaskan *C. opilio* did not contribute significantly to overall differences. Although sampling error may have been a factor (Gregorius, 1980) in detection of rare alleles, no private alleles were found in the North Atlantic. The minimal genetic differentiation among this circumpolar species contrasts with findings in halibut (*Hippoglossus*), herring (*Clupea*) and cod (*Gadus*) (Grant, 1987) where significant differentiation has been described across a similar geographic range. The close genetic affinity of the Bering Sea *C. opilio* collections with the collection from the North Atlantic and the detection of low-frequency Bering Sea *Chionoecetes* alleles in the North Atlantic suggest recent or ongoing gene flow. This possibility is supported by Garth (1958) whose range description includes a distribution of *C. opilio* northward (from the Bering Strait) and eastward through the Beaufort Sea and Davis Strait to the North Atlantic. This species tolerates very low temperatures; the optimum temperature for immature individuals has negative values even in the summer (Slizkin, 1990). Thus, it is plausible to hypoth-

[2] Morrison, R. 1997. Alaska Dep. Fish and Game, P.O. Box 920587, Dutch Harbor, AK 99692. Personal commun.

esize gene flow through these northern seas even in the presence of sea ice pack. Alternatively, it is possible that gene flow is restricted, but that the differentiating forces of drift, selection, and mutation have not yet produced significant detectable genetic divergence.

### Species differentiation, hybrids, and gene introgression

The morphological criteria for differentiating *C. bairdi* and *C. opilio* have been well described (Rathbun, 1925; Garth, 1958; Karinen and Hoopes, 1971). However, a few crabs in our study that met one or more morphological criteria were probably hybrid or recombinant individuals. Their composite genotypes were atypical of the parental species and were instead indicative of $F_1$ hybrids or backcross matings. Species differentiation in allelic frequencies was observed between *C. bairdi* and *C. opilio*, most notably for *AH-3**, *IDHP-1**, and *PROT-3**. The unusual composite genotypes were most clearly differentiated by the *PROT-3*100* allele in *C. bairdi* collections, and conversely, by the *PROT-3*88* allele in the *C. opilio* collections from the Bering Sea. The *PROT-3*100* allele contributed significantly to the among-regional differences in *C. bairdi*. This marker is also very useful for investigation of hybridization between these species.

### Gene flow and geographic barriers

Our findings are consistent with previous electrophoretic studies that infer that decapod crustaceans, especially large, mobile species, exhibit low levels of variation at allozyme markers (Nelson and Hedgecock, 1980). The high dispersal potential of marine species is often used to explain the low levels of variation detected among populations (Avise, 1994). Such distribution appears to be the case with *Chionoecetes* as well as with other marine organisms with similar geographic distributions in the North Pacific, Gulf of Alaska, and Bering Sea, such as Pacific halibut (Grant et al., 1984), Pacific herring (Grant and Utter, 1984), Pacific cod (*Gadus macrocephalus*) (Grant et al., 1987), Pacific ocean perch (*Sebastes alutus*) (Seeb and Gunderson, 1988), and red king crab (*Paralithodes camtschaticus*) (Seeb et al., 1990a).

Limits to the actual dispersal of marine species, despite high dispersal potential, may periodically or continuously limit gene flow in some directions (Avise, 1994 and references therein). The Alaska Peninsula–Aleutian chain appears to be a significant barrier to gene flow in some species, such as Pacific ocean perch (Seeb and Gunderson, 1988), Pacific herring (Grant and Utter, 1984), rock sole (*Pleuronectes bilineatus*) (Mulligan et al., 1995) and red king crab (Seeb et al., 1990a).

The Alaska Peninsula–Aleutian Chain appears to limit gene flow among *C. bairdi* populations as evidenced by the differentiation detected among regions above and below this geographic barrier. The lack of introgressed *C. opilio* alleles in the Gulf of Alaska and Southeast Alaska populations studied also supports this view. Our findings suggest that the numerous rare alleles observed in Bering Sea, and not Atlantic, populations of *Chionoecetes* may be ancient alleles that have been maintained over time in the large populations that have inhabited these waters; however, larger sample sizes of Atlantic Ocean *C. opilio* are needed to confirm this hypothesis. Detection of low-frequency Bering Sea *Chionoecetes* alleles in North Atlantic *C. opilio* and the lower heterozygosity of North Atlantic *C. opilio*, coupled with the lack of congeners in the North Atlantic, allow speculation that the genus *Chionoecetes* may have arisen in the North Pacific.

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# A decision rule based on the mean square error for correcting relative fishing power differences in trawl survey data

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**Abstract.**—Some combinations of trawler, trawl, and crew catch fish better than others. Systematic error enters catch per unit of effort (CPUE) data from trawl surveys through such relative differences in efficiency among sampling instruments. Correcting relative fishing power differences can remove bias due to systematic error but may also increase the variance of the mean CPUE estimate. As a result, the overall error of the estimate may actually become worse, even when the fishing power difference is statistically significant. A decision rule specified by the mean square error (MSE) of the mean CPUE estimate avoids this mistake: namely a correction that reduces the error in the mean CPUE estimate would be applied, a correction that increases the error would not be applied. I describe and demonstrate an algorithm, based on minimizing the MSE, for deciding to correct a fishing power difference. The strategy requires that a probability density function exist that models the CPUE data reasonably well.

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Trawl surveys are often used to collect data on catch observations standardized by fishing effort (the catch per unit of effort [CPUE]), and the mean CPUE is often interpreted as an index of abundance. Ideally, fishing power, or fish catching efficiency, must be held constant in trawl surveys lest altered catch rates be confounded with changes in abundance of fish or invertebrates. Unfortunately, the sampling instrument is a complex system that includes the vessel, vessel operators, and fishing gear, all of which may vary from survey to survey, introducing changes in fishing power (Gulland, 1956). Correcting fishing power differences seems necessary for proper interpretation of mean CPUE. However, methods have not been established for determining if an improved estimate of mean CPUE actually results from such correction.

Relative differences in fishing power make standardization in trawl surveys difficult. Technological changes in fishing gear, as well as replacement of older research vessels, may affect fishing power (Azarowitz, 1981; Byrne et al., 1991). Fishing power differences are an inherent part of multiple vessel surveys. Examples of this type of survey are annual and triennial surveys in several regions of the north Pacific Ocean and Bering Sea conducted by the Alaska Fisheries Science Center (AFSC) of the National Marine Fisheries Service (NMFS) (Harrison, 1992; Weinberg et al., 1994; Munro and Hoff, 1995; Goddard and Zimmermann[1]) and the International Young Fish Survey in the North Sea (Anonymous[2]). Koeller and Smith (1983) reported change in a single vessel's ability to measure speed over a 3-year period and hypothesized that this may have altered its fishing power from year to year. Operator effects have also been shown to account for fishing power differences among vessels (Munro and Hoff, 1995) and thus may be inferred for change in operators of a single vessel. (In what

[1] Goddard, P., and M. Zimmermann. 1993. Distribution, abundance, and biological characteristics of groundfish in the eastern Bering Sea based on results of the U.S. bottom trawl survey during June–September 1991. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Alaska Fish. Sci. Cent., 7600 Sand Point Way NE, Seattle, WA 98115-0070, Proc. Rep. 93-15, 324 p.

[2] Anonymous. 1986. Manual for the International Young Fish Surveys in the North Sea, Skagerrak, and Kattegat. International Council for the Exploration of the Sea, Palaegade 2-4, DK-1261, Copenhagen K, Denmark. ICES Council Meeting 1986/H:2.

follows, "vessel" refers to the entire system that comprises the sampling instrument, from the bow of the fishing vessel to the codend.)

A fishing power difference forces a choice between two estimators of mean CPUE, one that incorporates a fishing power correction and one that does not. Correcting a fishing power difference amounts to changing an observation to an estimate. The following model is used to estimate what a standard vessel would have caught had it executed exactly the same tow as was done by a nonstandard vessel:

$$\hat{x}_i = y_i \hat{FPC},$$

where $\hat{x}_i$ = estimated CPUE at station $i$ by the standard vessel;
$y_i$ = observed CPUE at station $i$ by the nonstandard vessel; and
$\hat{FPC}$ = estimated fishing power correction factor.

Each original observation, $y_i$, has no error beyond measurement error. Every $\hat{x}_i$ has error due to the variance of the estimate of FPC. Consequently the mean CPUE estimated from the $\hat{x}_i$ has at least two components of variation, one stemming from the usual sampling variance in the observations ($y_i$), the other due to uncertainty in the estimate of FPC. This added component of estimation error has been recognized as the cost of correcting systematic error in the observations, but only in passing, (Sissenwine and Bowman, 1978; Byrne et al., 1981; Koeller and Smith, 1983; Fanning, 1984).

Estimators are often chosen on the basis of their relative error, yet most researchers have ignored this in deciding whether or not to correct a fishing power difference. Investigations have been focused on estimating the difference but have not evaluated it in terms of estimating mean CPUE. Very few decision rules have been explicitly stated, most having been implied by testing the statistical significance of the fishing power difference itself. Early CPUE calibrations (Gulland, 1956; Robson, 1966) were based on multiplicative models of different sources of variability in CPUE data, including vessel effects. Log transformation of the data produced linear models with coefficients that could be estimated with regressions and for which classical hypotheses could be formulated and tested. Sissenwine and Bowman (1978), Kimura (1981), and Gavaris (1980) have followed this strategy in their decisions to apply FPCs. Gavaris (1980) estimated the FPC using the method of Bradu and Mundlak (1970) and reported approximate confidence intervals, without explicitly stating a decision rule. Fanning (1984) proposed an explicit decision rule using a beta-distributed index for the fishing power difference in paired observations. If the confidence interval included the value that represented identical fishing power, he recommended that the estimated FPC not be applied. Byrne and Fogarty (1985) tested the significance of fishing power differences using Hotelling's $t$-squared test when several species were considered simultaneously, or the nonparametric Friedman's test for a single species. They offered no interpretation of a significant fishing power difference, in particular, whether or not it should be corrected. The $t$-test was used by Byrne et al. (1991) to determine the significance of a fishing power difference. In response to a significant difference, they estimated an FPC using the method of Bradu and Mundlak (1970). They then produced confidence intervals for that estimate using a bootstrap approximation. However, they did not state an explicit decision rule based on those intervals.

Correcting a fishing power difference would be worthwhile only when it reduces the error in the estimate of mean CPUE. Statistical significance of a fishing power difference is not a compelling justification because the cost of the added uncertainty may out weigh the benefit of removing bias that entered through systematic error in CPUE data. If the estimate of a correction factor has a lot of uncertainty, then the error of the estimate of mean CPUE could actually become worse by correcting data, even for a statistically significant fishing power difference. A decision rule for correcting a fishing power difference must avoid this mistake by accounting for the cost of correcting as well as the benefit. Such a rule would permit choosing the estimate of mean CPUE that yields the lower total error.

## Methods

The notion of the mean square error (MSE) lends a useful structure for defining such a decision rule. The MSE is a widely recognized measure of error between an estimator and its parameter (Mood et al., 1974). The MSE is defined as

$$MSE\,[\hat{C}] = E\left[(\hat{C} - C)^2\right],$$

which is the expectation of the squared difference between the estimator of mean CPUE, $\hat{C}$, and the parameter being estimated, true CPUE or, $C$. The MSE can be rewritten as

$$MSE\,[\hat{C}] = \mathrm{Var}\,[\hat{C}] + b^2[\hat{C}],$$

or the sum of the variance and the squared bias of the estimator. By defining the following estimators,

$\hat{C}(\underline{w})$ = estimator as a function of uncorrected data

$\hat{C}(\underline{\hat{w}}_{\hat{FPC}})$ = estimator as a function of data corrected with an estimated *FPC*,

where $\underline{w} = (x_1, x_2, \ldots, x_{n_x}, y_1, y_2, \ldots y_n)$

= a mixed vector of CPUE observations from two vessels

and

$\underline{w}_{\hat{FPC}} = (x_1, x_2, \ldots, x_{n_x}, y_1 \hat{FPC}, y_2 \hat{FPC}, \ldots y_{n_y} \hat{FPC})$

= a mixed vector of CPUE observations and estimates,

a model for the decision rule can be stated as: Apply the FPC if

$$MSE\left[\hat{C}(\underline{w})\right] > MSE\left[\hat{C}(\underline{\hat{w}}_{\hat{FPC}})\right]$$

and do not apply the FPC if

$$MSE\left[\hat{C}(\underline{w})\right] \leq MSE\left[\hat{C}(\underline{\hat{w}}_{\hat{FPC}})\right].$$

(Note, this explication of the MSE of mean CPUE has been framed in terms of a single survey with two vessels. But the notion of MSE lends itself equally well to any situation in which data must be "corrected," including the common case of a single, nonstandard vessel conducting a standard survey.)

This decision rule is unattainable because it requires that the true value of the fishing power difference and CPUE sampling distributions be known. However, simulations can be used to estimate the mean square error. One such simulation strategy takes the following form: Assume a probability distribution for CPUE. Generate realizations of this distribution to represent a survey in which a fishing power difference is suspected. Impose an assumed fishing power difference on the simulated survey. Estimate the fishing power difference and apply the estimate to correct the assumed fishing power difference. (Estimating the fishing power difference may require further distributional assumptions and simulations, depending on the estimator and the kind of data it requires, especially if fishing power difference is to be estimated from experiments conducted independently of the survey.) The MSEs of the estimated mean CPUE are then calculated from the realizations with and with out the fishing power corrections. This procedure is repeated for a range of selected fishing power differences. Whether the observed fishing power difference (estimated from real data) falls within the range of the fishing power difference for which correcting reduces the MSE of the estimated mean CPUE can then be determined.

This general strategy is illustrated by constructing an algorithm to apply it to a real problem. Any algorithm for implementing this decision rule will depend on specific circumstances. In this case the particulars are defined by a fishing power problem in an annual survey of the eastern Bering Sea, conducted by the AFSC (Wakabayashi et al., 1985; Goddard and Zimmermann[1]). Two vessels systematically sample all strata, following interleaved station patterns that produce approximately equal numbers of CPUE observations. From these two sets of unpaired data a fishing power difference between two vessels is estimated for each of a number of species. The question is "Should this estimated FPC be used to correct CPUEs of one vessel to the fishing efficiency of the other?" This general MSE decision rule takes the following form (the specifics of the Bering Sea survey being addressed within this framework):

1 Simulate surveys from an appropriate sampling distribution for data collected by a "standard" vessel.
2 Impose a known fishing power difference on the CPUE data in each simulated survey. (In these examples half the data were altered to emulate a two-vessel survey.)
3 For each simulated survey, estimate an FPC to correct the fishing power difference that was imposed in the previous step. (FPCs may be estimated from simulation from independent experimental data or, as in these examples, estimated from the simulated survey itself. The important aspect is that the error structure of the FPC estimator be incorporated in the simulation process.)
4 Estimate the mean CPUE for each simulated survey with and without correcting for the fishing power difference.
5 Repeat steps 2 through 4 for a range of fishing power differences.
6 Compute MSEs for estimated mean CPUE for each level of fishing power difference.
7 Plot the estimated MSEs against the fishing power differences imposed in Step 2 (Fig. 1).
8 Determine the range of fishing power difference where the MSE for corrected data is lower than the MSE for uncorrected data (Fig. 1).

The region of increased error is centered around the value 1.0, which represents equal fishing powers, and is sandwiched between regions of reduced error (Fig. 1). The smaller the true fishing power difference the more likely that correcting it will lead to increased error in mean CPUE, and the greater the fishing

power difference the more likely that correcting it will improve error in mean CPUE. For the range of the relative fishing power difference for which correction increases (becomes worse), the MSE will be called the "noncorrection region." The two ranges of the relative fishing power difference for which correcting reduces (improves) the MSE will be referred to collectively as the "correction region."

This procedure has four critical elements: simulating the CPUE data, the estimator of FPC, the estimator of mean CPUE, and the sample size in each simulation. The CPUE data (kilograms per hectare) were simulated with the Δ-distribution. The Δ-distribution has been proposed as an appropriate distribution for data that include the value 0.0 and that are heavily skewed to the right (Pennington, 1983; McConnaughey and Conquest, 1992). The probability density function for the Δ-distribution has parameters $p$, the probability of an observation with the value 0.0, and $\mu$ and $\sigma$, the conventional defining parameters of the lognormal distribution, which are the population mean and standard deviation of the log-transformed elements, respectively (Aitchison and Brown, 1957). The parameters for this distribution were calculated with CPUE data for flathead sole (*Hippoglossoides elassodon*) and walleye pollock (*Theragra chalcogramma*) collected in the 1992 eastern Bering Sea survey (Table 1; Fig. 2). These two species were chosen to illustrate cases of moderate and extreme skewness to the right. The mechanism for imposing a fishing power difference is also part of simulating each survey. In these examples the relative difference was applied by multiplying each CPUE from the nonstandard vessel by a ratio that represented the true mean nonstandard CPUE over the true mean standard CPUE. Two-hundred surveys were simulated at each of twenty preselected fishing power differences (Table 2). In each simulated survey, half of the data were selected to represent the standard vessel and the fishing power difference was imposed on the other half of the data, representing the nonstandard vessel. The sample sizes in two of the simulations were based on the number of observations used to calculate the parameters of the Δ-distribution: 149 per vessel for pollock and 144 per vessel for flathead sole. The third simulation was based on 50 observations per vessel for flathead sole. The smaller sample size is similar to the number of tows made in the larger strata of the annual Bering Sea survey (Goddard and Zimmermann[1]).

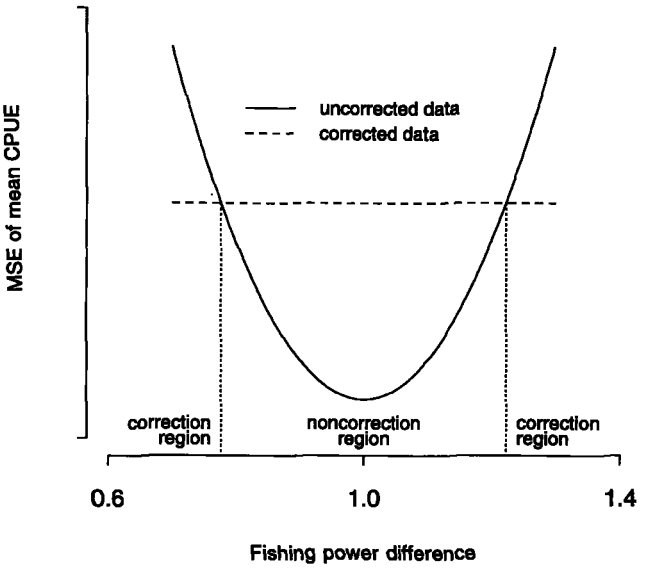


**Figure 1**

The noncorrection region that emerges from plotting mean square error of mean CPUE against the fishing power difference imposed on the simulated data. "Uncorrected data" refers to the scenario where mean CPUE was estimated without correcting the fishing power difference. "Corrected data" refers to the scenario where mean CPUE was estimated after correcting the fishing power difference.

**Table 1**

The Δ-distribution parameters and fishing power correction factors estimated from the 1992 Bering Sea survey data. Sample sizes are different because different vessels represented the "standard" vessel for each species.

| | Walleye pollock (*Theragra chalcogramma*) | Flathead sole (*Hippoglossoides elassodon*) |
|---|---|---|
| Δ-distribution parameters | | |
| $p$ (fraction of zeros) | 0.0336 | 0.1042 |
| $\mu$ (mean of log nonzeros) | 3.3590 | 1.5859 |
| $\sigma$ (SD of log nonzeros) | 2.1194 | 1.4985 |
| Number of observed CPUEs used to compute parameters | 149 | 144 |
| Estimated fishing power correction (FPC) factor | 1.32 | 0.76 |

The Kappenman estimator of the ratio of scale parameters (Kappenman, 1992) was used to estimate the FPC in each simulated survey. Inordinately large, rare observations are typical of trawl survey CPUE data (Koeller and Smith, 1983; Weinberg et al., 1994;

**Table 2**

Fishing power differences imposed on the simulated data.

| Catch ratio: nonstandard to standard | | Catch ratio: larger to smaller |
|---|---|---|
| 0.50 | Nonstandard vessel is | 2.00 |
| 0.57 | half as efficient | 1.75 |
| 0.67 | | 1.50 |
| 0.71 | | 1.40 |
| 0.77 | | 1.30 |
| 0.80 | | 1.25 |
| 0.83 | | 1.20 |
| 0.87 | | 1.15 |
| 0.91 | | 1.10 |
| 0.95 | | 1.05 |
| 1.00 | Identical fishing power | 1.00 |
| 1.05 | | 1.05 |
| 1.10 | | 1.10 |
| 1.15 | | 1.15 |
| 1.20 | | 1.20 |
| 1.25 | | 1.25 |
| 1.30 | | 1.30 |
| 1.40 | | 1.40 |
| 1.50 | | 1.50 |
| 1.75 | | 1.75 |
| 2.00 | Nonstandard vessel is twice as efficient | 2.00 |

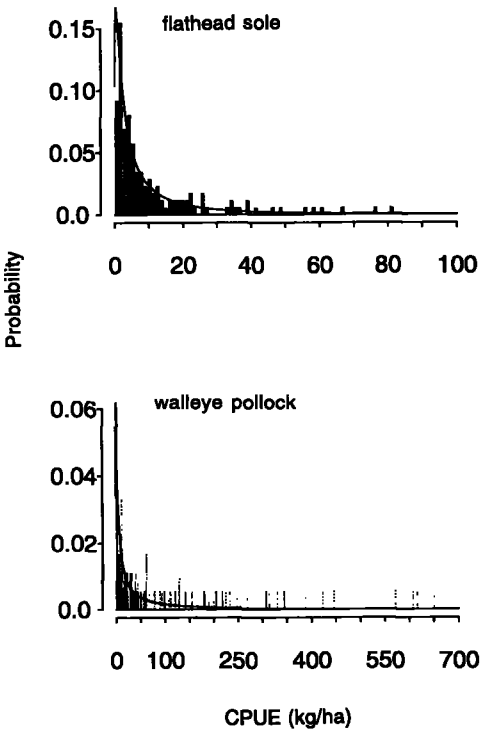


**Figure 2**

Histograms of catch-per-unit-of-effort (CPUE) data for flathead sole and walleye pollock overlayed by the probability density function for the Δ-distribution. The histograms are expressed as densities rather than as frequencies. The parameters specifying the Δ-distribution were estimated from the data in the histograms. The walleye pollock distribution is truncated to show reasonable detail. Not shown are the two most extreme values, 1,118.5 kg/ha and 2,906.8 kg/ha.

Goddard and Zimmermann[1]). If the rare, large observations typical of survey CPUEs are chance occurrences rather than the consequence of a fishing power difference, then a preferred estimator would be insensitive to them. The nonparametric Kappenman estimator has this property. Wilderbuer (1988) compared five FPC estimators (the ratio of means, the simple multiplicative model [Robson, 1966], the additive nested ANOVA, the multiplicative nested ANOVA, and the beta distributed index [Fanning, 1984]) and found all to have wide variability about the estimate of fishing power, indicating a sensitivity to rare large CPUEs. Wilderbuer et al. (1998) have extended this work to include the Kappenman estimator and have found it to have an estimation error equal to or lower than the others. For the Δ-distribution, $s$ determines heaviness of the right tail of the distribution. When the Δ-distribution is more symmetric in appearance and less heavy-tailed, all of the estimators reviewed by Wilderbuer (1988) may be reasonably well-behaved. When the Δ-distribution becomes skewed to the right and the magnitude of the rare, large observations becomes quite high, the insensitivity of the Kappenman estimator results in lower estimation error.

The arithmetic mean was used as the estimator for mean CPUE because it is unbiased. Any biases observed in the means estimated in the simulations would then be due to systematic error in the data caused by fishing power differences. Also, the arithmetic mean has been argued to be the best estimator of mean CPUE (Myers and Pepin, 1990; Smith, 1990) and is commonly used (e.g., Harrison, 1992; Weinberg, et al. 1994; Goddard and Zimmermann[1]).

The issue of design-based versus model-based estimation (Smith, 1990) is raised in the choosing of the arithmetic mean to estimate mean CPUE even though the data are simulated with a probability model that has known optimal estimators. Design-based estimation is followed here because that is the strategy employed in the analysis of the Bering Sea trawl surveys. A probability model is assumed in these examples solely to provide a parameter value for estimating the MSE. In a similar vein, it would seem that the question of relative efficiency could be

answered analytically rather than through a simulation, given a known probability model. Such a solution would be difficult or impossible because of the complicating factor of the estimated FPC. Even if a model-based estimation strategy were acceptable for estimating mean CPUE from uncorrected data, the appropriate probability model for the corrected data is not clear, especially if, as in these examples, the FPC estimator has an unknown distribution.

In this example, the two sets of simulated CPUE (standard and nonstandard prior to imposing the assumed fishing power difference) are independent and identically distributed random variables. This simulation ignored the possibility for spatial correlation among observations in a real survey. Because each station in the standard Bering Sea survey is 20 n mi from its nearest neighbor, I assumed that spatial correlation was negligible and did not attempt to build it into the simulations. This is consistent with current treatment of data collected on these surveys. A more complex procedure would be needed to simulate surveys with spatial correlation among observations.

## Results

For flathead sole, with a sample size of 144 per vessel, a clear region of increased error, the noncorrection region, appeared between approximately 0.77 and 1.14 in plots of MSE against the fishing power difference (Fig. 3A). The lowest MSE occurred with uncorrected data when there was identical fishing power (the value 1.0 on the x-axis). The FPC estimated for the original data, 0.76 (Table 1), fell just outside this region.

With a sample size of 50 per vessel, a clear noncorrection region appeared between approximately 0.56 and 1.19 for flathead sole (Fig. 3B). The FPC for the original data fell within this region. The minimum MSE occurred with uncorrected data. This minimum occurred, however, when the nonstandard vessel had a CPUE of about 23% less than that of the standard vessel rather than when the vessels had identical efficiencies (fishing power difference ratios of 0.87 and 1.0, respectively). The noncorrection region was also clearly asymmetric to the left with respect to a fishing power difference ratio of 1.0.

For walleye pollock, with a sample size of 149 per vessel, the noncorrection region was not as clearly defined because the lower bound occurred at some value less than 0.50; the upper bound was approximately 1.05 (Fig. 3C). The FPC estimated for the original data, 1.32 (Table 1), fell outside this region. The minimum MSE occurred with uncorrected data at a fishing power difference ratio near 0.67, where the nonstandard vessel caught 33% less than the standard. The noncorrection region was extremely

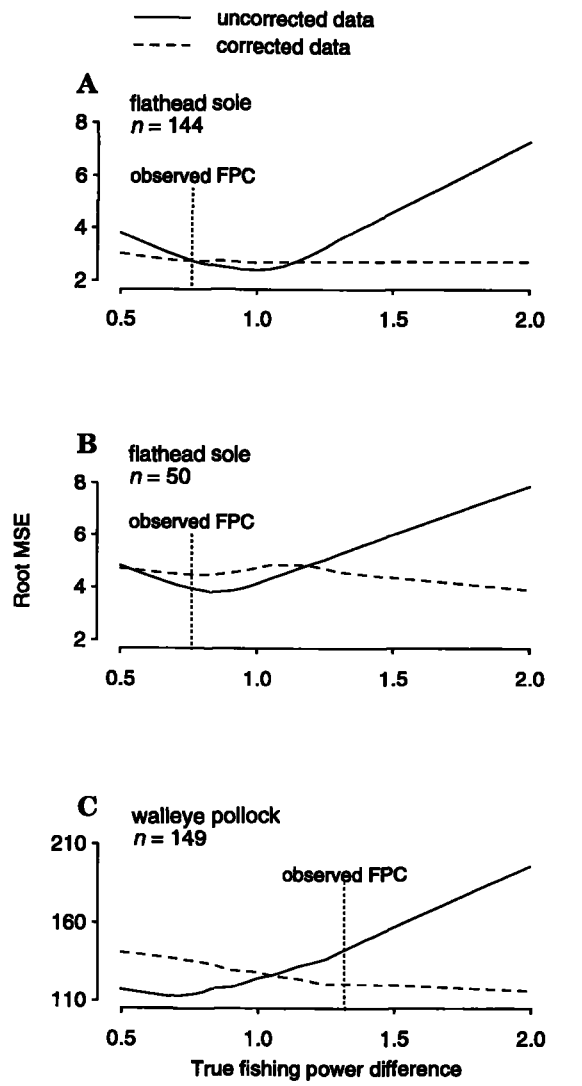


**Figure 3**

Simulation results: square root of the mean square error (MSE) of mean catch per unit of effort (CPUE) plotted against the true fishing power difference. The fishing power difference is expressed as the ratio of the true CPUE for the standard vessel over the true CPUE of the nonstandard vessel. "Corrected data" refers to MSEs computed from data in which the fishing power difference had been corrected. "Uncorrected data" refers to MSEs computed from data in which the fishing power difference had not been corrected. Sample size, $n$, refers to the number of stations realized for each vessel in each simulation. To illustrate general trends these results were smoothed with a scatterplot smoother called "lowess" in the statistical software package S-Plus (Becker et al., 1988).

asymmetric to the left with respect to a fishing power difference ratio of 1.0.

## Discussion

It is a well-established ideal to choose among estimators on the basis of their relative errors. These examples demonstrate that the approach can be functional in practice as well as in the abstract when deciding whether or not to apply an FPC. It is important to distinguish between the broader notion of a decision rule based on the MSE and the specifics given here as illustrations. These examples show that regions of increased and reduced MSE can be estimated. They demonstrate common features of the regions as well as ways the regions can vary. They show that the MSE strategy is functional but also underscore problems that can arise from inappropriate choices of estimators or simulation mechanisms. In all three cases a region of increased estimation error was successfully identified and each included the value 1.0, which represents identical fishing power. However, the breadth of the noncorrection region differed depending on sample and population variance. The three noncorrection regions also differed in their symmetry about the value 1.0, which was due to an interaction between the mechanism for imposing the fishing power difference on the simulated data and the sensitivity of the arithmetic mean to rare extreme observations.

CPUE variance broadened the noncorrection region. The flathead sole simulations demonstrated the effect of the sample variance, with the smaller sample size producing the broader region (Fig. 3, plots A and B). The pollock example produced a very broad region of increased error because the population variance was quite high (Table 1; Fig. 3C). These examples confirm the truism of the MSE: the greater the variance, the less important the systematic error due to a fishing power difference. The role of variance was clearly shown in the two flathead sole simulations where the FPC observed in the original survey fell within the noncorrection region for the higher variance case, and outside the noncorrection region for the lower variance case (Fig. 3, plots A and B).

Asymmetry in the noncorrection regions was a function of the simulation mechanism. However, the problem serves to reinforce the idea that high variance tends to reduce the relative importance of bias or systematic error and reduces the benefit of correcting it. Fishing power was assumed to be a simple multiplicative effect in these simulations. The variance was altered, as well as the bias, when the fishing power difference was multiplied against Δ-distributed data, an undesirable consequence. Because the arithmetic mean is sensitive, the rare, inordinately large CPUEs exert high leverage on it. This leverage itself was altered with a multiplicative fishing power difference. For the highly skewed pollock data, the change in variance was much greater than the change in bias (Fig. 4). When the standard vessel was less efficient, the uncorrected data produced a lower MSE because the fishing power difference reduced the leverage of the rare large tows, reduc-

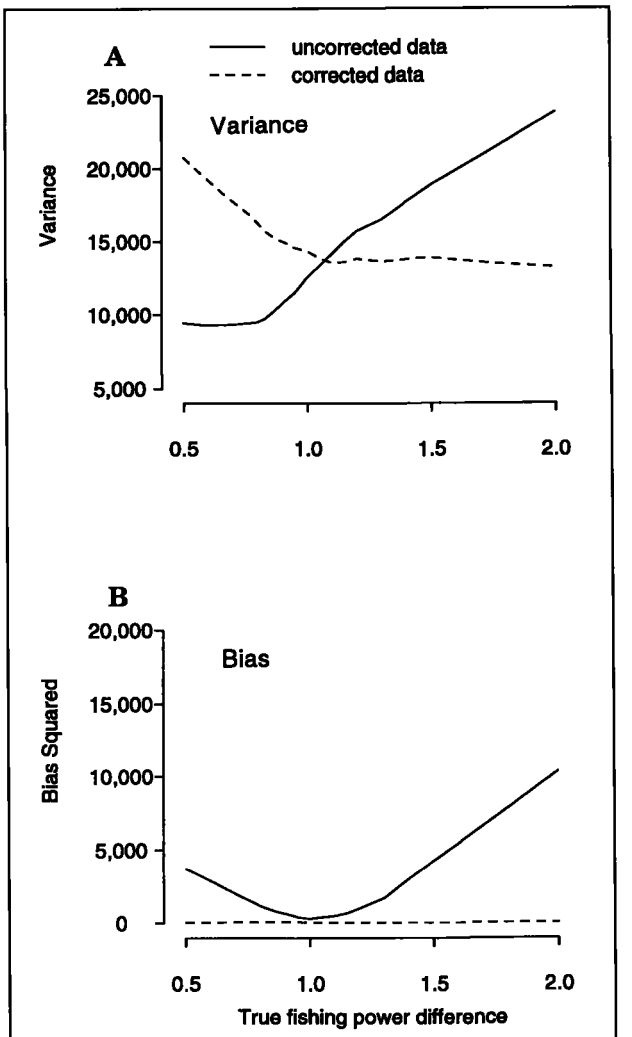


**Figure 4**

Components of the mean square error of the estimated mean catch per unit of effort (CPUE) of walleye pollock. "Corrected data" refers to variances and biases computed from data in which the fishing power difference had been corrected. "Uncorrected data" refers to variances and biases computed from data in which the fishing power difference had not been corrected. To illustrate general trends these results were smoothed with a scatterplot smoother called "lowess" in the statistical software package S-Plus (Becker et al., 1988).

ing the variance of the mean CPUE (Fig. 4A). The noncorrection region of data thus extended far to the left (Fig. 3C). When the nonstandard vessel was more efficient, the imposed fishing power difference had the opposite effect, increasing the variance of the mean calculated from uncorrected data (Fig. 4A). Correcting even moderate fishing power differences reduced the MSE (Fig 3C), but by reducing variance, not by correcting systematic error. This problem is purely a consequence of the fishing power mechanism in the simulations. An improved mechanism is needed to render the MSE-based decision rule a clearer tool. In this case, with highly skewed CPUE distributions, there may be a cut-off point beyond which a fishing power difference would not be imposed, because the rare, large tows are more likely to be chance occurrences than indicators of fishing power. Note that the bias did behave as expected: the uncorrected data produced a minimum when the fishing powers were identical, and corrected data produced a constant bias that was always lower than that of the uncorrected data (Fig. 4B). The pollock example illustrates how an MSE-based decision rule can be deceiving under an improperly specified model.

The noncorrection region itself is an estimate, with error around the upper and lower bounds of the range. The observed fishing power difference or correction factor will also be an estimate with its own error. Between these two sources of uncertainty, the upper and lower bounds of the noncorrection region are not as clear as they might appear in an application. Thus, a conservative approach would be to decide against using an FPC even when the observed value falls a little outside the noncorrection region. For this reason, and because improved precision generally increases certainty, it would pay to narrow the noncorrection region as much as possible through estimators with less sensitivity to the rare, large observations that characterize much CPUE data and through careful modeling of the process leading to the fishing power difference.

This decision strategy can also be used to re-evaluate old or changing fishing power problems. The concept of minimizing the MSE can accommodate changes in state-of-the-art estimation and allow the consequence of change to be examined. The decision rule remains valid regardless of improvements in simulation strategies, estimators, or understanding of processes leading to fishing power differences. The strategy can also be used to decide if experiments are warranted to calibrate the fishing power of research vessels. Such experiments tend to be very expensive yet limited in scope. Will it be possible to attain a sample size great enough to produce meaningfully narrow noncorrection regions?

A decision not to apply an FPC by these methods does not in any way imply that the fishing power difference is trivial or unimportant. For instance, if one of two vessels in a survey had a catch rate 30% lower than the other, and both vessels had equal numbers of observations, then the estimated mean CPUE could be in error by as much as 15%. An error of this magnitude could have a profound influence on a heavily exploited, closely managed stock. Yet such a fishing power difference may go uncorrected because, to correct it, would involve a risk of error of even greater magnitude. A decision against correcting is only a conclusion about the feasibility of applying an FPC, not the cost of having the systematic error in the data. Once a fishing power difference occurs in survey data, an irrevocable mistake has been made. The final estimate will have increased error, whether it is due to bias added by systematic error or due to variance added by estimating and correcting for the bias. This example illustrates the importance of maintaining standard survey techniques by illustrating the cost, in terms of precision, of correcting fishing power differences.

The decision to apply an estimated FPC is difficult. Statistical significance of a fishing power difference does not necessarily permit inference regarding the consequence of applying a correction factor when estimating mean CPUE. These three examples demonstrate the usefulness of this decision procedure. Even under difficult circumstances, high variance and an estimator sensitive to rare, large observations, the noncorrection regions are easy to defend because they are based on a clear goal—that of minimizing the error of the estimate of mean CPUE.

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# Annual and between-sex variability of yellowfin sole, *Pleuronectes asper*, spring–summer distributions in the eastern Bering Sea

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**Abstract.**—Annual and between-sex variations in yellowfin sole, *Pleuronectes asper*, distributions in the eastern Bering Sea during spring and summer were examined by analyzing research survey data, including a standard 15-year time series from 1982 to 1996, as well as exploratory nearshore samples. Yellowfin sole were most concentrated nearshore; abundance gradually decreased with increasing bottom depth to trace numbers beyond 100 m. Male yellowfin sole were distributed nearer to shore than females in all years.. Proportions of males (no. males/no. both sexes), therefore, increased nearshore with decreasing bottom depth. Males outnumbered females by two to one in waters less than 30 m deep. Yellowfin sole during 1982–84 were distributed in deeper waters than during 1985–96. The shallower distributions after 1984 were attributed to greater percentages of mature fish that reside in nearshore spawning areas (< 30 m) during spring–summer. High biomass estimates (>3 million metric tons) during 1982–84 were attributed in part to increased availability of yellowfin sole within the standard survey area.

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Yellowfin sole, *Pleuronectes asper*, of North America has a Pacific coast distribution from British Columbia (49°N) north to the Chukchi Sea (70°N) and a distribution along the Asian coast that ranges from the Sea of Japan (35°N) north to the Gulf of Anadyr (Fadeev, 1970; Hart, 1973; Bakkala, 1981; Wilderbuer et al., 1992). The eastern Bering Sea shelf has supported the largest concentration of yellowfin sole (Bakkala, 1993), with survey biomass estimates exceeding 2 million metric tons (t) since the early 1980s (Wilderbuer et al., 1992).

Spring–summer (June–August) distributions of yellowfin sole in the eastern Bering Sea are dependent upon the timing of their annual cross-shelf migration from overwintering grounds near the shelf-slope break (about 200 m bottom depth) to nearshore waters (<50 m bottom depth) of Bristol Bay north to Nunivak Island (Bakkala, 1981; Wakabayashi, 1989). This migration is thought to follow the ice edge as it recedes during spring (Bakkala, 1981). Many juvenile yellowfin sole are likely nonmigratory and remain nearshore under ice-cover during winter (Fadeev, 1970). Juvenile and adult distributions, therefore, overlap during spring–summer when adults enter nearshore waters to spawn (Nichol, 1995, 1997).

Past yellowfin sole abundance in the eastern Bering Sea has varied with the magnitude of fishery exploitation. A predominantly foreign-led commercial trawl effort (Japan and U.S.S.R.) accounted for annual landings in excess of 400,000 t from 1959 to 1962. This trawl effort led to a decline of the stock and to significantly lower annual catches (<100,000 t) through the 1970s (Wilderbuer et al., 1992). Lower exploitation rates during the late 1970s coincided with a major increase in stock abundance that appeared to peak in the early 1980s. Considering the high abundance, annual yellowfin sole catches have been moderate since 1982, averaging 147,433 t (Table 1). Commercial trawl catches of yellowfin in recent years have been limited by fishery management time and area closures owing to bycatch of species such as Pacific halibut (*Hippoglossus stenolepis*), Pacific herring (*Clupea pallasi*), Tanner crab (*Chionoecetes bairdi*), and red king crab (*Paralithodes camtschaticus*) (Witherell, 1995). Despite moderate exploitation, annual survey biomass estimates have fluctuated widely since the early 1980s (Wilderbuer[1]). These fluctua-

[1] Wilderbuer, T. K. 1996. Yellowfin sole. Chapter 3 *in* Plan team for groundfish fisheries of the Bering Sea/Aleutian Islands (ed.), Stock assessment and fishery evaluation

*continued on next page*

**Table 1**

Standard AFSC survey yellowfin sole (*Pleuronectes asper*) biomass and population estimates, percentage of male and female CPUE (kg/hectare) in nearshore (<30 m bottom depth) waters, sex-proportions, and mean CPUE-weighted bottom depths by sex, for years 1982–96. Commercial catch estimates for yellowfin sole in the eastern Bering Sea are also included.

| Year | Survey biomass (metric tons) | % CPUE[1] < 30 m | | Population numbers (billions) | Proportion male (m/m+f)[2] | Mean depth (m)[3] | | Commercial catch (metric tons)[4] |
|---|---|---|---|---|---|---|---|---|
| | | Males | Females | | | Males | Females | |
| 1982 | 3,377,838 | 20.56 | 9.81 | 20.67 | 0.492 | 45.0 | 52.9 | 95,712 |
| 1983 | 3,535,269 | 22.04 | 5.41 | 16.94 | 0.486 | 46.3 | 58.5 | 108,385 |
| 1984 | 3,141,188 | 16.96 | 5.62 | 14.26 | 0.434 | 47.3 | 58.7 | 159,526 |
| 1985 | 2,443,666 | 29.63 | 11.39 | 10.60 | 0.437 | 43.3 | 55.2 | 227,107 |
| 1986 | 1,909,866 | 31.05 | 13.38 | 7.96 | 0.436 | 42.8 | 54.7 | 208,597 |
| 1987 | 2,613,067 | 27.47 | 13.18 | 10.35 | 0.438 | 44.6 | 53.6 | 181,428 |
| 1988 | 2,402,369 | 23.94 | 9.86 | 10.09 | 0.426 | 45.0 | 55.6 | 223,156 |
| 1989 | 2,316,249 | 28.83 | 20.05 | 9.66 | 0.454 | 42.3 | 48.3 | 153,165 |
| 1990 | 2,183,708 | 24.30 | 12.46 | 9.06 | 0.435 | 44.6 | 53.0 | 83,970 |
| 1991 | 2,393,268 | 19.22 | 5.94 | 9.54 | 0.453 | 44.5 | 53.8 | 115,842 |
| 1992 | 2,172,900 | 34.89 | 19.01 | 8.21 | 0.452 | 42.3 | 53.4 | 149,569 |
| 1993 | 2,465,443 | 31.64 | 11.59 | 10.03 | 0.442 | 43.8 | 54.2 | 106,101 |
| 1994 | 2,610,474 | 32.34 | 13.73 | 10.70 | 0.442 | 40.1 | 51.0 | 144,544 |
| 1995 | 2,009,671 | 33.02 | 13.66 | 8.24 | 0.445 | 40.2 | 51.3 | 124,740 |
| 1996 | 2,298,560 | 31.28 | 9.83 | 9.62 | 0.460 | 43.9 | 56.8 | 129,659 |

[1] $\%CPUE=(\sum CPUE_{i,d<30}/\sum CPUE_{i,d=all}) \times 100$ where $CPUE_{id}$ = station CPUE of the $i$th sex within the $d$th depth range. Note that this estimate is derived from the AFSC survey which did not cover the entire nearshore area.
[2] Proportion male = population number of males divided by population number of males and females.
[3] Mean depths are weighted by CPUE (kg/hectare) values at each tow location.
[4] Total retained and discarded catch estimates for yellowfin sole from foreign (1982–87), joint-venture (1982–90), and domestic (1987–present) fisheries in the eastern Bering Sea (Wilderbuer[1]).

tions are inconsistent with age-structured stock synthesis models (Methot, 1990) that predict relatively stable abundance levels after 1981 (Wilderbuer[1]).

Large scale spring–summer Alaska Fisheries Science Center (AFSC) resource assessment surveys of the eastern Bering Sea shelf began with a baseline survey in 1975 (Pereyra et al.[2]) and have continued annually since 1979 with the primary purpose of estimating the abundance of important groundfish and crab species, including yellowfin sole (Gunderson, 1993). In 1982, a change in the standard survey trawl from a 400-mesh "eastern" trawl to a larger 83–112 "eastern," increased the catch efficiency for most flatfish species including yellowfin sole (Bakkala, 1993). Survey gear has remained constant since 1982. Although these surveys cover most of the shelf area north of the Alaska Peninsula and south of latitude 60°N (Fig. 1), nearshore waters have been excluded owing to shallow bottom depths and variable bottom substrate. Areas such as Togiak Bay (Fig. 1), where commercial trawlers have successfully targeted yellowfin sole in waters as shallow as 5–6 m (Low and Narita, 1990), have been excluded from resource assessment. Recognition that yellowfin sole spawn during the survey period (June–August) and that nearshore spawning grounds extend into these nonsurveyed areas (Nichol, 1995) has prompted speculation as to whether fluctuations in survey biomass may be due to annual variation in yellowfin sole distributions that overlap surveyed and nonsurveyed areas.

This study investigates two potential sources of variation in yellowfin sole distribution during spring-summer, which may partially account for fluctuations in survey biomass estimates. In this paper, I describe variations in yellowfin sole distribution patterns between sexes and among years. Data from exploratory nearshore samples are included to demonstrate problems associated with the exclusion of nearshore areas from resource assessments.

[1] (*continued from previous page*) report for the groundfish resources of the Bering Sea/Aleutian Islands region as projected for 1997. North Pacific Fishery Management Council, 605 W. 4th Avenue Suite 306, Anchorage, AK 99501.

[2] Pereyra, W. T., J. E. Reeves, and R. G. Bakkala. 1976. Demersal fish and shellfish resources of the eastern Bering Sea in the baseline year 1975. Northwest and Alaska Fisheries Center Proc. Rep. NOAA-NMFS, 619 p. Alaska Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA 98115-0070.

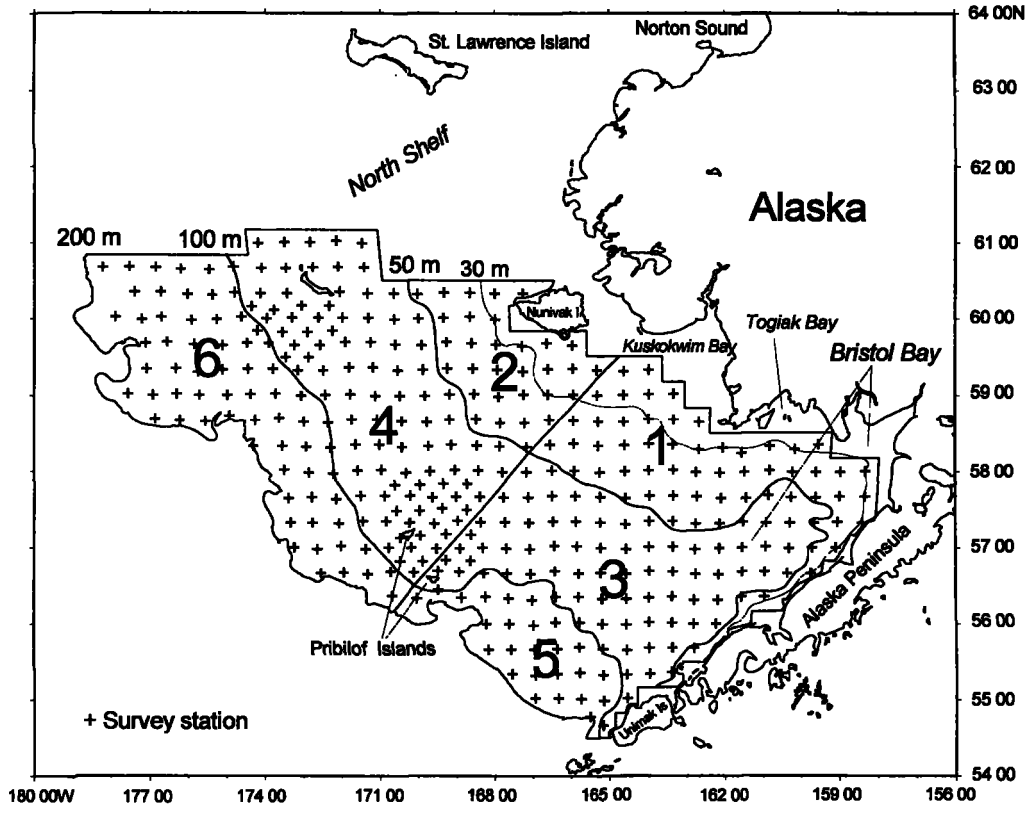



**Figure 1**

Standard Alaska Fisheries Science Center eastern Bering Sea survey stations. Large numerals (1–6) indicate strata areas: strata 1–2, <50 m; strata 3–4, 50–100 m; strata 5–6, 100–200 m.

## Materials and methods

### Surveys and gear

**Standard AFSC** Owing to differences in standard trawl gear used prior to 1982, only the 1982–96 standard surveys are considered here. About 350 standard stations, ranging in depth from 16 m to 230 m, were sampled annually for each of the 1982–96 AFSC surveys (Fig. 1; Table 2). Survey stations were spaced 37 km (20 nautical miles) apart, following a 37 × 37 km grid pattern. Surveys generally began in inner Bristol Bay, followed transects directed north and south, and progressed east to west with each finished transect. Trawls were towed for about 30 min at a speed of 5.6 km/h (3 knots) at each station during daylight hours. The standard AFSC sampling gear, an 83–112 "eastern" trawl, was characterized by average vertical and horizontal wing openings of 2.6 m and 16.5 m, respectively. Effective net spread and height measurements were obtained by means of a commercial trawl net-mensuration system (Scanmar) that was used during most tows. Footrope and headrope lengths were 25.3 m and 34.1 m, respectively. Paired 55-m dandylines (bridles) were attached to each wing and to 1.8 m × 2.7 m steel V-doors. Chain extensions measuring 61 cm in length were attached from each end of the footrope to the lower dandyline to improve bottom contact of the footrope. Two chartered commercial trawl vessels were employed each year to complete the standard survey. A total of 9 vessels ranging from 30.0 to 39.6 m in length have been used since 1982.

Total yellowfin sole catch weights (kg) as well as random sex-specific length-frequency samples (total length in cm) were collected at each station (haul) where the species was captured. Haul positions, bottom depths, and surface and bottom temperatures were also recorded at each station.

**AFSC exploratory tows** Additional 30-minute tows in waters nearer shore than the standard survey area were made during the course of the AFSC surveys with the same trawl gear and sampling procedures. Sampling depths ranged from 9.0 m nearshore to 29.3 m offshore. A total of twenty-five nearshore tows, 13 in the Togiak Bay area and 12 in the Kuskokwim Bay area, were made during the 1988–91 standard

**Table 2**

Summary of AFSC groundfish surveys on the eastern Bering Sea shelf. Tows in which yellowfin sole (YFS, *Pleuronectes asper*) were captured are noted parenthetically.

| Survey | Area[1] | Gear[2] | Date | Bottom depth (m) | Number of tows[3] | Number of YFS measured |
|---|---|---|---|---|---|---|
| Standard | EBS | 83-112 | June–Aug 1982 | 18–137 | 329 (251) | 37,023 |
| | | | June–Aug 1983 | 20–134 | 354 (270) | 33,924 |
| | | | June–Aug 1984 | 18–134 | 355 (279) | 33,894 |
| | | | June–Aug 1985 | 18–154 | 353 (270) | 33,824 |
| | | | June–Aug 1986 | 18–148 | 354 (251) | 30,470 |
| | | | June–Aug 1987 | 18–112 | 342 (235) | 31,241 |
| | | | June–Aug 1988 | 18–130 | 353 (249) | 27,121 |
| | | | June–Aug 1989 | 18–110 | 354 (236) | 29,510 |
| | | | June–Aug 1990 | 16–126 | 352 (247) | 30,491 |
| | | | June–Aug 1991 | 18–119 | 351 (248) | 27,985 |
| | | | June–Aug 1992 | 16–152 | 336 (231) | 23,626 |
| | | | June–Aug 1993 | 18–163 | 355 (243) | 26,647 |
| | | | June–Aug 1994 | 16–113 | 355 (257) | 24,420 |
| | | | June–Aug 1995 | 16–154 | 356 (249) | 22,111 |
| | | | June–Aug 1996 | 20–114 | 355 (247) | 27,190 |
| Exploratory | Kuskokwim Bay area | 83–112 | June 1988 | 13–27 | 4 (4) | 786 |
| | | | June 1989 | 9–20 | 4 (4) | 734 |
| | | | June 1990 | 13–29 | 2 (2) | 408 |
| | | | June 1991 | 13–29 | 2 (2) | 293 |
| | Togiak Bay area | 83-112 | June 1988 | 13–29 | 5 (5) | 1264 |
| | | | June 1989 | 16–27 | 5 (5) | 1438 |
| | | | June 1990 | 11–26 | 2 (2) | 515 |
| | | | June 1991 | 15 | 1 (1) | 107 |
| Nearshore beam trawl | Togiak Bay area | PSB | May, 1995 | 2–30 | 28 (28) | 4134 |

[1] EBS = eastern Bering Sea shelf area from the Alaska Peninsula north to latitude 62° N.
[2] 83-112 = Eastern otter trawl with 25.3 m (83 ft) headrope and 34.2 m (112 ft) footrope. PSB = plumb-staff beam trawl with a 3.1 m (10 ft) aluminum beam.
[3] Number in parentheses indicates number of tows in which yellowfin sole were captured.

surveys (Fig. 2; Table 2). These tows were conducted to collect preliminary data on spawning yellowfin sole, which were known from commercial trawl reports to occur in these nearshore areas. Extensive survey coverage of this area has been limited owing to the shallow bottom depths.

**Nearshore beam-trawl survey** A 3.1-m plumb staff beam trawl with specifications detailed in Gunderson and Ellis (1986) was used aboard a chartered 9.7-m (32-ft) purse-seine or gillnet vessel. This survey successfully sampled a total of 28 stations in the shallow waters of the Togiak Bay area, from 18 May to 28 May 1995 (Fig. 2; Table 2). Sampling depths ranged from 1.8 m nearshore to 30.2 m offshore. Tows were made during daylight hours and were less than 10 min in duration. All yellowfin sole were sexed, measured, and assigned a maturity code. For the purpose of this examination, maturity was classified as either mature or immature. Females were considered mature if ovaries were yolked or recently spent. Males were considered mature if testes were swollen, opaque colored, running with sperm, or recently spent.

## Analysis

Yellowfin sole distributions were described in terms of catch per unit of effort (CPUE; kg/hectare) for each of the 1982–96 AFSC standard surveys. Calculation of CPUE followed area-swept methods described by Alverson and Pereyra (1969), whereby catch is the total weight (kg) of yellowfin sole within a station tow and effort is the area (hectare) swept by the path of the trawl. Area swept was computed as the product of the distance fished and the effective net-spread

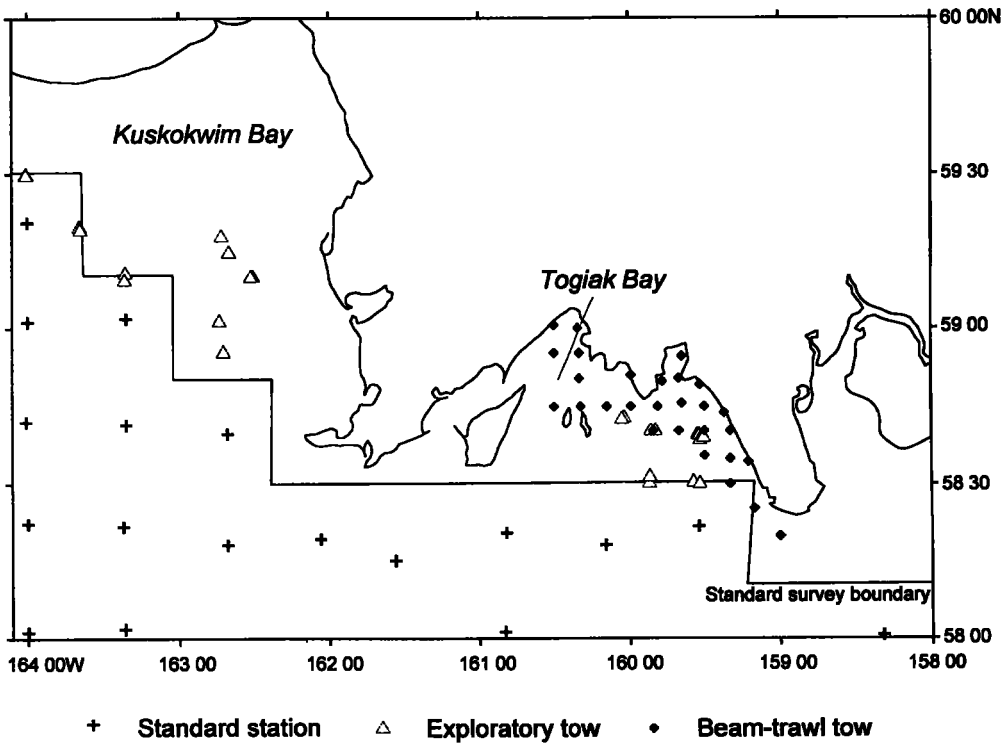



**Figure 2**

Geographic location of exploratory (1988–91) and beam-trawl tows (1995) made inshore of the standard AFSC survey stations.

for each tow. All fish within the path of the trawl were assumed captured. Male and female catch rates at each station were calculated as follows:

$$CPUE_i = CPUE \cdot (Weight\ Proportion\ of\ ith\ sex) = CPUE \cdot \left( \frac{\sum_{j=1}^{n_i} aL_{ij}^b}{\sum_{j=1}^{n} aL_j^b} \right), \quad (1)$$

where $CPUE$ = catch per unit of effort (kg/hectare) of all yellowfin sole at a station;
$CPUE_i$ = catch per unit of effort (kg/hectare) of the $i$th sex;
$n$ = total number of fish;
$n_i$ = number of fish of the $i$th sex;
$L$ = total length (cm) of the $j$th fish, males and females included;
$L_i$ = total length (cm) of the $j$th fish and $i$th sex;
$a$ = 0.007441; and
$b$ = 3.130.

Constants $a$ and $b$ were calculated with nonlinear regression (nlin procedure; SAS Institute, 1989) with the equation: $W = aL^b$ ($n$=796, $r^2$=0.99), where $W$=individual yellowfin sole weights (g) measured during the 1987 standard AFSC survey. Prior to estimating $a$ and $b$, a test comparing the length-weight relations between males and females was performed. A test of the null hypothesis of no difference between male and female linear log(length)-log(weight) revealed no significant difference in either slopes (analysis of covariance; $F$=2.46; df=1,792; $P$=0.12) or intercepts ($F$=2.05; df=1,793; $P$=0.15). Sexes were therefore combined to estimate constants $a$ and $b$ above.

Annual yellowfin sole "survey biomass" was estimated as:

$$Biomass = \sum_{k=1}^{n} \left( \overline{CPUE}_k \cdot A_k \right), \quad (2)$$

where $\overline{CPUE}_k$ = the mean of station CPUE values (Eq. 1) within the $k$th stratum (Fig. 1); and
$A_k$ = the area (hectares) of the $k$th stratum.

Proportions of males (no. males/no. both sexes) at each station were averaged across stations by depth

group (10–19 m, 20–29 m, etc.), weighted by the station CPUE (no. fish/hectare). For nearshore beam-trawl samples, variance surrounding mean male-proportions was estimated following Cochran (1977) for estimation of proportions in cluster sampling. For standard and exploratory surveys, the error structure of proportion means was approximated by the boot-strap method (Efron and Tibshirani, 1993). The station-specific data were randomly resampled and the mean estimated 1000 times. Twenty-fifth and 975th quantiles were chosen for the 95% confidence bounds.

## Results

### Between-sex variation

Male yellowfin sole within the standard survey area were distributed closer to shore than were females in all years, 1982–96 (Fig. 3; Table 1). In addition to having an overall distribution in deeper water, females also appeared to have a more extended northwesterly distribution than males (Fig. 3). Males outnumbered females near shore, whereas farther off shore (>60 m bottom depth), females outnumbered males (Fig. 4). The proportion of males (no. males/no. both sexes) and CPUE increased with decreasing depth (Fig. 4). Togiak and Kuskokwim Bay area samples from exploratory trawls were also characterized by a higher proportion of males as well as greater overall yellowfin sole concentrations. The proportion of males from Togiak and Kuskowim Bay areas averaged 0.60 and 0.67, respectively (Fig. 4).

Sex proportions also varied between mature and immature yellowfin sole. Among beam-trawl samples from the Togiak Bay area (Fig. 2), the overall mean proportion of males was 0.54 (SE=0.0033). Among mature fish, however, the proportion of males averaged 0.65 (SE=0.0067) and among immature fish, mostly small <20 cm fish, the proportion of males averaged 0.50 (SE=0.0024). Within the spawning area (<30 m), the proportion of males among mature fish averaged 0.68 (SE=0.0056) (Fig. 5).

### Among-year variation

Yellowfin sole spring–summer distributions varied from year to year, although the most notable difference was for years 1982–84 when distributions of males in particular within the standard AFSC survey area were shifted off shore (deeper waters) relative to subsequent years (1985–96) (Fig. 3). A greater mean CPUE-weighted bottom depth in conjunction with a decreased percentage of nearshore (<30 m) CPUE (kg/hectare) during 1982–84 confirmed a bathymetric shift to deeper waters for both male and female distributions in relation to subsequent years (Table 1). Interestingly, yellowfin sole biomass levels, as well as the overall proportion of males within the standard AFSC survey, were considerably higher during 1982–83 than in subsequent years (Table 1).

## Discussion

### Between-sex variation

Distributional differences between male and female yellowfin sole exist primarily because males mature earlier than females. Standard AFSC surveys, exploratory nearshore samples, and Togiak area beam-trawl samples have shown conclusively that male yellowfin sole outnumber females in the nearshore areas (<30 m bottom depth) of the eastern Bering Sea during spring–summer. Given that males mature approximately 4 years earlier than females (Wilderbuer et al., 1992), spawning males should considerably outnumber spawning females. Because yellowfin sole spawn primarily in nearshore areas (<30 m) during spring–summer (Nichol, 1995), mature males outnumber mature females by nearly 2:1 in this region. In deeper waters, females outnumber males because of the abundance of larger (25–32 cm TL) immature females that generally do not move into the spawning area (Nichol, 1997).

Factors such as differential life-spans and differential catchability between sexes have been shown to cause similar sex-ratio patterns in other species (Beverton, 1964). Such factors were assumed negligible in this case. Since 1982, maximum ages for yellowfin sole males and females averaged 25.7 and 26.1 years,[3] respectively, and have not differed significantly (paired $t$-test; $P$-value=0.7758, df=28), suggesting similar life-spans for males and females. Beverton (1964) discussed the potential effects of differential natural mortality, fishing mortality, and catchability on sex-ratios of plaice (*Pleuronectes platessa* L.) in the North Sea. The possibility that male yellowfin sole may be more readily captured by trawl gear, at least among immature fish, is unlikely given that the sex proportion among immature fish in the spawning area was near 0.5 (Fig. 5). The possibility that spawning males are more catchable than females owing to differential spawning behavior, as Beverton (1964) reported for plaice, is not known for

[3] Ages were determined by the Age and Growth Unit of the Alaska Fisheries Science Center (AFSC) from annual otolith collections made during the standard AFSC groundfish trawl surveys in the eastern Bering Sea.

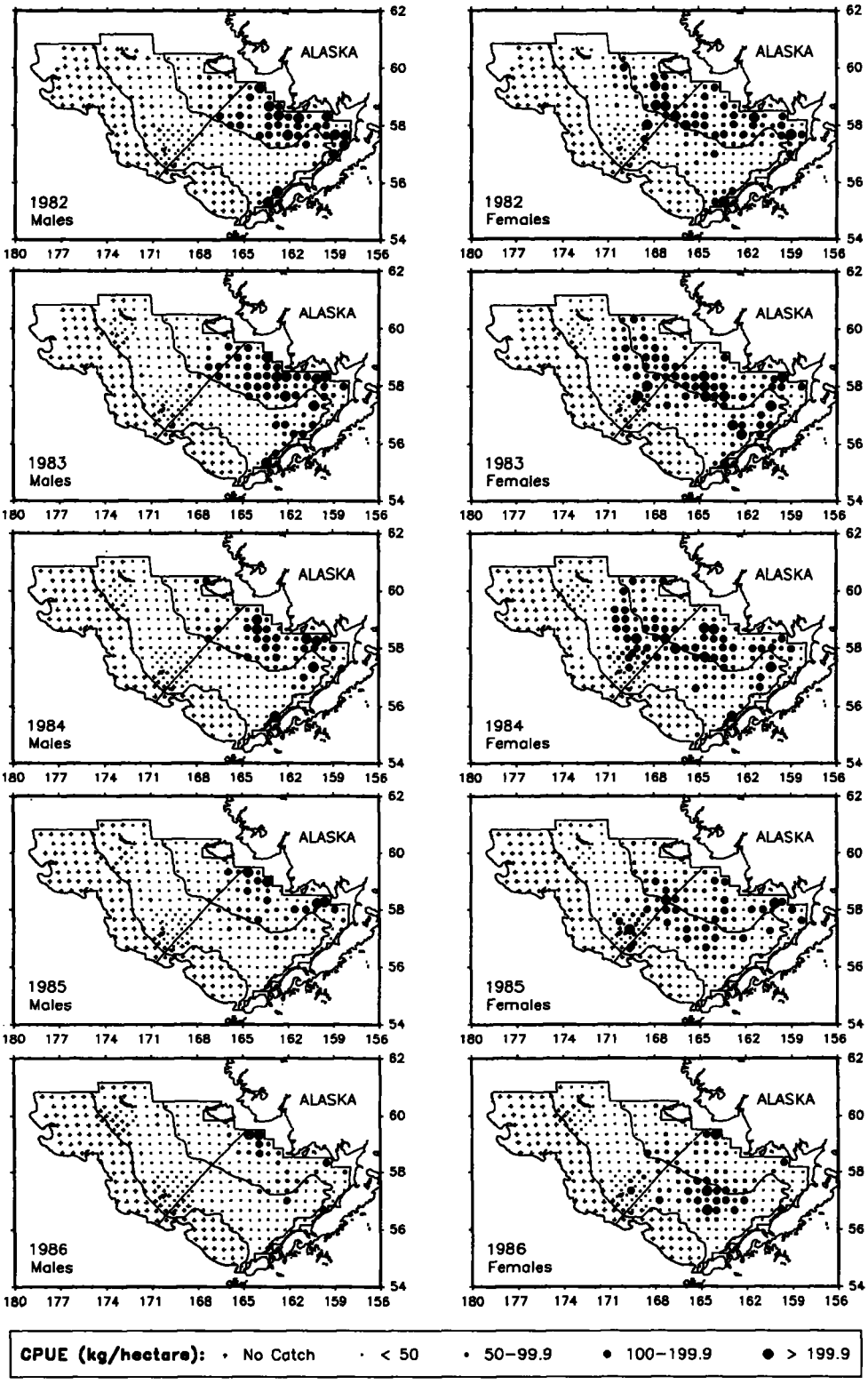
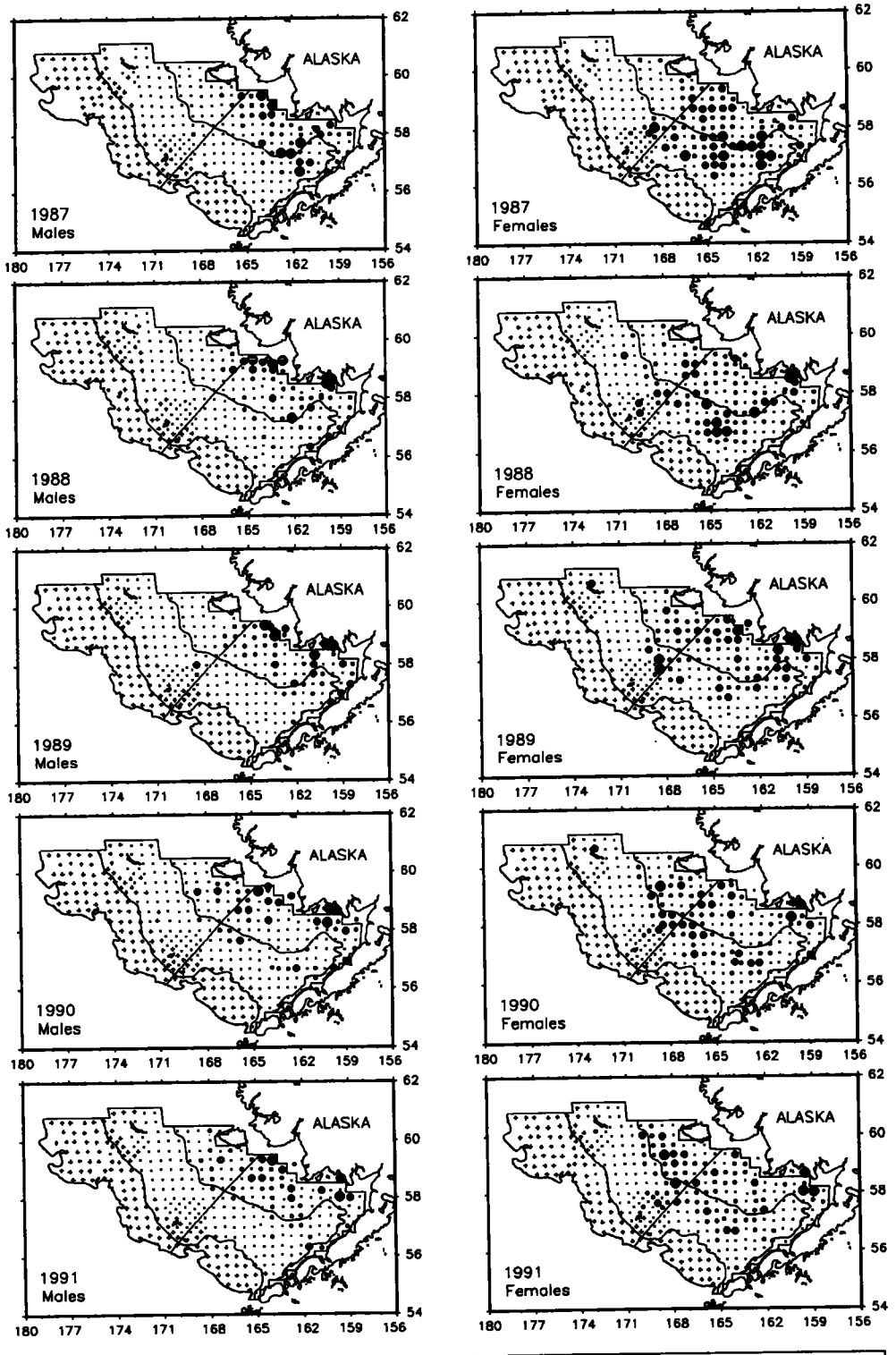



**Figure 3**

Geographical distribution of male and female yellowfin sole (*Pleuronectes asper*) in terms of catch per unit of effort (CPUE; kg/hectare) for each year, 1982–96.

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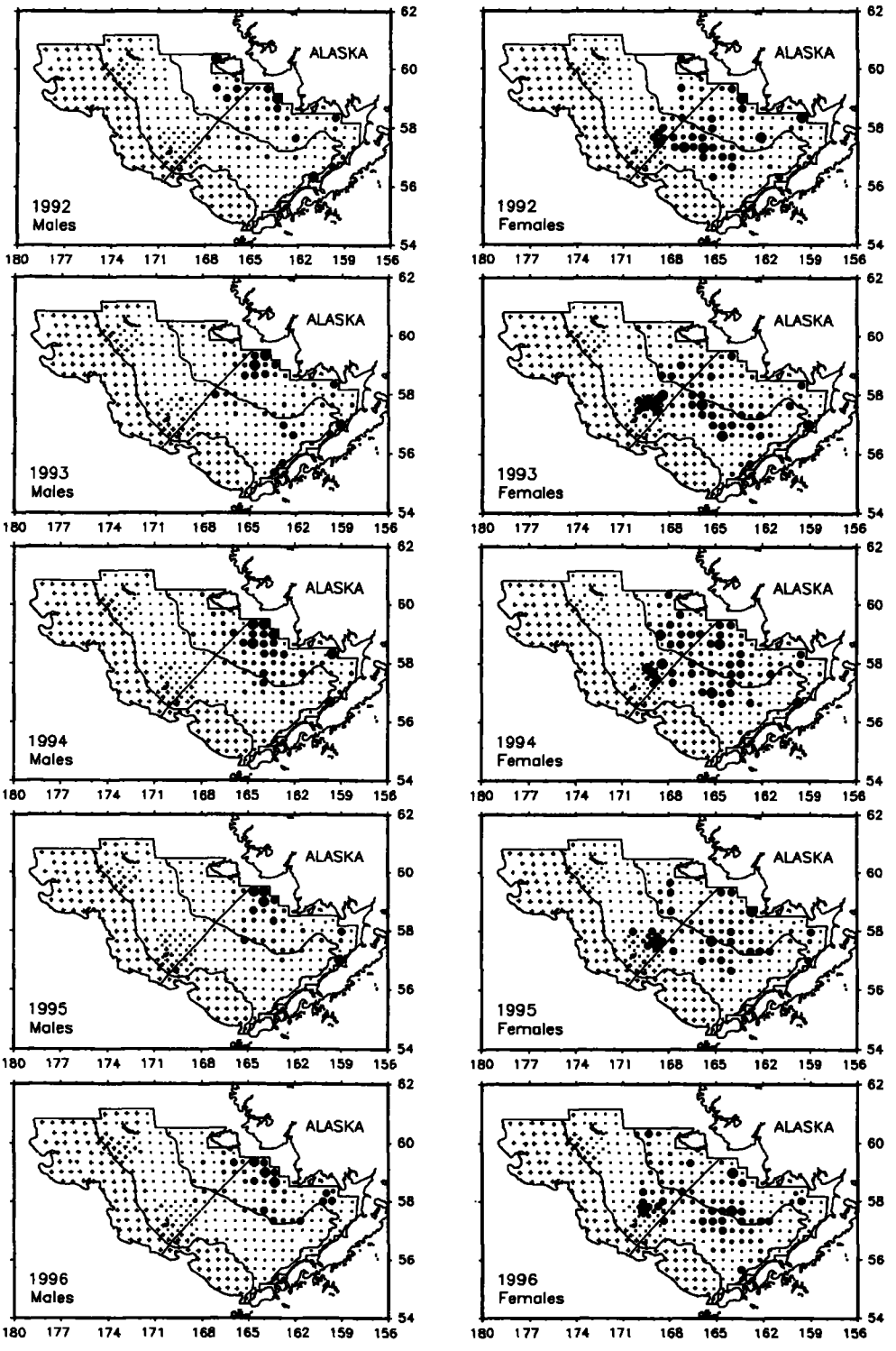


**Figure 3 (continued)**

yellowfin sole. However, because yellowfin sole males were dominant inshore and females were dominant offshore, the more likely cause for the sex-proportion patterns observed here was the differential distribution patterns between sexes.

## Among-year variation

Spring–summer distributions during 1982–84 may have been deeper than those in subsequent years, in part, because the population was younger and less mature. Wilderbuer et al. (1992) indicated that older (>17 years) yellowfin sole were an insignificant part of the population prior to the mid-1980s compared with later years and indeed, length distributions were skewed toward smaller length groups during the 1982–84 surveys compared with later years (Fig. 6). Given estimated lengths at 50% maturity of 20.3 and 28.8 cm TL for male and female yellowfin sole, respectively (Wilderbuer et al., 1992), many of the fish constituting the strong modes from 1982 to 1984 were sexually immature. Certainly there was a progression from immaturity to maturity for many of these fish. Nichol (1997) showed that larger (25–32 cm) immature females nearing maturity maintain a deeper bathymetric distribution than mature spawning fish during spring–summer. With increasing maturity of the population, therefore, we would expect to see a distribution shift to shallower spawning waters in years after 1984. Smaller males (22–27 cm TL) and females (25–32 cm TL) constituted a large proportion of the yellowfin sole biomass from 1982 to 1984 (Fig. 7). High concentrations of 22–27 cm males that resided at 40–49 m bottom depth during 1982–84 were not apparent from 1985 to 1996. Similarly, prominent modes of 25–32 cm females at 30–39 m and 70–79 m depths during 1982–84 were not nearly as apparent during 1985–96 (Fig. 7).

Why then was the proportion of males within the standard area higher during 1982–83 than other years? The most plausible explanation is that the deeper overall yellowfin sole distributions during these years rendered the population more available to the survey. Nearshore areas not

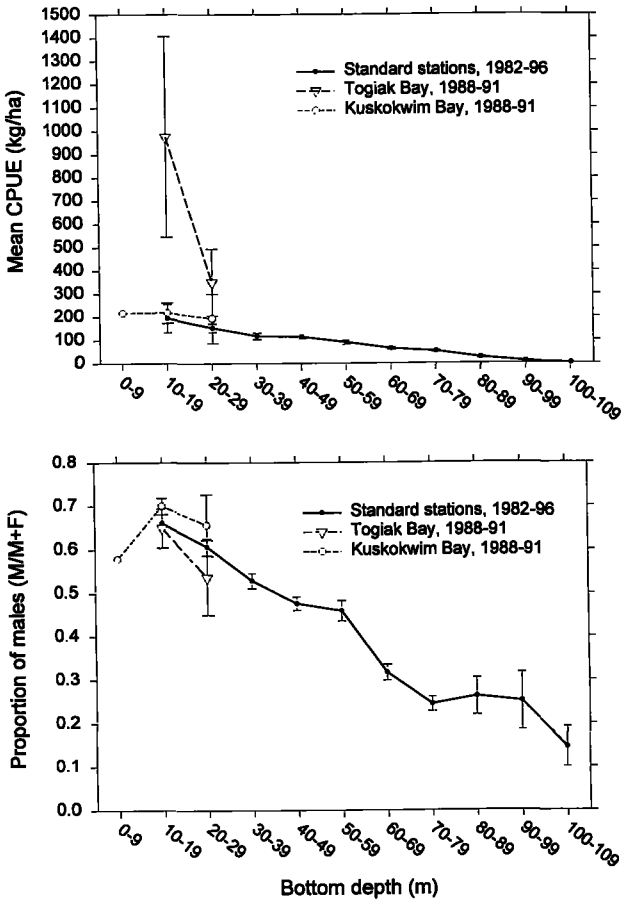


**Figure 4**

Mean catch per unit of effort (CPUE; kg/hectare) and mean proportion of males (no. males/no. both sexes) of yellowfin sole (*Pleuronectes asper*) at standard Alaska Fisheries Science Center trawl stations (1982–96) and at sites in nearshore Togiak Bay and Kuskokwim Bay areas (1988–91). Mean proportions are weighted by the CPUE (no. fish/hectare) at each station within each depth grouping. Bars are 95% confidence intervals.

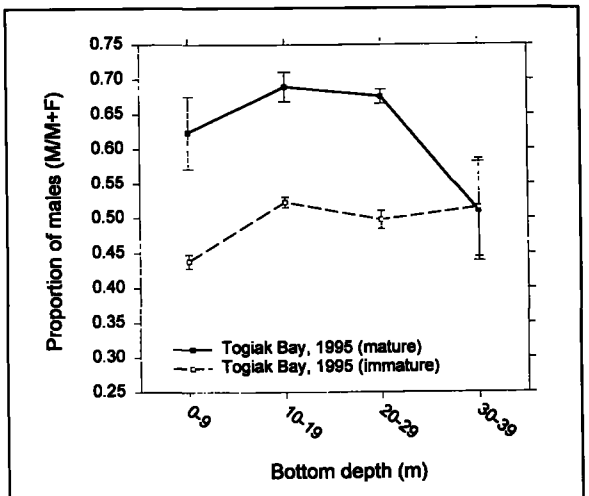


**Figure 5**

Mean male proportions (no. males/no. males and females) of mature and immature yellowfin sole (*Pleuronectes asper*) by bottom depth during the 1995 beam-trawl survey of Togiak Bay. Mean proportions are weighted by the CPUE (no. fish/hectare) at each station within each depth grouping. Bars are 95% confidence intervals.

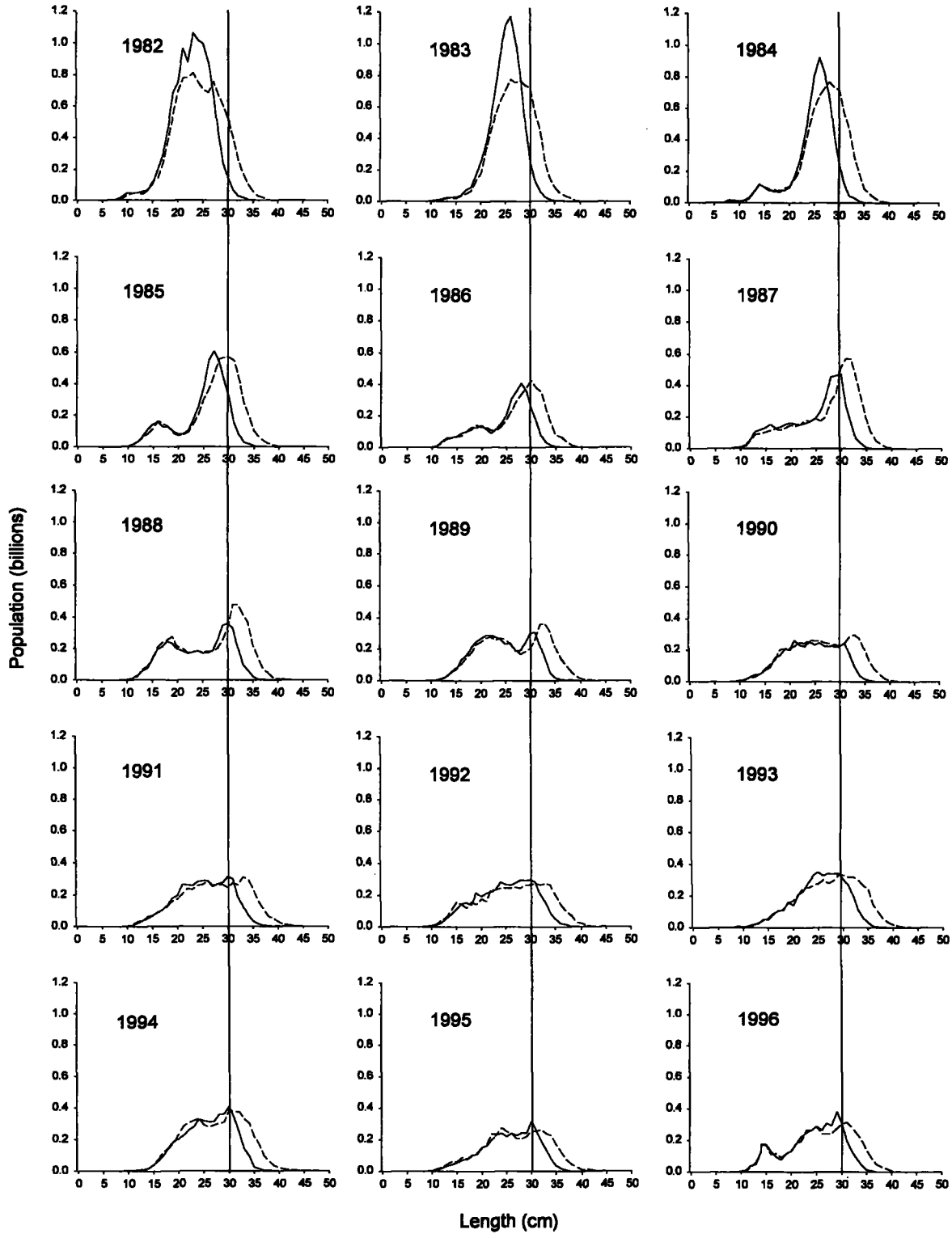


**Figure 6**

Length composition of male (solid line) and female (dashed line) yellowfin sole (*Pleuronectes asper*) in terms of population numbers for years 1982–96. The vertical lines provide a reference for fish length at 30 cm TL.

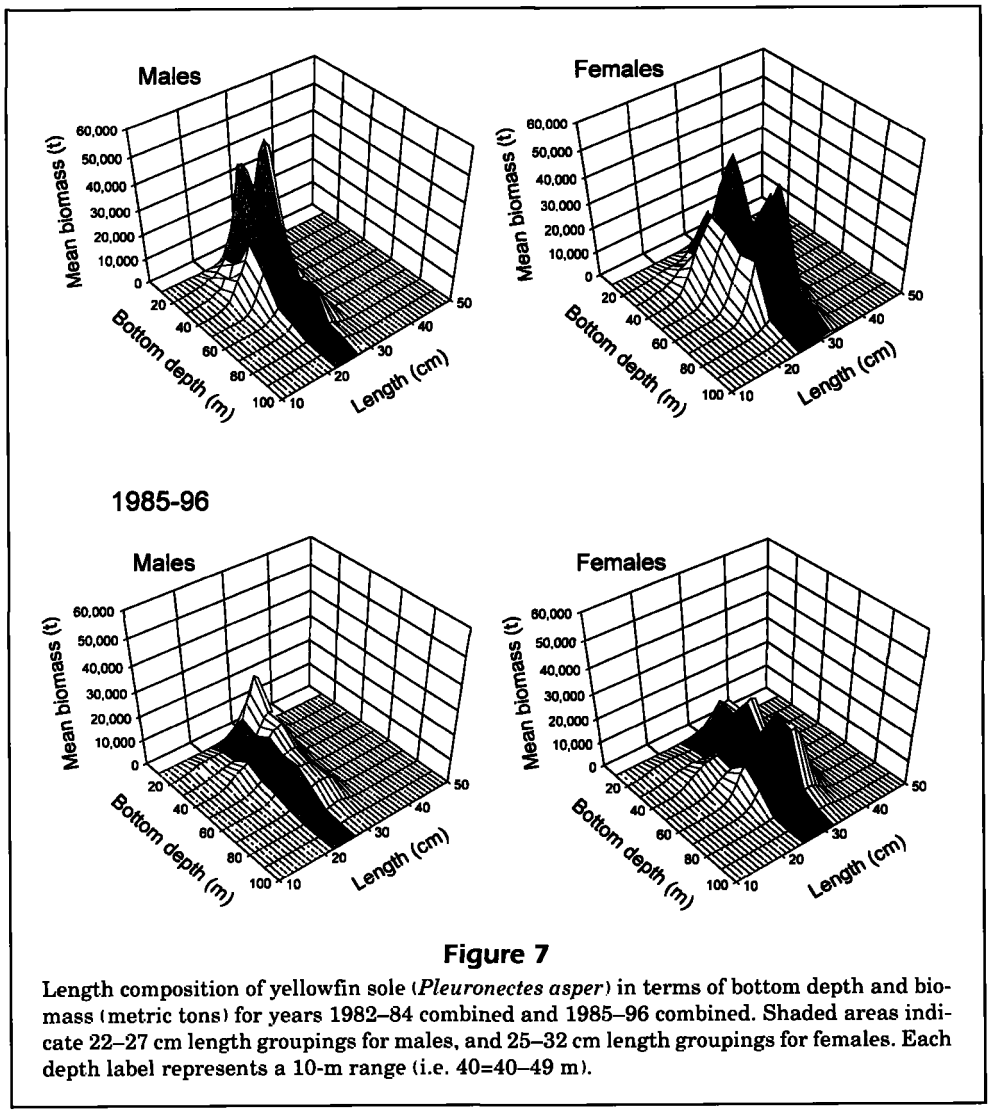


**Figure 7**

Length composition of yellowfin sole (*Pleuronectes asper*) in terms of bottom depth and biomass (metric tons) for years 1982–84 combined and 1985–96 combined. Shaded areas indicate 22–27 cm length groupings for males, and 25–32 cm length groupings for females. Each depth label represents a 10-m range (i.e. 40=40–49 m).

sampled during the standard AFSC surveys likely contained more males than females. Hence, a shift of the population to deeper waters possibly exposed a higher proportion of males to the survey gear than during subsequent years.

## Effects of distribution on survey biomass

Given that the standard AFSC survey area does not encompass the entire yellowfin sole distribution, annual distributional shifts between surveyed and nonsurveyed areas may explain the annual biomass fluctuations observed within the standard AFSC survey area. Yellowfin sole biomass estimates within the standard AFSC survey area have fluctuated from a high of 3.5 million t in 1983 down to 1.9 million t in 1986 (Table 1). These fluctuations are *not* possible according to yellowfin sole life history and the relatively light fishing exploitation of this species since the late 1970s (Wilderbuer et al., 1992). Stock synthesis models based on catch-at-age data (Methot, 1990) predict much more stable changes in yellowfin sole biomass (Fig. 8). Even though these models incorporate survey biomass estimates as auxiliary information (Wilderbuer[1]), predicted biomass estimates from 1982 to 1984 were much lower than what survey estimates indicated. I propose that the deeper overall spring–summer distributions from 1982 to 1984 contributed to an inflation of survey biomass estimates in contrast with subsequent years, owing to increased availability of yellowfin sole to the AFSC survey. Strong year classes that were present in the survey area during 1982–84 may have become less accessible to the survey gear during later years owing to their sexual maturation and subsequent migration into shallower nearshore spawning waters.

Nearshore areas from the standard survey boundary to the coastline (excluding river systems and in-

ner bays) totaled approximately 40,184 km$^2$ (Fig. 1). In contrast, the two nearest shore strata within the AFSC survey area total 77,871 km$^2$ (stratum 1) and 41,027 km$^2$ (stratum 2), respectively. The coastline areas, thus, offered yellowfin sole a considerable refuge from the AFSC bottom trawl survey. According to past samples from Togiak Bay and Kuskokwim Bay areas (Table 2), yellowfin sole are more concentrated in the coastline areas than within the standard AFSC survey area (Fig. 4). Considering the vast unsampled areas near shore, as well as the large yellowfin sole concentrations that inhabit these areas, annual fluctuations in biomass within the standard AFSC area should be expected.

Biomass estimates generated from standard AFSC eastern Bering Sea trawl surveys are considered a relative measure of population abundance. However, because nonsurveyed nearshore areas contain higher concentrations of yellowfin sole and because males outnumber females there, standard area biomass estimates underestimate male abundance. Distribution plots suggest a more extended northwesterly distribution of females compared with males. Within the northwest area (subareas 2, 4, and 6) the average proportion of males from 1982 to 1996 was 0.33 ± 0.016 (95% confidence) compared with 0.50 ± 0.010 in the southeast area (subareas 1, 3, and 5). The lack of males in the northwest area may be an indication that a large percentage of males missed by the survey inhabit nearshore waters of Kuskokwim Bay and waters east of Nunivak Island (Fig. 1).

Bottom temperature may be one factor that has influenced the availability of yellowfin sole to the standard AFSC survey. Except for the years 1982–84, when fish availability was affected more by population structure, biomass estimates were generally lower during colder years (Fig. 9). Midshelf bottom temperatures were chosen to represent annual temperature regimes because water exchange is minimal when compared with the inner shelf (< 50 m) and outer shelf (>100 m) waters (Coachman, 1986; Wilderbuer et al., 1992). Distribution patterns, as well as timing of the annual yellowfin sole cross-shelf migration, may in part be dependent upon the annual temperature regime. Fadeev (1965) indicated that spring yellowfin sole migrations occurred one month earlier than usual during years when warm water developed earlier on the eastern Bering Sea shelf. Pola et al. (1985) also demonstrated, using simulation models, that summer yellowfin and rock sole distributions could be established two months earlier in a warm year than in a cold year. If ice-edge

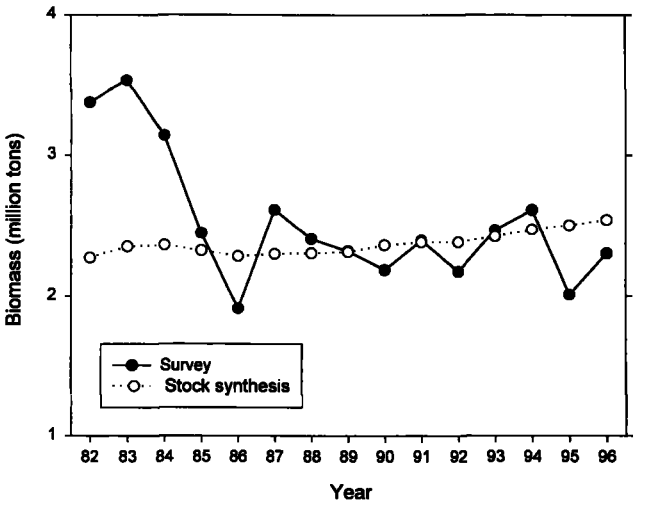


**Figure 8**

Comparison of yellowfin sole (*Pleuronectes asper*) biomass estimates from the AFSC survey and from stock synthesis analysis. Stock synthesis estimates incorporate the selectivity of the survey sampling gear and use survey biomass estimates as auxiliary data, but they are based on catch-at-age-data.

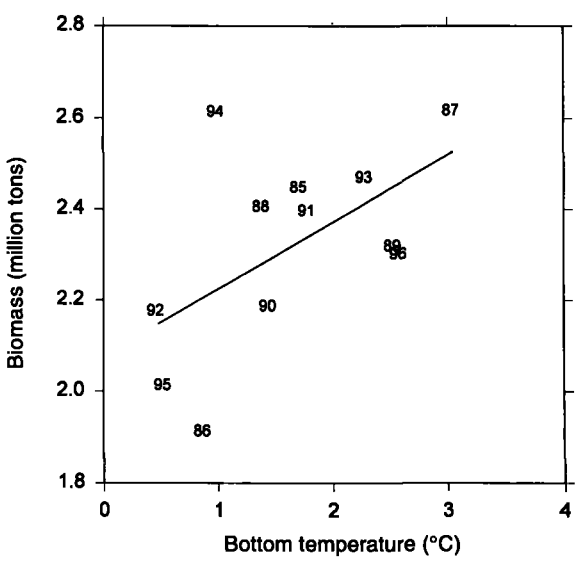


**Figure 9**

Increase in estimates of yellowfin sole (*Pleuronectes asper*) biomass as related to mean midshelf (50–100 m) bottom temperatures for years 1985–1995. Line represents the linear regression of biomass (dependent variable) against bottom temperature (independent variable); $r^2 = 0.32$, $n = 12$, slope = 0.15 (two-tailed $P$=0.054), intercept = 2.08. Note that 1982–84 data were excluded because the population structure was unique during those years.

retreat determines the timing of inshore yellowfin sole migration (Bakkala, 1981), and subsequently the timing of spawning, distribution patterns at the time of the survey could be affected. Increasing percentages of spent yellowfin sole during the June 1993 AFSC survey (Nichol, 1995) indicated that spawning activity progresses within the duration of the survey. Spring–summer surveys conducted in warmer years may intercept higher proportions of spent individuals that no longer inhabit the unavailable nearshore spawning areas.

Interannual variation of yellowfin sole biomass estimates within the eastern Bering Sea may be reduced under alternative survey designs (McAllister, 1995). I recommend the incorporation of additional standard stations in nearshore areas, such as the exploratory tows made in Togiak and Kuskokwim Bays (Fig. 2), and east of Nunivak Island. The addition of such stations would likely reduce interannual variation of survey biomass estimates as well as provide a more accurate representation of the population sex-composition.

## Acknowledgments

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**Abstract.**—Pacific red snapper, *Lutjanus peru*, collected from commercial hook-and-line gear and shrimp trawls off the southeast coast of Baja California Sur, Mexico, were aged by using scales and otoliths (whole-otolith and sectioned-otolith readings). Comparison of ages determined from these structures revealed that scales tend to underestimate ages beyond 5 years, often by more than 1 year, and that they are the least precise structures for ageing. Sectioned otoliths gave greater estimates of age than whole-otolith counts (mean differences <1 yr) and were the most precise structure. The von Bertalanffy growth function described *L. peru* growth satisfactorily with length-at-age determined from whole otoliths and sectioned otoliths. Parameters for the entire population were $L_\infty$ = 97.32 cm, $K$ = 0.1111/yr, $t_0$ = −0.316 yr ($n$=1180). No significant differences in length-at-age were found between sexes. The largest individual was a 31-year-old 99.2-cm-TL male, constituting a maximum age, and length record for this species. A multiple regression model of whole-otolith age as a function of otolith and fish measurements provided satisfactory results. Total mortality rates were significantly lower for females ($Z$=0.282/yr) than for males ($Z$=0.366/yr).

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# Age, growth, mortality, and population characteristics of the Pacific red snapper, *Lutjanus peru*, off the southeast coast of Baja California, Mexico

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The Pacific red snapper, *Lutjanus peru* (Nichols and Murphy), known as "huachinango" in Mexico, is distributed throughout the lower Gulf of California to Peru and found in offshore schools over rocky bottoms to depths exceeding 100 m. It is a commercially important species in Mexico as well as in Central and South America (Thomson et al., 1987; Gutiérrez Vargas, 1990; Ramírez Rodríguez and Rodríguez Medrano, 1990).

*Lutjanus peru* is fished in most Mexican states along the Pacific coast. The highly valued product is generally marketed whole and transported to inland cities, or occasionally exported. Nationwide, it shares a market with its congener, the Gulf of Mexico red snapper *Lutjanus campechanus* Poey. From 1980 to 1988, the reported catches of both species averaged 6556 metric tons (t) per year (SD 1290 t/yr), of which 56% originated in the Pacific.[1] In Baja California Sur, Pacific red snapper is fished on a small artisanal scale; near Cerralvo Island, *L. peru* ranks within the six most important exploited finfishes (Fig. 1) (Ramírez Rodríguez and Rodríguez Medrano, 1990). As is the case with other snappers, juveniles of this species aggregate over soft bottoms where they are caught as bycatch during shrimp trawling activities (Van Der Heiden, 1985; author's personal observations).

Information on the biology of *L. peru* is limited despite its ecological and commercial importance. Gorelova (1979) performed feeding experiments on juvenile *L. peru* caught off the coast of Peru, whereas Ruiz Santos (1983) studied the reproductive biology of the species off the southwest coast of Mexico and Ruiz and Madrid (1992) studied the biology of a parasitic isopod and its effects on *L. peru* hosts off Michoacán. With the exception of Rocha Olivares and Gómez Muñoz (1993), age and growth of the Pacific red snapper have been estimated either from scales in Mexico (Castro, 1981; Ruiz Luna et al., 1985; Aguilar Salazar, 1986) or from length-frequency distributions in Costa Rica (Gutiérrez Vargas, 1990). The use of scales, however, may result in less than accurate age estimates for some

[1] Anuarios Estadísticos de Pesca, Secretaría de Medio Ambiente Recursos Naturales y Pesca. Av. Progreso Núm. 5, Colonia Del Carmen, Coyoacan. Delegación Coyoacan 04110, México, D.F.

species, including systematic underestimations (e.g. Bilton, 1973; O'Gorman et al., 1987; see review by Beamish and McFarlane, 1987, and papers therein).

Because of the lack of reliable information on biological parameters for this commercially important tropical species, this work represents the first comprehensive study of growth and mortality of a *L. peru* population based on otolith age determinations. A comparison of age estimates from whole and sectioned otoliths and from scales is made to assess their relative usefulness. Growth and mortality rates are estimated, and other aspects of the biology are presented for an exploited population of the Pacific red snapper off the southeast coast of Baja California Sur.

## Materials and methods

### Study area and sampling scheme

This study took place in Bahía de La Paz, one of two major bays in the Gulf of California (Walker, 1960). The most important fishing grounds for *L. peru* lie within and southeast of the Bay, around Espíritu Santo-Partida and Cerralvo Islands (Fig. 1). Peak catches occur during the summer.

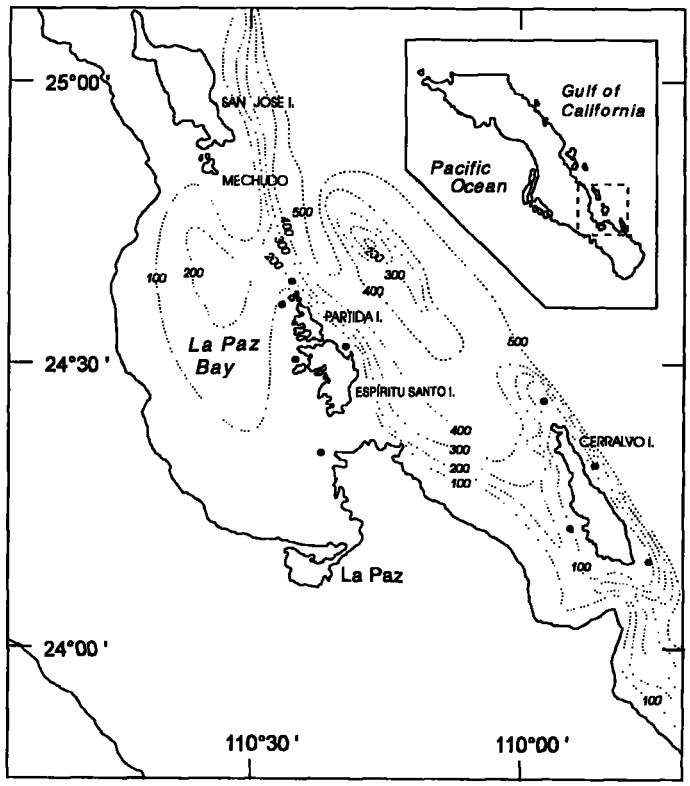


**Figure 1**

Map of study area showing approximate positions (•) of fishing grounds and sampling sites of Pacific red snapper *Lutjanus peru*. Depth contours are in fathoms.

Pacific red snapper were collected from March 1989 to March 1991. Most samples came from La Paz City fish market, which was sampled at least weekly, March 1989 to February 1991. Snappers were also collected monthly with baited hook and line, May 1989 to February 1991. Juvenile red snappers were collected as shrimp trawler bycatch during February and March 1991. Biological samples were taken from all fish collected ($n$=2605). In the market, sampling time was limited to the period before fish were stored, therefore biological sampling was restricted to the first 20 randomly selected individuals from each 4-cm length interval. Biological samples consisted of both sagittae, at least 10 scales from underneath the left pectoral fin, and testes and ovaries, which were fixed in 10% buffered formalin and used for sex determination and reproduction studies. Total and standard lengths (TL and SL, respectively) were measured to the nearest mm; total and gutted weights (TW and GW, respectively) were recorded to the nearest 2 or 5 g, depending on fish size. Since fish were gutted on landing, some data and samples could not be obtained from the market. However, many gutted fishes could be sexed from gonadal remains. In 1989, when samples were most abundant, 3085 additional fishes were measured to construct sex-specific length-frequency distributions.

### Sample processing and age determination

Because the left and right sagittae did not differ morphometrically[2] or in weight (paired $t$-tests, $P$>0.5) in a random subsample of 50 fishes representative of the length range available and since no differences were found in their marking pattern or number of rings, the right otolith was used for age determination when available. Otoliths were submerged in 90% glycerol for 24 hours before they were viewed under a dissecting scope with reflected light over a darkened background. Otoliths embedded in thermoplastic cement were sectioned with a low-speed saw. Three sections (0.3 mm thick), including the primordium and the flanking regions, were made orthogonal to the anteroposterior axis of the structure. Sections were glued to glass slides with cyanoacrylate-based cement and prepared for observation as de-

[2] Measurements compared are those described in Rocha Olivares and Gomez Muñoz (1993).

scribed for whole otoliths. Scales were mounted intact between two glass slides and observed under a dissecting microscope at different magnifications with transmitted light.

Organisms were aged by counting the number of growth marks found in scales (scale age), whole otoliths (whole-otolith age), and sectioned otoliths (sectioned-otolith age). Because a large number of fishes occurred within a restricted length range (Fig. 2), age estimates for whole-otolith ring counts were made on 50 randomly subsampled otoliths from each 2-cm fish-length interval ($n$=1356) (FAO, 1982). After whole-otolith age determinations were made, a stratified random subsample of these otoliths was sectioned ($n$=151) and the corresponding scales were used for ageing (10 per fish). Only nonregenerated scales were used for age determinations.

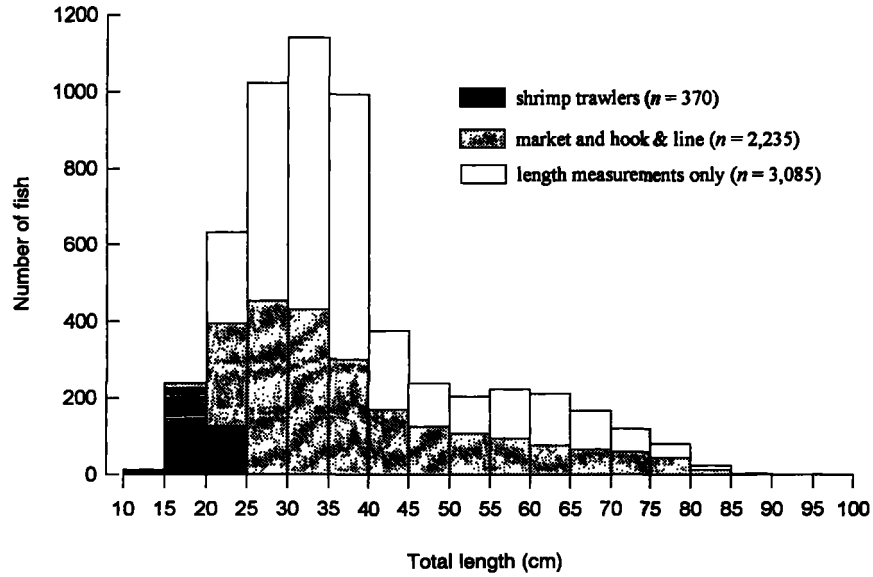


**Figure 2**

Length-frequency distribution of *Lutjanus peru* collected by hook-and-line and shrimp trawling activities in the southeast coast of Baja California Sur, Mexico. Only fishes from trawls, hook and line, and the market were used for the ageing study.

Two independent whole-otolith age determinations were made at different times by two readers. A third estimate was then made three months later for those otoliths with different ages. Lack of consensus resulted in the otolith being discarded as "noninterpretable," and excluded from the growth analysis. An effort was made to note the cause for rejection. Sectioned otoliths and scales were subject to two reading rounds by one reader separated by a three-month interval.

Estimates of the precision (variation between different reading rounds for each structure) and of the corroboration (variation among structures) were assessed by comparing the percentage of discordant determinations between two data sets (%D) and the index of average percent error of Beamish and Fournier (%E) (1981).

Following the method proposed by Boehlert (1985) of using objective criteria and multiple regression models to determine fish age from otolith measurable parameters, an effort was made to predict Pacific red snapper whole-otolith age by using otoliths and fish morphometrics. This method, originally conceived to save time and costs as well as to reduce the subjectivity involved in otolith reading, was implemented on *L. peru* data and the resulting model used to determine the age of fishes whose otoliths could not be read. Independent variables included otolith weight (to the nearest mg), width, length, ventral radius, anterior radius, fish TL, GW, their logarithmic transformations and squared terms, and a modified condition factor $K$ (gutted weight/ $TL^3$). Data from a stratified random subsample (FAO, 1982) from the whole-otolith age determinations were used for this analysis ($n$=285). A stepwise procedure with an inclusion level of $P$=0.05 was used to select variables for the model. Homoscedasticity and normality were evaluated by residual analysis (Zar, 1984).

## Growth

Individual length-at-age (whole-otolith and sectioned-otolith) data were used to fit the von Bertalanffy growth function (VBGF):

$$L_t = L_\infty\left(1-e^{-K(t-t_0)}\right)$$

where $L_t$ = length at age $t$;
$L_\infty$ = asymptotic length;
$K$ = growth coefficient; and
$t_0$ = age at which fish length would be zero if it grows according to the model.

Hotelling's $T^2$ test (Bernard, 1981) was used to compare growth parameters.

Observed length-at-age data were obtained from whole-otolith readings for most fishes ($n$=1170) and from sectioned-otolith readings for the largest specimens ($n$=10). To correct for within-year growth, ages were assigned as follows. Since translucent margin deposition on the otolith peaks in July (Rocha Olivares and Gomez Muñoz, 1993; Fig. 3), only fishes caught during this month were assigned integer ages. For the rest, subsequent growth was accounted for by assigning fractional ages in proportion to the elapsed time (e.g. a fish with two annuli caught in January was assigned 2.5 years).

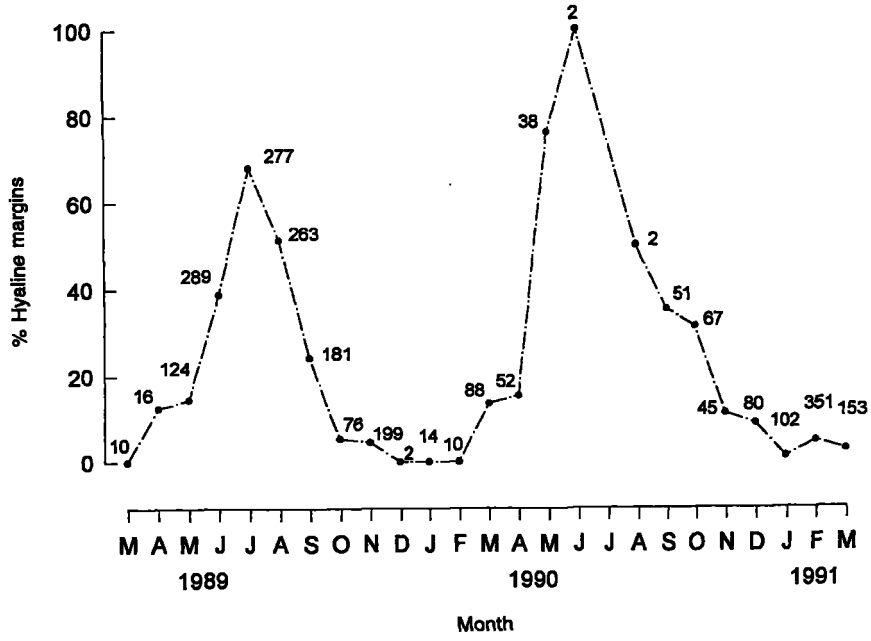


**Figure 3**

Percentage of translucent margins of the whole otoliths of *Lutjanus peru*. Sample sizes are shown next to symbols.

Length–weight relationships were fitted to the data and used to calculate the von Bertalanffy asymptotic weight ($W_\infty$). Growth performance $\phi = \log_{10}(K) + 2/3 \log_{10}(W_\infty)$ was computed from the growth parameters (Manooch, 1987).

All coefficients of determination reported for nonlinear models were computed by using the following expression (Draper and Smith, 1981):

$$R^2 = 1 - \frac{\sum (y - \hat{y})^2}{\sum (y - \bar{y})^2},$$

where $y$ = observed values;
$\hat{y}$ = predicted values; and
$\bar{y}$ = mean values.

### Mortality

An age-length key was constructed from whole-otolith ages for the sexes combined and applied to the length-frequency distributions to construct population age distributions by sex. Total mortality rate ($Z$) was determined from the descending limb of the resulting catch curves for males, females, and pooled sexes. Hoenig's (1983) combined regression equation was used to obtain another estimate of $Z$. Owing to the lack of data concerning fishing effort and the unavailability of unfished areas, no direct estimation of the natural mortality rate ($M$) was possible. Instead, empirical relationships between $M$ and $K$ were used to obtain approximate estimates (Pauly, 1980; Ralston, 1987). A mean bottom temperature of 14°C was assumed for calculating $M$. This temperature prevails throughout most of the Gulf at depths between 100 and 300 m (Maluf, 1983).

## Results

### Population parameters and morphometric relations

During the sampling period *L. peru* abundance was variable, and in some months (e.g. March and December 1989 and July to August 1990), sample size was small because of limited supply. Sex determination was possible for only 13.1% of the specimens used for length-frequency distributions (males:females= 1:0.84; $H_0$=1:1 ratio, $\chi^2_c$=2.85, $P$=0.091). In the biological sampling, the sex ratio was 1:0.85 ($H_0$=1:1 ratio, $\chi^2_c$=5.36, $P$=0.021), indicating that no bias was introduced in the length-frequency sampling with only gonad fragments.

Macroscopic gonad differentiation occurs in *L. peru* between 30 and 35 cm TL (Table 1). A significant fraction of the catch included individuals smaller than 50 cm TL (38% of a total of 2171 kg of gutted fish).

**Table 1**

Total length composition (cm) of the biological sample of Pacific red snapper by sex. The column labeled "unsexed" groups fishes with undifferentiated gonads (almost all of those <30 cm) and those gutted and with no traces of gonadal tissue (most of those between 30 and 40 cm and all of those > 40 cm).

| Size range | Males | Females | Unsexed | Total |
|---|---|---|---|---|
| 10.1–15.0 | 0 | 0 | 24 | 24 |
| 15.1–20.0 | 0 | 0 | 259 | 259 |
| 20.1–25.0 | 4 | 5 | 366 | 375 |
| 25.1–30.0 | 23 | 23 | 404 | 450 |
| 30.1–35.0 | 67 | 59 | 305 | 431 |
| 35.1–40.0 | 109 | 76 | 117 | 302 |
| 40.1–45.0 | 66 | 46 | 59 | 171 |
| 45.1–50.0 | 40 | 28 | 56 | 124 |
| 50.1–55.0 | 32 | 24 | 52 | 108 |
| 55.1–60.0 | 37 | 17 | 38 | 92 |
| 60.1–65.0 | 26 | 25 | 26 | 77 |
| 65.1–70.0 | 26 | 23 | 18 | 67 |
| 70.1–75.0 | 21 | 29 | 11 | 61 |
| 75.1–80.0 | 9 | 30 | 7 | 46 |
| 80.1–85.0 | 5 | 9 | 0 | 14 |
| 85.1–90.0 | 0 | 3 | 0 | 3 |
| 90.1–95.0 | 0 | 0 | 0 | 0 |
| 95.1–100.0 | 1 | 0 | 0 | 1 |
| Total | 466 | 397 | 1742 | 2605 |

Male and female length compositions were significantly different (Kolmogorov-Smirnov two-sample test, $D$=0.0836, 0.01<$P$<0.05). Although the largest specimen was a 99.2-cm-TL male (Table I), females predominated beyond 70 cm (sex ratio 1:1.97).

Conversion equations for lengths (cm) and weights (kg) did not differ between sexes (ANCOVA, $P$>0.05); therefore data were pooled:

$TL$=1.246$SL$ + 0.104 ($n$=2603, $r^2$=0.997, $P$<0.001)

$TW$=1.207$GW$ − 0.020 ($n$=841, $r^2$=0.988, $P$<0.001)

$GW=1.763 \times 10^{-5}\ TL^{2.877}$ ($n$=2350, $R^2$=0.990, $P$<0.001)

$TW=1.816 \times 10^{-5}\ TL^{2.905}$ ($n$=844, $R^2$=0.980, $P$<0.001).

Exponents of the length-weight relationships were significantly different from three ($t$-test, $P$<0.05).

## Age determination

Concentric annuli and circuli were observed in most otoliths and scales. Most scales were found to be interpretable, although circuli were never as clearly defined as otolith annuli. Most samples ($n$=92) presented less than 40% regenerated scales. A correlation was found between the percentage of regenerated scales and fish length ($r$=0.310, $P$<0.001).

**Table 2**

Values of percent disagreement (%D) and percent average error (%E) for whole-otolith, sectioned-otolith, and scale age determinations for individual structures (precision) and between the structure and whole-otolith age (between structures) of Pacific red snapper. No. = number of determinations. Rejections are otoliths not included in the analysis for being too large (size) or for lacking a clear marking pattern (other).

| | Index | | Rejections | | |
|---|---|---|---|---|---|
| Age | %D | %E | No. | Size | Other |
| Precision | | | | | |
| Whole-otoligh | 16.90 | 3.89 | 143 | 7 | 1 |
| Sectioned-otolith | 10.42 | 2.13 | 144 | 1 | 6 |
| Scale | 34.01 | 4.19 | 147 | 2 | 2 |
| Between structures | | | | | |
| Sectioned-otolith | 26.36 | 2.82 | 129 | | |
| Scale | 58.65 | 8.86 | 133 | | |

Of the 1356 otoliths used for whole-otolith age determinations, 186 were discarded for the following reasons: large size prevented the enumeration of all the growth rings (2.2%), breakage or loss (1.4%), deformities or abnormal calcification (2.3%), and non interpretable otoliths as defined in the "Methods" section (7.8%). Whole-otolith ages were available for 1170 individuals ranging from 10.2 to 83.5 cm TL.

A number of scales and otoliths were also rejected in the comparison of whole-otolith, sectioned-otolith, and scale ages (Table 2). Noninterpretable otoliths were included in the computation of precision indices, but not in the between-structures indices. Most of the rejections of whole otoliths were due to size, but a similar proportion of sectioned otoliths lacked a clear marking pattern. Sectioned otoliths and scales were the most and least precise structures, respectively, for age determination (Table 2). The %D indicates a factor of three difference in the precision of sectioned otoliths and scales. However, the %E shows that such differences are less important (less than a factor of two) because this index incorporates the difference in age estimations (Beamish and Fournier, 1981). The difference between whole-otolith ages and sectioned-otolith or scale ages was much larger (Fig. 4). Sectioned-otolith ages were found to be at least twice as similar to whole-otolith ages as scale ages according to %D, and more than three times as similar according to %E (Table 2).

The magnitude of the discrepancies in age determinations among structures increased with both age and length of the fish (Fig. 4). Differences between scale

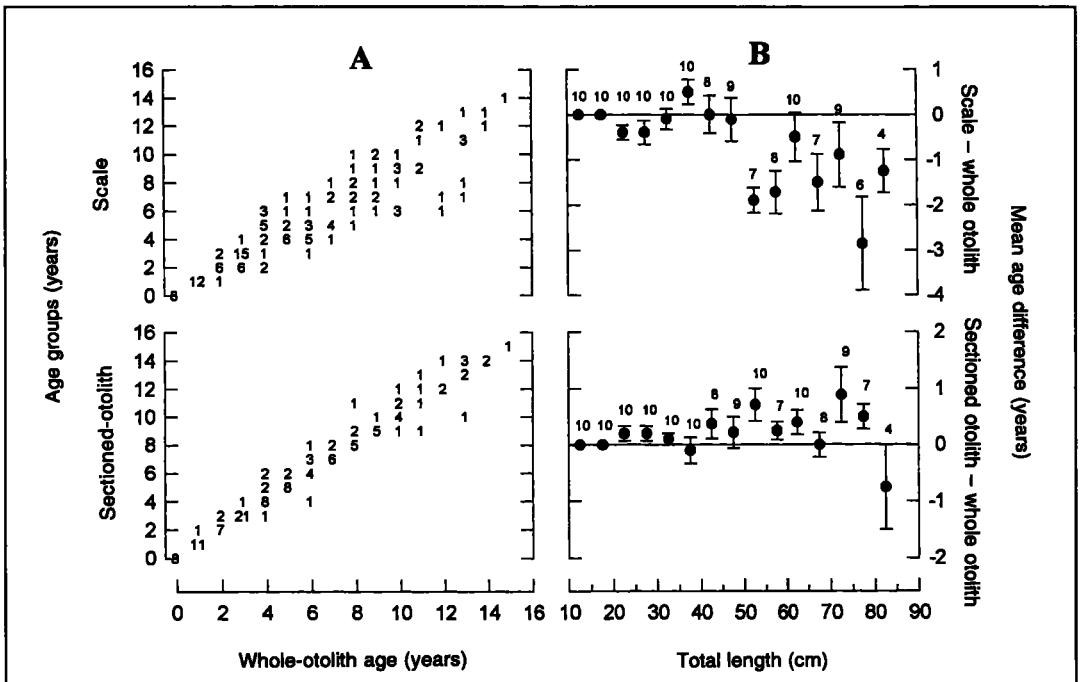


**Figure 4**

(**A**) Scatter plots of sectioned-otolith and scale ages against whole-otolith ages. Numbers represent the frequency of occurrence. (**B**) Mean age difference (± standard error of the mean) of scale and sectioned-otolith ages minus whole-otolith age against length of *Lutjanus peru*.

and whole-otolith ages were as large as six years, whereas for sectioned otoliths, differences did not exceed three years (Fig. 4A). Scale ages were consistently lower than whole-otolith ages in fish larger than 50 cm TL, whereas the largest sectioned-otolith and whole-otolith age deviations were found in fish above 40 cm TL (Fig. 4B). The mean sectioned-otolith and whole-otolith age deviations did not exceed one year, although mean scale and whole-otolith age deviations often exceeded one year.

Six independent variables with highly significant coefficients were included in the multiple regression model (Table 3). The model explained 96% of the variability in the data with a standard error of less than one year. A linear regression of whole-otolith age on otolith weight alone accounted for 93% of the variance. The residuals revealed a trend indicating a certain degree of heteroscedasticity but were normally distributed ($\chi^2$=10.41, $P$=0.005). Whole-otolith ages determined with the multiple regression model for 28 fish with unreadable otoliths were very close to the VBGF (see "Discussion" section).

**Table 3**

Regression coefficients for the multiple regression model of whole-otolith age as a function of otolith and fish measurements of Pacific red snapper. SE = coefficient standard error, SEE = standard error of the estimate. $R$ = multiple correlation coefficient; No. = number of observations.

| Variable | Coefficients | SE | $P$ |
|---|---|---|---|
| Intercept (c) | –6.183 | 1.0940 | 0.000 |
| Total length squared | 1.306E-03 | 1.4910E-04 | 0.000 |
| ln(Gutted weight) | 1.353E-05 | 3.1700E-06 | 0.000 |
| Otolith weight squared | 5.915 | 0.7313 | 0.000 |
| Otolith width squared | –7.391E-01 | 2.4400E-01 | 0.000 |
| ln (otolith ventral radius) | 2.153E-02 | 7.6050E-03 | 0.005 |
| Otolith weight | –1.014E-02 | 3.3360E-03 | 0.003 |
| | | $R$ = | 0.9797 |
| | | SEE = | 0.6469 |
| | | No. = | 283 |

## Growth

Mean observed length-at-age were not significantly different between sexes, ($t$-tests, 0.95>$P$>0.09), however male and female VBGF parameters computed separately from individual data were significantly different ($T^2$=609.5, $P$<<0.001) (Fig. 5). The 99% Roy-Bose simultaneous confidence intervals indicated that the three VBGF parameters significantly contributed to the observed difference in predicted growth (6.091≤$L_\infty$

(male) – $L_\infty$(female) ≤ 8.419, –0.026 ≤ $K$(male) – $K$(female) ≤ –0.020, –0.511 ≤ $t_0$(male) – $t_0$(female) ≤ –0.344).

Of the thirty otoliths too large for whole-otolith reading, ten were randomly selected, sectioned, and read, yielding ages of 15 years and above. The VBGF parameters computed from all available data, including whole-otolith and sectioned-otolith ages ($n$=1180) were considered to be representative of the population (asymptotic standard error): $L_\infty$ = 97.32 cm (1.816), $K$ = 0.1111/yr (4.073 × $10^{-3}$), $t_0$ = –0.316 (0.0569) ($n$=1180, $R^2$=0.93). The asymptotic length was converted to an asymptotic weight of $W_\infty$ = 10.84 kg. The growth performance of *L. peru* was $\phi$ = 1.736. The age composition of the sampled males differed significantly from that of the females (Kolmogorov-Smirnov two-sample test, $D$=0.0843, 0.01<$P$< 0.05) (Fig. 6).

### Mortality

The length range of most age groups was on the order of 20 cm (Table 4: Fig. 7A). Catch curves were constructed for males, females, and pooled sexes. Total mortality rates ($Z$) were calculated without the extreme age groups and those not fully recruited to the fishery (Fig. 8). Total instantaneous mortality rate for females, estimated from the catch curves, was significantly lower compared with those for males ($t$=–2.112, df=52, $P$<<0.001). Hoenig's formula should be applied to the maximum age of "the largest few fish" (Hoenig, 1983). On the basis of this recommendation and the fact that only one out of 5690 fishes measured in this study was larger than 90 cm, this 31-year-old fish was interpreted as an outlier and a $t_{max}$ = 26 years was considered more representative of the population. This value yielded a $Z$ = 0.172/yr, which is considerably lower than the catch curve estimates. The estimates of $M$ obtained from the empirical relationships 0.222/yr (Pauly, 1980) and 0.248/yr (Ralston, 1987) were compatible with the catch curve mortality estimates giving exploitation rates $F/Z$) ranging from 0.121 (females) to 0.393 (males).

## Discussion

### Sampled length range

The accurate estimation of growth parameters depends, among other factors, on the adequate sampling of the length range of a species. The fish used in this study covered most of the known length range of the Pacific

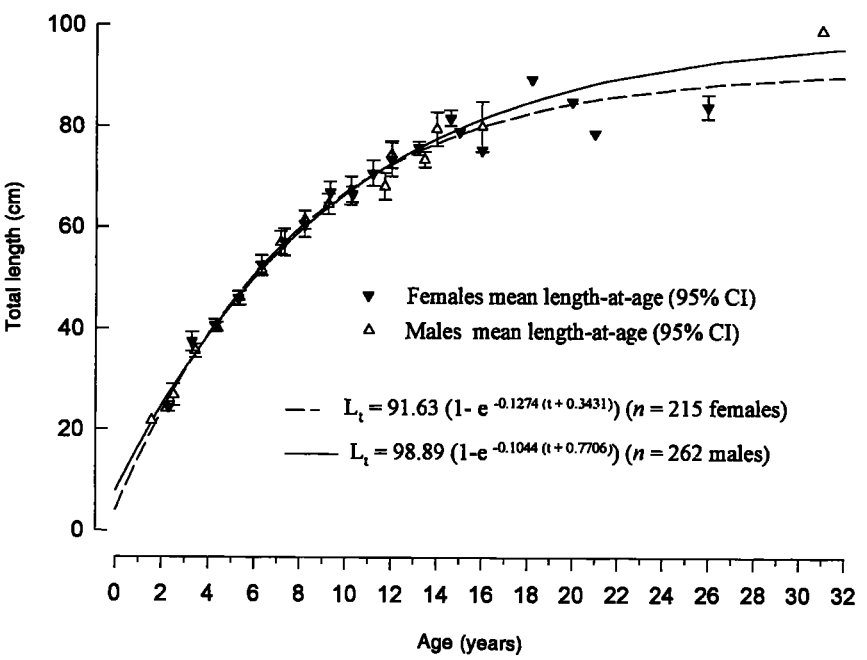


**Figure 5**

Fitted VBGF curves and mean length-at-age (whole-otolith and sectioned-otolith) for *L. peru* females (dashed line, filled triangles) and males (solid line, open triangles). 95% CIs are shown.

red snapper (10 to ca. 100 cm TL). The lower size limit of *L. peru* in the hook-and-line catch (18.3 cm) was very close to that reported for *L. campechanus* fished with similar size hooks in the Gulf of Mexico (18.0 cm) (Nelson and Manooch, 1982). This might indicate a comparable vulnerability due to morphological similarity. Because fishermen do not typically change hook size to target small snappers (personal observation), the preponderance of small fish in the catch (ca. 61% in numbers) that had not yet recruited to the spawning population was not due to gear selectivity. The upper limit of the range was also sampled and a length record is reported for the species. Thus it seems unlikely that the growth parameters of *L. peru* may be biased owing to inadequate sampling of its length-range.

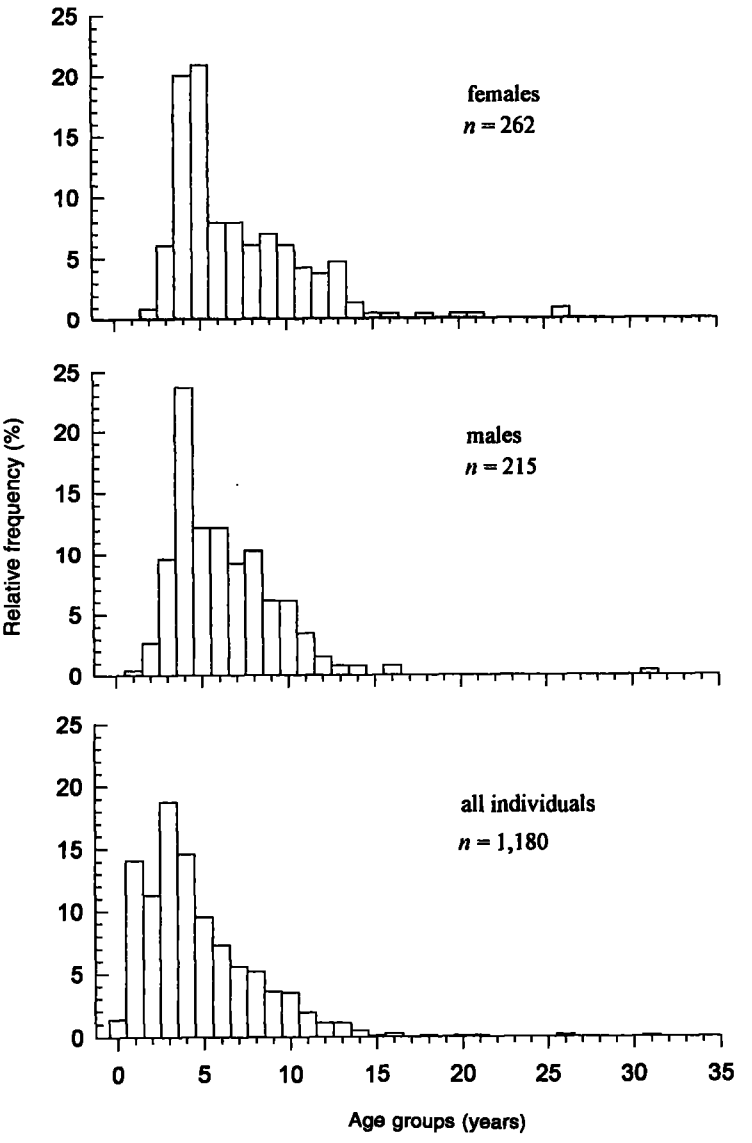


**Figure 6**

Age structure of *Lutjanus peru* females, males, and sexes combined of directly aged specimens collected at La Paz fish market or caught by hook-and-line and shrimp trawling activities off the southeast coast of Baja California Sur. Data represent whole-otolith ages (up to 15 years) and sectioned-otolith ages (beyond 15 years). Most of the unsexed individuals are undifferentiated fish but some are reproductively active adults that could not be sexed.

## Age determination

The monthly fluctuation in the percentage of translucent margins suggests that the period of translucent ring formation takes place in the summer during the spawning season (Fig. 3). This observation enabled Rocha Olivares and Gómez Muñoz (1993) to indirectly validate whole-otolith rings as annuli in *L. peru* up to 10 years old.

The greater precision of sectioned otoliths suggested by %D and %E resulted from a more direct access to the marking patterns of the structure. Different degrees of wear and tear were noted on the anterior margin of large scales, which contributed to age determination variability within reading rounds. Comparison of individual age estimates of *L. peru* from whole otoliths, sectioned otoliths, and scales provided evidence supporting age underestimation by the latter. This underestimation by scales has also been observed in the Antarctic fish *Notothenia gibberifrons* Lonnberg (Coggan et al., 1990). Libby (1985) also concluded that whole-otolith ages were more accurate and less subjective than scales for ageing the anadromous alewife, *Alosa pseudoharengus* (Wilson). As in other species, however, this effect does not seem to be very important during the first five years in *L. peru*. For example, Lou (1992) found that either scales or sectioned otoliths provided reliable age estimates up to five years in the tropical parrotfish *Scarus schlegeli* (Bleeker), and Lowerre-Barbieri et al. (1994) reported similar findings in weakfish, *Cynoscion regalis* (Bloch and Schneider), to age six. Apparently, otoliths are more reliable structures than scales (Beamish and McFarlane, 1987) over most ages, and this study extends this observation to the Pacific red snapper.

A number of studies have compared whole and sectioned otoliths as alternative structures for age determination. The magnitude of the difference between whole-otolith and sectioned-otolith age varies from species to species, but the general trend is an underestimation of whole-otolith ages in older fishes. Wilson and Boehlert (1990) found that sectioned-otolith ages produced smaller $L_\infty$ estimates than whole-otolith ages, but growth rates were similar for both in the canary rockfish, *Sebastes pinniger* (Gill). In the long-lived orange roughy, *Hoplostethus atlanticus* Collett, Smith et al. (1995) found that sectioned-otolith ages exceeded whole-otolith ages after the age of reproductive maturity. Ferreira and Russ (1994) found in the Great Barrier reef coral trout, *Plectropomus leopardus* (Lacépède), that the mean difference between sectioned-otolith and whole-otolith readings remains within one year in fishes up to 12 years, but increases abruptly to almost four years for age groups 13 and 14. Pearson et al. (1991) found that whole-otolith ages tend to be as much as eight years less than broken-and-burnt otolith ages in the shortbelly rockfish, *S. jordani* Gilbert. In *L. peru*, discrepancies between whole-otolith and sectioned-otolith ages were not extreme, but whole-otolith age determinations were not reliable beyond the 15th annulus. It would be useful to extend these observations to other populations of *L. peru* to assess the variability of this pattern.

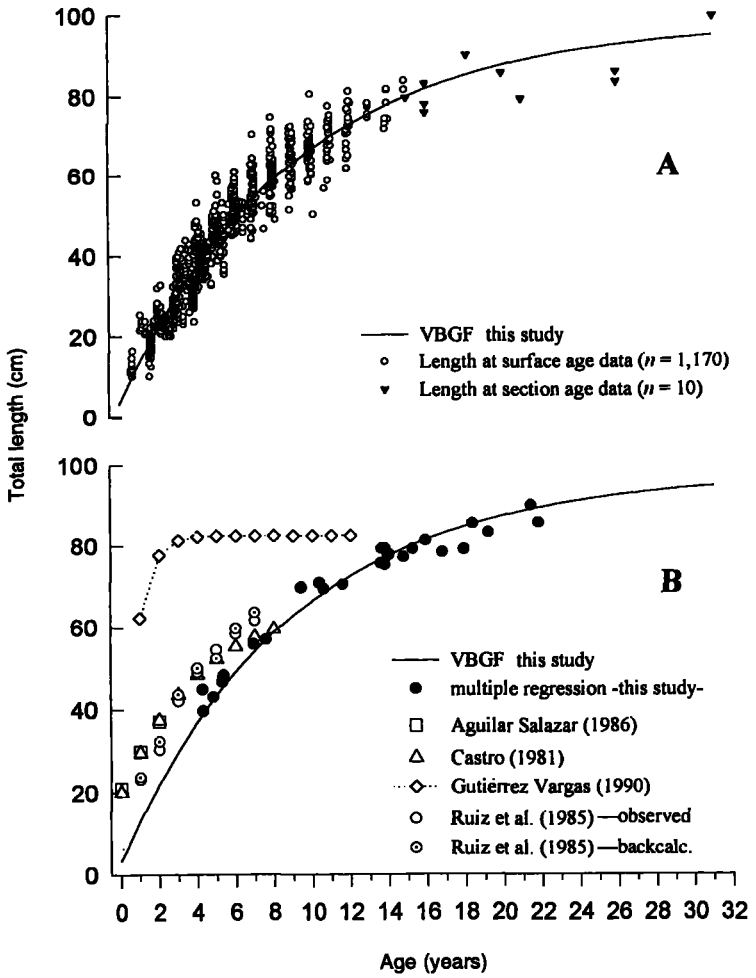


**Figure 7**

(**A**) Scatter plot of all length-at-age data used for VBGF parameter estimation. Length-at-whole-otolith age (circles), length-at-sectioned-otolith age (triangles), and VBGF curve obtained from this study (solid line). (**B**) VBGF curve from this study (solid line) and lengths at age reported in other studies of age and growth of *Lutjanus peru*. Mean observed lengths at age (open circles) and mean back-calculated (dotted open circles) from Ruiz et al. (1985); mean observed length at age from Aguilar Salazar (1986) (squares), mean observed length at age from Castro (1981) (triangles). Diamonds joined by a dotted line indicate the von Bertalanffy growth curve reported by Gutiérrez Vargas (1990). Filled circles represent age estimates obtained with the multiple regression model for "unreadable" otoliths.

The coefficient of determination of the multiple regression model is affected by the degree of colinearity of the independent variables. Although not all the assumptions required for the use of a multiple regression model are met by the data set, including homoscedasticity, this does not preclude its results to serve as a first-order age approximation. Otolith weight appears to be a very good predictor of age in this species, as it has been observed in *P. leopardus* (Ferreira and Russ, 1994). The model was used to estimate the age of those otoliths that had been discarded as unreadable and for which all variables were available, placing the predicted ages very close to the VBGF curve (Fig. 7B). The success of this method suggests that it could be implemented for routine age determination of this species.

## Growth

The growth of *L. peru* was satisfactorily described by the generalized VBGF. The absence of a significant difference in mean length-at-age between sexes and the significantly different growth parameters might seem contradictory. However, the graphic representation of the data revealed that both sexes have very similar growth schedules during

the first 10–12 years (Fig. 5). The very few males sampled beyond the ascending limb of the curve may have prevented a more constrained curve fit in this region.

The results of this and other studies made in Mexico and Costa Rica reveal the following patterns: 1) scale-based studies, using traditional methods for growth parameter estimation, yield higher growth rates resulting from age underestimation if large fishes are involved (Table 5, reference A) but not so if only small fishes are included (Table 5, reference B); 2) small asymptotic lengths may result from a restricted length range (Fig. 7B); 3) length-frequency based methods for growth parameter estimation yield fewer age classes and unrealistic growth rates, which have been observed elsewhere (Grimes, 1987; see also Rocha Olivares, 1991, for examples of unpublished data). It is possible that part of the observed differences in the growth parameters of *L. peru* between peninsular and continental populations are "true"; however the diversity of fishing gears and selectivities used in different states (Aguilar Salazar, 1986) and the poor effort invested in systematic biological data collection make interpopulation comparisons difficult.

The presence of an individual of ca. 100-cm TL represents a length record for the species. The sectioned-otolith age of this fish (31 years) also constitutes a record for the maximum age of an eastern Pacific lutjanid, and adds *L. peru* to the list of long-lived snappers (i.e. exceeding 30 years of age): *L. bohar* (38 years), *L. adetti* (37 years), *L. sebae* (35 years) (Loubens, 1980), *L. malabaricus* (46 years) (Mathews and Samuels, 1985), and *L. quinquelineatus* (32 years) (Newman et al., 1996). When compared with the growth trends observed in the family, growth performance of *L. peru* ($\phi$=1.74) falls above the mean value for lutjanids (1.65) but within the expected range (1.08–2.15; SD=0.35) (Munro, 1983). Furthermore, the combination of $L_\infty$ = 97.32 cm and $K$ = 0.1111/yr of the Baja California population of Pacific red snapper is very close to the functional relationship of $\log_{10}(K)$ versus $\log_{10}(L_\infty)$ reported by Manooch (1987) for snappers (Lutjanidae) and groupers (Serranidae).

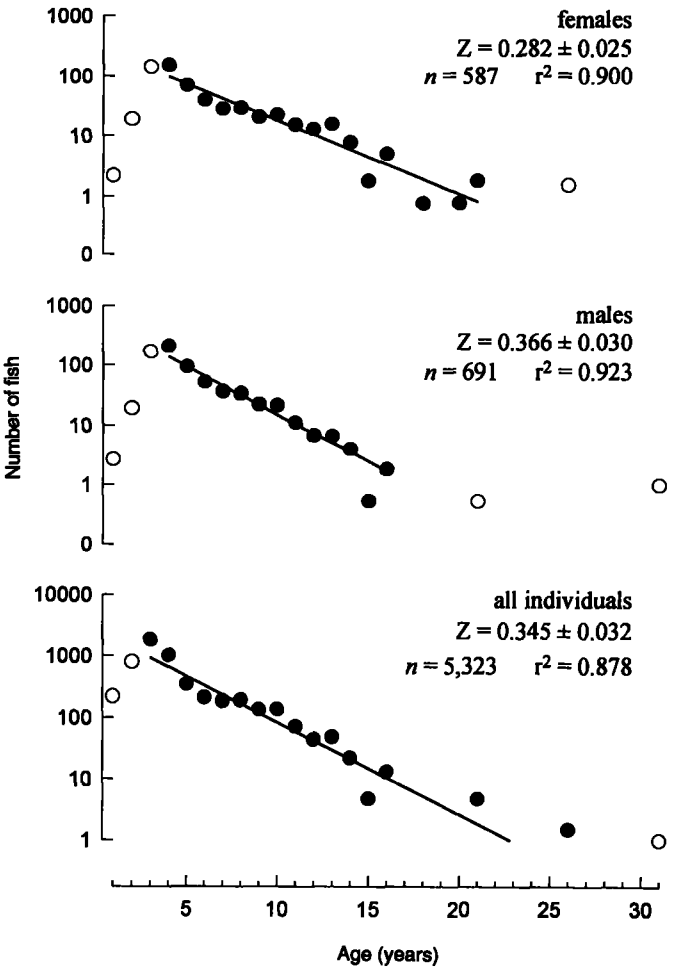


**Figure 8**

Catch curves and estimates of total mortality of *Lutjanus peru* females, males and sexes combined, caught by hook and line off the southeast coast of Baja California Sur. The age composition was computed with an age-length key and the length composition of the massive and biological samples. Total mortality rates $Z$ (per year ± standard error) are presented for females, males, and the entire population. Black dots represent data points included in the calculation of the slope (solid line).

## Mortality

In this study, estimates of $M$ were restricted to the use of empirical relationships between $M$ and $K$ because no effort data were available and no unfished areas could be sampled. It has been repeatedly observed that these two parameters are inversely related across a large number of fish taxa (Pauly, 1980). Hoenig's (1983) empirical formula yielded an unrealistically low estimate of mortality, as it probably would in other long-lived snappers. When compared to total mortality rates ($Z$), estimates of $M$ are consistent and yield much lower exploitation rates and $F/M$ ratios than those reported for other lutjanids (cf. Table 8.2 in Ralston, 1987), probably as the result of an overestimation of $M$ by the empirical formulae.

Male predominance in population sex ratios is not uncommon among lutjanids (cf.

Table 5.1 in Grimes, 1987). Populations of *L. peru* studied in Baja California Sur and Michoacán off continental Mexico show this bias (1:0.82, $n$=785; Ruiz Luna et al., 1985). In lutjanids, evidence suggests that skewed sex ratios probably reflect differential growth and mortality between sexes (Grimes, 1987). Other reproduction studies on lujanids have also suggested a tendency for females to be more common at larger sizes. The population sampled in this study shows significant differences in mortality rates

**Table 4**

Age-length key used in the construction of the catch curves of Pacific red snapper, *L. peru*. Ages represent whole-otolith ages except for fish older than 15 years for which sectioned otoliths were used.

| Length Group (cm) | Age group (year) | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 0+ | 1+ | 2+ | 3+ | 4+ | 5+ | 6+ | 7+ | 8+ | 9+ | 10+ | 11+ | 12+ | 13+ | 14+ | 15+ | 16+ | 18+ | 20+ | 21+ | 26+ | 31+ | Total |
| 10.1–15.0 | 15 | 8 | | | | | | | | | | | | | | | | | | | | | 23 |
| 15.1–20.0 | 1 | 107 | 2 | | | | | | | | | | | | | | | | | | | | 110 |
| 20.1–25.0 | | 50 | 69 | 8 | | | | | | | | | | | | | | | | | | | 127 |
| 25.1–30.0 | | 1 | 58 | 62 | | | | | | | | | | | | | | | | | | | 121 |
| 30.1–35.0 | | | 4 | 102 | 17 | | | | | | | | | | | | | | | | | | 123 |
| 35.1–40.0 | | | | 40 | 70 | 7 | | | | | | | | | | | | | | | | | 117 |
| 40.1–45.0 | | | | 9 | 67 | 37 | 2 | | | | | | | | | | | | | | | | 115 |
| 45.1–50.0 | | | | | 17 | 53 | 26 | 2 | 1 | | | | | | | | | | | | | | 99 |
| 50.1–55.0 | | | | | 1 | 9 | 47 | 26 | 6 | | 1 | | | | | | | | | | | | 90 |
| 55.1–60.0 | | | | | | 6 | 8 | 24 | 23 | 10 | 3 | | | | | | | | | | | | 74 |
| 60.1–65.0 | | | | | | | 3 | 11 | 20 | 9 | 11 | 3 | 1 | | | | | | | | | | 58 |
| 65.1–70.0 | | | | | | | | 1 | 6 | 17 | 20 | 7 | | | | | | | | | | | 51 |
| 70.1–75.0 | | | | | | | | 2 | 5 | 6 | 4 | 10 | 8 | 7 | 1 | | | | | | | | 43 |
| 75.1–80.0 | | | | | | | | | | | 1 | 2 | 3 | 6 | 1 | 1 | 2 | | | 1 | | | 17 |
| 80.1–85.0 | | | | | | | | | | | 1 | | 1 | | 4 | | 1 | | | | | | 7 |
| 85.1–90.0 | | | | | | | | | | | | | | | | | | 1 | 1 | | 2 | | 4 |
| > 90 | | | | | | | | | | | | | | | | | | | | | | 1 | 1 |
| Total | 16 | 166 | 133 | 221 | 172 | 112 | 86 | 66 | 61 | 42 | 41 | 22 | 13 | 13 | 6 | 1 | 3 | 1 | 1 | 1 | 2 | 1 | 1180 |

**Table 5**

Comparison of growth parameters of *Lutjanus peru* obtained in studies from Mexico and Costa Rica (F-W=Ford-Walford plot, NL=nonlinear regression, $n$=sample size, LFA=length-frequency analysis, obs=observed lengths, back=back-calculated lengths, NA=not applicable).

| | Reference | | | | |
|---|---|---|---|---|---|
| | A | B | C | D | E |
| Study site | Michoacan | Michoacan Guerrero Oaxaca | Baja California Sur (Los Cabos region) | NW Costa Rica | Baja California Sur (Bahía de La Paz region) |
| Structure used | scales | scales | scales | NA | otoliths |
| Method | F-W | F-W | F-W | LFA | NL |
| Data | obs. back | obs. | back | NA | obs |
| $L_\infty$ (cm) | 81.5 79.5 | 82.64 | 66.71 | 83.34 | 92.85 |
| $K$ (per yr) | 0.196 0.191 | 0.11 | 0.23 | 1.46 | 0.12 |
| $t_0$ (yr) | 0.725 0.786 | 1.48 | –0.54 | 0.04 | 0.14 |
| $n$ | 1068 412 | 175 | 208 | 5902 | 1180 |
| Age range (yr) | 1–7 1–7 | 0–2 | 0–8 | 1–12 | 0–31 |
| Size range (cm) | 23–62 24–64 | 21–37 | 20–59 | 24–82 | 10–99 |

A = Ruiz et al. (1985); B = Aguilar Salazar (1986); C = Castro (1981); D = Gutierrez Vargas (1990); and E = this study.

between sexes. The higher mortality rate of males may account for the biased sex ratio. In no other lutjanid species has such a large difference in total mortality been observed between males and females. Whether this difference results from different availability to the fishing gear, spatial segregation, or foraging behaviors ($F$-associated difference), or from differences in predator vulnerability or natural longevity ($M$-associated difference) requires further research.

In this paper I have compared the merit of scales, whole otoliths, and sectioned otoliths to age the Pacific red snapper, *L. peru*. As is the case for other tropical and semitropical fishes, the usefulness of whole-otolith age determination is limited up to a certain age, after which, sectioned otoliths are the only reliable method for ageing and scales should be avoided. Age determinations from whole and sectioned otoliths of fishes covering most of the known size range of *L. peru* were used to determine the VBGF parameters. A 31-year-old fish measuring 99.2 cm is reported and constitutes a record size and age. Total mortality rates were higher for males resulting in a preponderance of females among the older fishes.

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# Enhancing diet analyses of piscivorous fishes in the Northwest Atlantic through identification and reconstruction of original prey sizes from ingested remains

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**Abstract.**—Biological interactions among species can play a dominant role in structuring marine fish communities. Specifically, predation may represent a significant source of mortality for larval and juvenile fishes. Analysis of predator diet requires accurate information on the identity as well as the sizes of prey consumed. In examinations of stomach contents of piscivorous fishes, the condition of recovered prey items varies substantially not only in the large range of digestive states encountered but also in the occurrence of partially consumed fishes. To estimate the original sizes of well-digested and partially consumed prey fishes we constructed a series of predictive equations relating total length, fork length, and weight of fish to seven morphometric measurements including dorsoventral body depth, eye diameter, caudal peduncle depth, pectoral-fin length, opercle length, cleithrum length, and dentary length for ten common prey fishes in the Northwest Atlantic. All relationships were highly significant, with coefficients of determination typically exceeding 0.90 and mean percent prediction errors less than 10%, indicating that reliable original size estimates are obtainable from incomplete fish remains. To aid in field-based identification of prey fishes, we extracted and examined opercles, cleithra, and dentaries from each fish. Careful examination of bones revealed prominent diagnostic characteristics with clear differences among family taxa, demonstrating their potential utility as identification tools. Used collectively, the predictive equations and the diagnostic features of the bones should allow for inclusion in diet analyses of prey items previously designated as unidentifiable or unmeasurable, and thus increase the amount of dietary information obtainable from stomach contents analyses of Northwest Atlantic piscivores.

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Biological interactions among species can significantly affect the dynamics of marine fish populations (Overholtz et al., 1991; Rothschild, 1991). Specifically, predation by piscivorous fishes is recognized as an important mechanism in structuring fish communities (Hackney, 1979; Lyons and Magnuson, 1987; Tonn et al., 1992), particularly in the role it plays to potentially regulate natural mortality rates and recruitment of larval and juvenile fishes (Sissenwine, 1984; Houde, 1987; Bailey and Houde, 1989). In order to estimate consumption rates of key predators, details are needed on the types and sizes of prey fishes consumed across spatial and temporal scales. However, because of the substantial variability in the condition of recovered prey items, the collection of stomach contents data in the field is often limited to only those items that are readily identified and measured, resulting in the loss of potentially important diet information.

Identification of piscine prey ingested by fish, avian, and mammalian predators has frequently involved the use of diagnostic bones including vertebrae (Pikhu and Pikhu, 1970; Feltham and Marquiss, 1989; Carss and Elston, 1996), pharyngeal arches (McIntyre and Ward, 1986; Raven, 1986), opercular bones (Newsome, 1977), the axial skeleton

and hypurals (Trippel and Beamish, 1987), and cleithra and dentaries (Hansel et al., 1988). Measurements of the dimensions of diagnostic bones have often then been used to estimate original prey size (Trippel and Beamish, 1987; Hansel et al., 1988; Carss and Elston, 1996). Previous studies on the food habits of piscivores have used fish otoliths as an aid in prey identification and original prey size estimation (Jobling and Breiby, 1986). However, acidic preservatives, such as formaldehyde, can dissolve otoliths, resulting in unreliable otolith length and fish length relationships (McMahon and Tash, 1979). In addition to bones, external morphological measurements, such as eye diameter and caudal peduncle depth, have been used successfully to reconstruct prey body size for recently consumed prey fishes (Crane et al., 1987; Scharf et al., 1997). However, the majority of fish feeding studies employing such techniques have been directed at freshwater piscivores, whereas researchers examining the diets of marine fishes have utilized these techniques much less frequently (Crane et al., 1987; Scharf et al., 1997). Moreover, no such techniques are currently available to enhance diet analyses and more completely define the role of piscivorous fishes in structuring fish communities in the Northwest Atlantic.[1]

Here, we generate a series of predictive regression equations to estimate prey fish total length, fork length, and weight for ten fish species. Original fish size is estimated from four external morphometric measurements including maximum body depth, eye diameter, caudal peduncle depth, and pectoral-fin length, as well as from length measurements of three diagnostic bones: the opercle, the cleithrum, and the dentary. The prey species used here include several of commercial and recreational importance and commonly occur in the diets of marine piscivores in the Northwest Atlantic, representing approximately 52% of the total fish prey consumed by piscivorous fishes during 1973–90 (Grosslein et al., 1980; Langton and Bowman, 1981).[2] We also identify and describe the unique characteristics of the three diagnostic bones for each fish species and assess their potential value as tools for field identification of prey fishes recovered from predator stomachs.

## Materials and methods

Over 700 fish representing ten species in five families ranging in size from 52 to 340 millimeters (mm) total length (TL) were measured and dissected (Table 1). Fish were collected as part of Food Chain Dynamics Investigation (FCDI) (NEFSC, NMFS) research cruises conducted on Georges Bank during June and August of 1995 and 1996. FCDI research cruises were sponsored through the National Oceanic and Atmospheric Administration Coastal Ocean Program-Georges Bank Predation Study. Fish were also collected from waters off the Northeast U.S. coast during September and October of 1996 as part of the NEFSC Fall bottom trawl surveys. Additional fish were collected by personnel from the Massachusetts Division of Marine Fisheries as part of a coastal trawling survey conducted in May and September of 1996. All fish were immediately frozen until they could be returned to the laboratory. In the laboratory, fish were thawed and weighed wet to the near-

[1] Rountree, R. A. 1997. Food Chain Dynamics Investigation (FCDI). Northeast Fisheries Science Center (NEFSC), National Marine Fisheries Service (NMFS), 166 Water St., Woods. Hole, MA 02543. Personal commun.

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**Table 1**

Family, species, number ($n$), and size range (total length in millimeters) of prey fishes used to construct predictive equations.

| Family | Species | Common name | $n$ | Size range |
|---|---|---|---|---|
| Clupeidae | *Alosa pseudoharengus* | Alewife | 137 | 73–282 |
| | *Alosa aestivalis* | Blueback herring | 38 | 83–134 |
| | *Clupea harengus* | Atlantic herring | 84 | 97–269 |
| Scombridae | *Scomber scombrus* | Atlantic mackerel | 56 | 158–330 |
| Stromateidae | *Peprilus triacanthus* | Butterfish | 108 | 54–193 |
| Ammodytidae | *Ammodytes dubius* | Sand lance | 75 | 109–209 |
| Gadidae | *Urophycis chuss* | Red hake | 45 | 108–340 |
| | *Merluccius bilinearis* | Silver hake | 95 | 75–300 |
| | *Melanogrammus aeglefinus* | Haddock | 47 | 79–202 |
| | *Gadus morhua* | Atlantic cod | 31 | 52–140 |

est 0.01 gram (g) before external measurements were completed to the nearest 0.01 mm with digital calipers. To remove diagnostic bones, fish were placed in boiling water for 30–90 seconds, depending on fish size. Bones were then extracted from the soft tissue and measured to the nearest 0.025 mm with an ocular micrometer (2.75×).

Least squares regression equations (StataCorp., 1995) were generated to predict original total length, fork length, and weight from measurements of body depth, eye diameter, caudal peduncle depth, pectoral-fin length, opercle length, cleithrum length, and dentary length. The left eye, left pectoral fin, and diagnostic bones from the left side of each fish were used consistently unless damaged. Body depth was measured as the maximum linear dorsoventral distance with fins depressed. Eye diameter was measured horizontally along the anteroposterior axis. Caudal peduncle depth was measured dorsoventrally. Pectoral-fin length was measured from the anterior most point of fin insertion to the tip of the longest fin ray. Opercle length was measured as the maximum linear dorsoventral distance, usually from the dorsal most point to the tip of the primary ray (Fig. 1). Cleithrum length was measured from the tip of the dorsal process to the tip of the ventral process (Fig. 2). Dentary length was defined as the maximum linear anteroposterior distance from the symphyseal margin located anteriorly between the left and right dentaries to the posterior tip of the dorsal or ventral process, whichever was longer (Fig. 3). A series of least squares regression equations to predict fish weight from total or fork length for each species was also generated. To further assess the strength of individual bivariate relationships, mean percent prediction errors (Smith, 1980) were determined for each regression by averaging the percent prediction error calculated for each observation as

$$[(Observed - Predicted) / Predicted] \times 100.$$

Forward and backward stepwise linear regressions (StataCorp., 1995) were performed in an attempt to identify the best set of predictor variables. To ensure that all variables in the stepwise model were individually significant, the value of the $F$-statistic used to determine variable inclusion was set at four (Draper and Smith, 1981).

Opercles, cleithra, and dentaries were also carefully examined to identify distinguishing characteristics that may be potentially useful for identification of each fish species. Several features of each bone were examined for differences among species, including the general shape of each bone; the numbers and orientation of ridges on the opercle and the curvature of opercle margins; the numbers, sizes, and shapes of cleithrum processes; and the presence or absence of teeth on the dentary, with attention given to overall tooth size, shape, and orientation, as well as the shapes and relative lengths of dentary processes.

## Results

### Predictive equations

Regressions relating external morphological measurements to total and fork length were all highly significant ($P<0.0001$), with $r^2$ values ranging from 0.63 to 0.99 and mean percent prediction errors ranging from 2.68 to 10.83 (Table 2). Regressions from measurements of eye diameter to predict original fish length were typically more variable than those from other external measurements. This was likely due to measurement error associated with damage of the soft adipose tissue surrounding the eye incurred during the freezing and thawing processes. Regressions relating diagnostic bone measurements to total and fork length were also highly significant ($P<0.0001$), with $r^2$ values ranging from 0.81 to 0.99 and mean percent prediction errors ranging from 1.26 to 8.48 (Table 3). Compared with regressions from external morphological measurements, variation in diagnostic bone measurements typically explained more of the variation in original fish length (94% of $r^2$ values >0.90) and bones were generally more precise in predicting fish length (87% of mean %PEs < 5.00). Stepwise linear regressions indicated that cleithrum length was the most consistent predictor of original fish length and it was included in the best set of predictor variables for 8 of 10 species (Table 4). Pectoral-fin length was included in the best set of predictors for 6 species, whereas dentary length was included for 5 species. The remaining independent variables were included in the best set of predictors for either 3 or 4 species, respectively.

Regressions relating external morphological measurements and diagnostic bone measurements to fish weight were also each highly significant ($P<0.0001$), with $r^2$ values ranging from 0.71 to 0.99 (Table 5). Mean percent prediction errors for regressions predicting fish weight ranged from 5.97 to 39.17. These were typically higher compared with prediction errors for regressions predicting fish length, indicating that estimates of original fish length were more precise than estimates of original prey weight. Similar to length regressions, diagnostic bone measurements yielded higher $r^2$ values and lower mean percent prediction errors when regressed against fish weight compared with external morphological mea-

surements. Stepwise linear regressions indicated that body depth, caudal peduncle depth, and cleithrum length were the most consistent predictors of original fish weight and were included in the best set of predictor variables for 8, 9, and 8 species, respectively (Table 6). Pectoral-fin length was included in the best set of predictor variables for 5 species, whereas opercle length was included for 3 species. Dentary length and eye diameter appeared to be the least consistent predictors of fish weight and were included in the best set of predictor variables for 1 and 0 of the species, respectively. Lastly, measurements of total and fork length were significantly related to total weight for each species ($P<0.0001$) with

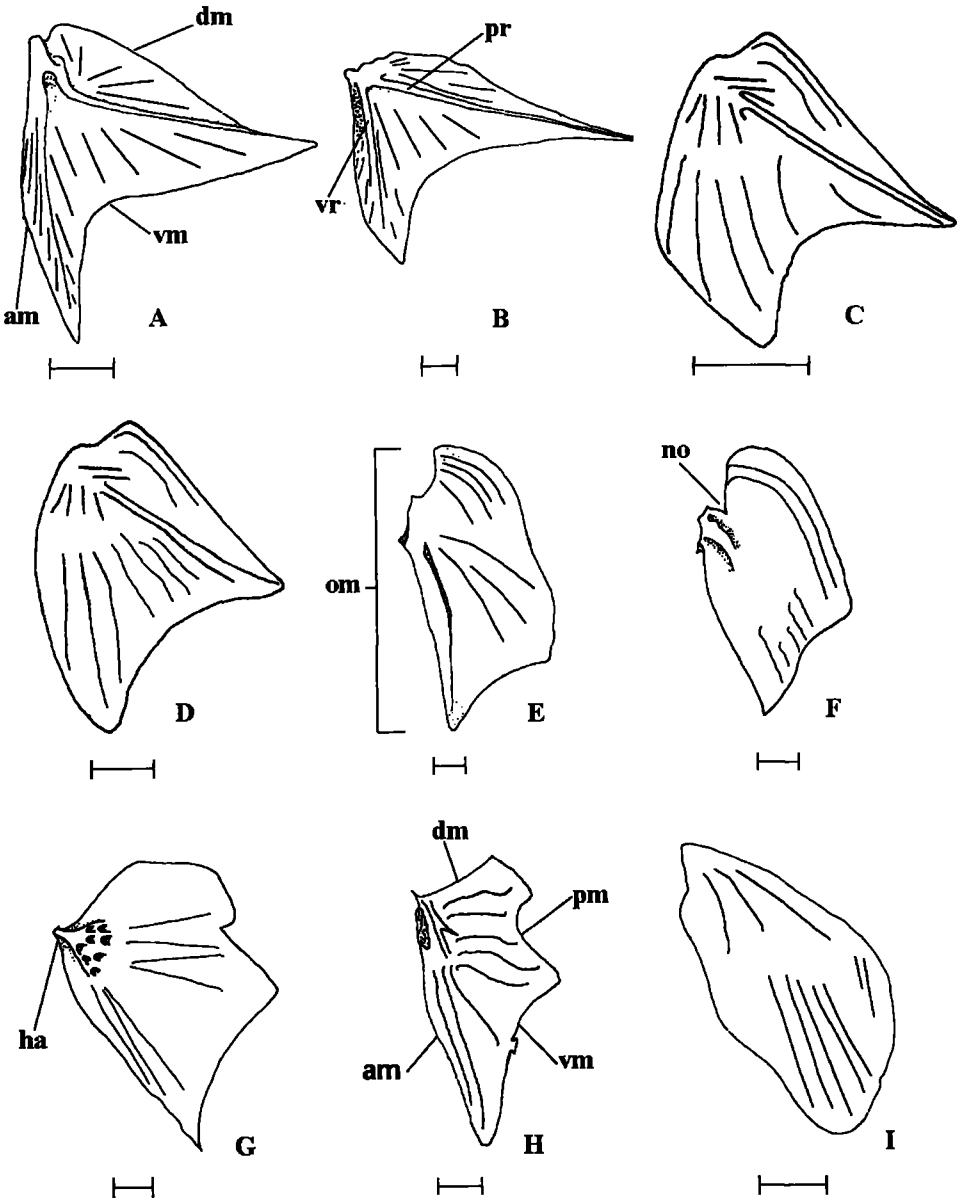


**Figure 1**

Left opercles from nine species of marine fishes in the Northwest Atlantic: (**A**) silver hake; (**B**) red hake; (**C**) Atlantic cod; (**D**) haddock; (**E**) alewife; (**F**) Atlantic herring; (**G**) Atlantic mackerel; (**H**) butterfish; (**I**) sand lance. Opercles are presented in lateral view. Abbreviations: dm = dorsal margin; vm = ventral margin; am = anterior margion; pr = posterior ridge; vr = ventral ridge; om = opercular measurement; no = notch; ha = hyomandibular articulation site; pm = posterior margin; . Scale bars = 2.0 mm.

$r^2$ values typically greater than 0.95 and mean percent prediction errors generally less than 10% (Table 7).

## Diagnostic bones

For each of the bones examined here, clear differences in diagnostic features exist among family taxa. Distinguishing bone characteristics were also evident among genera within the families Gadidae and Clupeidae. Differences between two species from the same genus (*Alosa*) were, however, difficult to discern from the three bones used here. Therefore, bone illustrations are presented for only nine species, with alewife, rather than blueback herring, representing the genus *Alosa*.

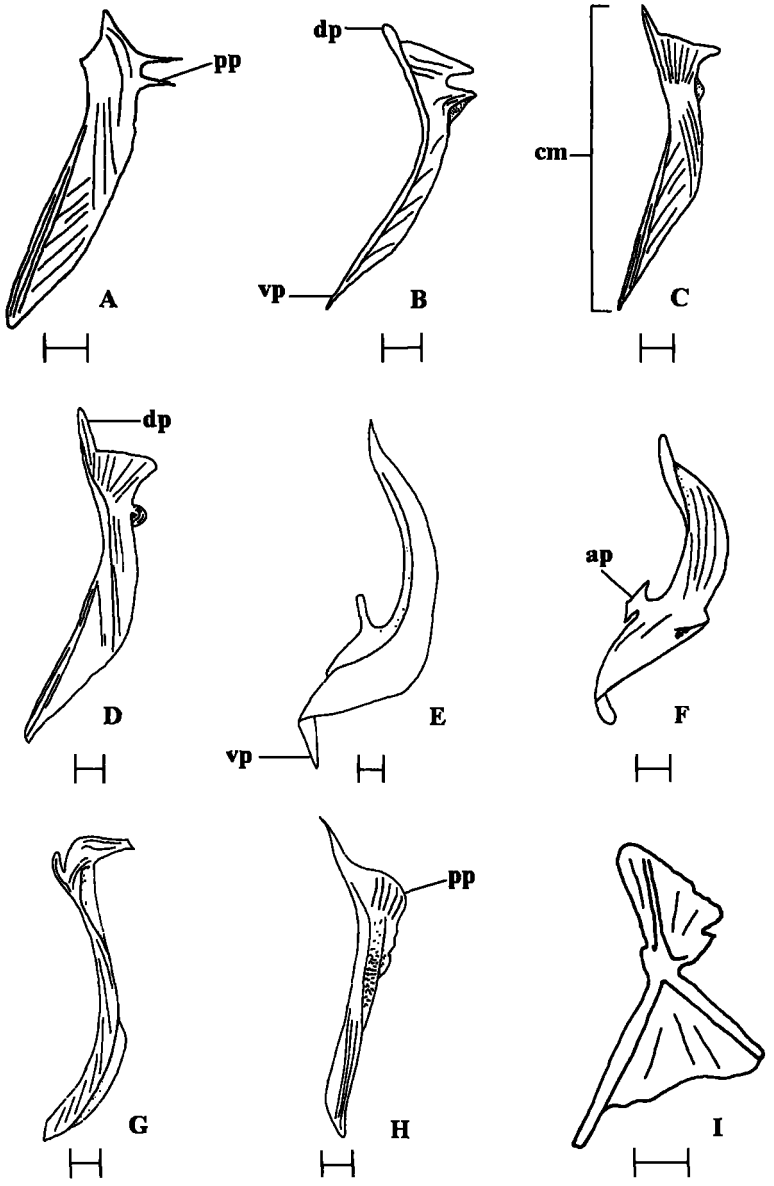


**Figure 2**

Left cleithra from nine species of marine fishes in the Northwest Atlantic: (**A**) silver hake; (**B**) red hake; (**C**) Atlantic cod; (**D**) haddock; (**E**) alewife; (**F**) Atlantic herring; (**G**) Atlantic mackerel; (**H**) butterfish; (**I**) sand lance. Cleithra are presented in lateral view. Abbreviations: pp = posterior process; dp = dorsal process; vp = ventral process; cm = cleithrum measurement; ap = anterior process; Scale bars = 2.0 mm.

## Opercles

The opercle is the largest and most dorsal bone in the opercular series, which consists of the opercle, the subopercle, and the interopercle. Together, these three bones provide the skeletal support for the muscular operculum, or gill cover in fishes. The opercle articulates with the opercular process of the hyomandibula. The articulation site is located in the anterodorsal region of the opercle, and represents a consistent morphological feature for orientation of the bone during examination. The opercles of the fishes examined here can be differentiated by two major diagnostic characteristics. First, the general shape of the opercle is clearly unique to several of the families examined. The opercles of some families share a general triangular shape with three well-defined margins, whereas others are not triangular and possess four definable margins. A second distinctive feature is the presence or absence of ridges originating at the site of hyomandibular articulation and extending ventrally or posteriorly along the margins of the opercle.

Of the taxa examined here, silver hake (*Merluccius bilinearis*) and red hake (*Urophycis chuss*) have opercles with the most pronounced triangular shape and three clearly defined margins (Fig. 1, A and B). The hake opercles are further distinguished by the presence of two prominent ridges originating at the site of hyomandibular articulation and extending ventrally and posteriorly along the anterior and dorsal margins, respectively. Hake opercles differ

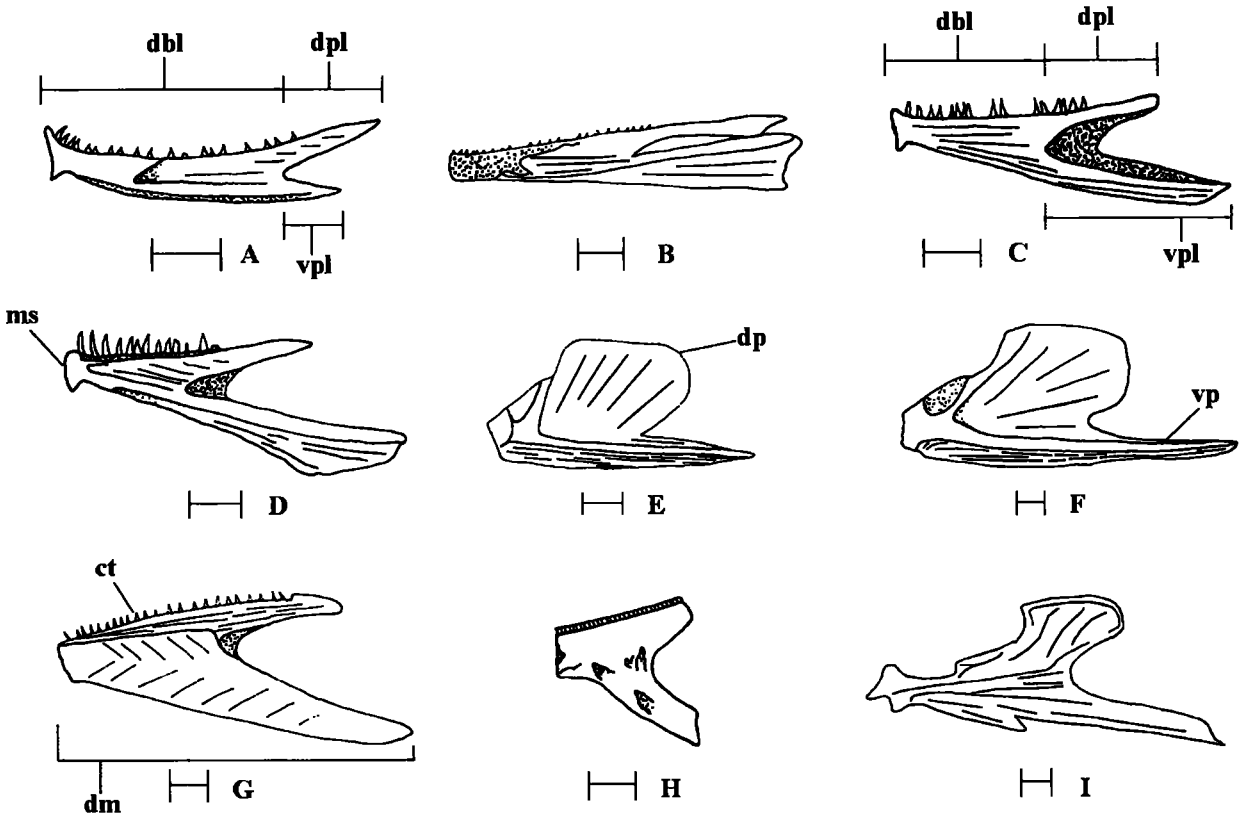


**Figure 3**

Left dentaries from nine species of marine fishes in the Northwest Atlantic: (**A**) silver hake; (**B**) red hake; (**C**) Atlantic cod; (**D**) haddock; (**E**) alewife; (**F**) Atlantic herring; (**G**) Atlantic mackerel; (**H**) butterfish; (**I**) sand lance. Dentaries are presented in lateral view. Abbreviations: dbl = dentary body length; dpl = dorsal process length; vpl = ventral process length; ms = mandibular symphysis; dp = dorsal process; vp = ventral process; ct = conical teeth; dm = dentary measurement. Scale bars = 2.0 mm.

slightly because the posterior region of the red hake opercle is longer in relation to the body of the opercle than that of silver hake and is also narrower, ending in a sharper point in contrast with the opercle of silver hake. The opercles of Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) share a general triangular shape with the hakes, although it is less pronounced in cod and haddock (Fig. 1, C and D). Opercles of Atlantic cod and haddock can be further separated from hake opercles by the presence of only one prominent ridge, which extends posteriorly from the site of hyomandibular attachment, rather than the two ridges found in hake. There appear to be no consistent, observable differences between the opercles of Atlantic cod and haddock. The opercles of alewife (*Alosa pseudoharengus*) and Atlantic herring (*Clupea harengus*) are not triangular and have a distinct notch that is dorsal to the site of hyomandibular articulation along the dorsal margin, with a pronounced curvature along the posterior margin (Fig. 1, E and F). The opercles of alewife and Atlantic herring each possess one ridge, extending ventrally from the site of hyomandibular articulation along the anterior margin, and each also has four definable margins. Alewife and Atlantic herring opercles differ mainly in the shape of the dorsal notch—the notch being cup-shaped in alewife, compared with v-shaped in Atlantic herring. In Atlantic mackerel (*Scomber scombrus*), the opercle has a pronounced dorsal curvature with a notch located centrally along the posterior margin (Fig. 1G). The ridge extending from the hyomandibular articulation site is unique to Atlantic mackerel in that it branches out broadly as it extends posteriorly from the articulation site. The opercles of butterfish (*Peprilus triacanthus*) are unique in general shape, resembling a butterfly wing, with four clearly defined margins and a ridge extending ventrally from the hyomandibular articulation site along the anterior margin (Fig. 1H). Sand lance (*Ammodytes dubius*) represent the only species examined here with opercles not possessing ridges along any margins. Sand lance opercles also

**Table 2**

Least squares regression equations relating measurements of body depth (BD), eye diameter (ED), caudal peduncle depth (CP), and pectoral–fin length (PF) to total length (TL) and fork length (FL) for ten prey species in the Northwest Atlantic. All measurements are in millimeters. $s_b$ = standard error of the regression coefficient; $r^2$ = coefficient of determination; %PE = mean percent prediction error; $n$ = number of fish measured; Range = size range in total length. Fork lengths were not measured for red hake, silver hake, or Atlantic cod.

| | Total length | | | | Fork length | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Species | Equation | $s_b$ | $r^2$ | %PE | Equation | $s_b$ | $r^2$ | %PE | $n$ | Range |
| Alewife | $TL = 3.881BD + 11.012$ | 0.073 | 0.95 | 4.38 | $FL = 3.469BD + 10.856$ | 0.067 | 0.98 | 4.04 | 137 | 73–282 |
| | $TL = 24.906ED - 61.344$ | 0.781 | 0.88 | 7.30 | $FL = 23.335ED - 57.728$ | 0.562 | 0.96 | 6.13 | 137 | 73–282 |
| | $TL = 12.876CP - 1.784$ | 0.182 | 0.97 | 3.53 | $FL = 11.348CP + 1.313$ | 0.163 | 0.99 | 3.31 | 137 | 73–282 |
| | $TL = 6.840PF + 0.532$ | 0.100 | 0.99 | 3.15 | $FL = 5.982PF + 1.785$ | 0.093 | 0.98 | 3.34 | 66 | 73–282 |
| Blueback herring | $TL = 4.970BD + 1.439$ | 0.268 | 0.91 | 3.59 | $FL = 4.620BD - 1.573$ | 0.246 | 0.91 | 3.66 | 38 | 83–134 |
| | $TL = 25.318ED - 35.605$ | 2.117 | 0.80 | 5.33 | $FL = 23.792ED - 37.352$ | 1.865 | 0.82 | 5.42 | 38 | 83–134 |
| | $TL = 13.684CP + 0.194$ | 0.752 | 0.90 | 3.53 | $FL = 12.585CP - 1.782$ | 0.754 | 0.89 | 4.06 | 38 | 83–134 |
| | $TL = 7.760PF + 2.935$ | 0.383 | 0.92 | 3.58 | $FL = 7.198PF - 0.005$ | 0.358 | 0.92 | 3.79 | 38 | 83–134 |
| Atlantic herring | $TL = 4.561BD + 27.341$ | 0.089 | 0.97 | 4.22 | $FL = 4.036BD + 26.880$ | 0.081 | 0.97 | 4.17 | 84 | 97–295 |
| | $TL = 26.717ED - 51.235$ | 0.594 | 0.96 | 5.08 | $FL = 23.633ED - 42.586$ | 0.537 | 0.96 | 5.00 | 84 | 97–295 |
| | $TL = 16.303CP - 17.288$ | 0.296 | 0.97 | 4.55 | $FL = 14.441CP - 12.792$ | 0.257 | 0.97 | 4.35 | 84 | 97–295 |
| | $TL = 7.507PF + 1.533$ | 0.101 | 0.99 | 2.68 | $FL = 6.631PF + 4.306$ | 0.102 | 0.98 | 2.95 | 84 | 97–295 |
| Atlantic mackerel | $TL = 5.203BD + 37.203$ | 0.122 | 0.97 | 3.67 | $FL = 4.641BD + 39.790$ | 0.118 | 0.97 | 3.89 | 56 | 158–330 |
| | $TL = 33.706ED - 81.239$ | 3.027 | 0.70 | 10.83 | $FL = 30.404ED - 68.847$ | 2.652 | 0.71 | 10.28 | 56 | 158–330 |
| | $TL = 40.081CP - 0.837$ | 0.700 | 0.98 | 2.78 | $FL = 35.874CP + 5.213$ | 0.592 | 0.99 | 2.61 | 56 | 158–330 |
| | $TL = 9.037PF - 1.242$ | 0.178 | 0.98 | 3.02 | $FL = 8.068PF + 5.346$ | 0.172 | 0.98 | 3.06 | 56 | 158–330 |
| Butterfish | $TL = 2.860BD + 1.650$ | 0.038 | 0.98 | 3.32 | $FL = 2.384BD + 5.638$ | 0.034 | 0.98 | 3.57 | 108 | 54–193 |
| | $TL = 20.065ED - 21.148$ | 0.635 | 0.90 | 7.48 | $FL = 16.700ED - 13.166$ | 0.544 | 0.90 | 7.52 | 108 | 54–193 |
| | $TL = 17.960CP + 7.962$ | 0.290 | 0.97 | 3.57 | $FL = 14.950CP + 11.046$ | 0.264 | 0.97 | 4.03 | 108 | 54–193 |
| | $TL = 3.766PF + 15.966$ | 0.060 | 0.98 | 4.33 | $FL = 3.126PF + 18.121$ | 0.064 | 0.98 | 5.54 | 63 | 54–193 |
| Sand lance | $TL = 7.308BD + 58.774$ | 0.455 | 0.78 | 6.07 | $FL = 7.045BD + 57.497$ | 0.463 | 0.76 | 6.16 | 75 | 109–209 |
| | $TL = 49.467ED - 45.022$ | 4.358 | 0.64 | 8.29 | $FL = 47.921ED - 43.479$ | 4.313 | 0.63 | 8.45 | 75 | 109–209 |
| | $TL = 35.928CP + 8.185$ | 1.562 | 0.88 | 4.32 | $FL = 34.923CP + 7.599$ | 1.575 | 0.87 | 4.48 | 75 | 109–209 |
| | $TL = 14.993PF - 31.272$ | 0.934 | 0.78 | 6.52 | $FL = 14.542PF - 30.374$ | 0.933 | 0.77 | 6.75 | 75 | 109–209 |
| Red hake | $TL = 6.398BD + 10.340$ | 0.210 | 0.96 | 7.40 | | | | | 45 | 108–340 |
| | $TL = 28.474ED - 91.519$ | 0.860 | 0.96 | 6.37 | | | | | 45 | 108–340 |
| | $TL = 26.384CP - 17.165$ | 0.627 | 0.98 | 5.18 | | | | | 45 | 108–340 |
| | $TL = 6.885PF - 0.693$ | 0.146 | 0.98 | 3.92 | | | | | 45 | 108–340 |
| Silver hake | $TL = 6.460BD + 18.219$ | 0.164 | 0.94 | 7.00 | | | | | 95 | 75–300 |
| | $TL = 21.998ED - 31.654$ | 0.504 | 0.95 | 7.05 | | | | | 95 | 75–300 |
| | $TL = 22.823CP + 22.881$ | 0.345 | 0.98 | 4.63 | | | | | 95 | 75–300 |
| | $TL = 4.946PF + 20.269$ | 0.070 | 0.99 | 3.36 | | | | | 60 | 75–300 |
| Haddock | $TL = 4.199BD + 21.964$ | 0.173 | 0.93 | 5.30 | $FL = 4.066BD + 19.660$ | 0.164 | 0.93 | 4.83 | 47 | 79–202 |
| | $TL = 20.069ED - 35.473$ | 1.375 | 0.83 | 7.97 | $FL = 19.525ED - 36.724$ | 1.291 | 0.84 | 7.87 | 47 | 79–202 |
| | $TL = 18.465CP + 16.596$ | 0.699 | 0.94 | 4.90 | $FL = 17.922CP + 14.205$ | 0.638 | 0.95 | 4.54 | 47 | 79–202 |
| | $TL = 7.367PF - 10.712$ | 0.260 | 0.95 | 4.69 | $FL = 7.106PF - 11.430$ | 0.263 | 0.94 | 4.90 | 47 | 79–202 |
| Atlantic cod | $TL = 4.249BD + 21.367$ | 0.133 | 0.97 | 4.03 | | | | | 31 | 52–140 |
| | $TL = 19.393ED - 19.490$ | 1.053 | 0.92 | 7.33 | | | | | 31 | 52–140 |
| | $TL = 17.999CP + 9.806$ | 0.480 | 0.98 | 3.72 | | | | | 31 | 52–140 |
| | $TL = 6.728PF + 7.681$ | 0.185 | 0.98 | 3.48 | | | | | 31 | 52–140 |

possess only two clearly definable margins and are curved along the entire posterior margin (Fig. 1I).

## Cleithra

In higher teleost fishes, the cleithrum is the ventral most bone of the pectoral girdle, which consists of the supracleithrum, the cleithrum, and the postcleithrum. The cleithrum attaches directly to the scapulocoracoid, which articulates with the base of the pectoral fin. Together, the left and right cleithra form the frame of the body wall directly posterior to the branchial cavity. The cleithra of the fishes examined here can be differentiated by their general shape as

well as the numbers, locations, and shapes of the processes. The majority of the cleithra described here have a gently sloping curvature along the dorsoventral axis, whereas others are clearly more sharply curved. Most families examined here possess cleithra with dorsal and ventral processes that end sharply; others possess varying numbers and shapes of posterior and anterior processes.

The cleithra of silver hake and red hake are gently curved along the dorsoventral axis and each has two posterior processes located directly ventral to the dorsal process (Fig. 2, A and B). The ventral process of the red hake ends in a sharper point and is not as broad as that of silver hake, and the posterior processes are broader than those of silver hake. Atlantic cod and haddock have gently curved cleithra with a general shape similar to that of the cleithra of silver and red hake (Fig. 2, C and D). However, the cleithra of Atlantic cod and haddock contain only one posterior process that is broader than the posterior processes of the hake cleithra, and the dorsal processes of Atlantic cod and haddock cleithra end sharply and are much more pronounced than those of the hake cleithra. The main difference between the cleithra of Atlantic cod and haddock is in the shape of the posterior process; the process is distinctly more hook-shaped in Atlantic cod than in haddock. The cleithra of alewife and Atlantic herring are each sharply curved and possess an anterior process located medially along the dorsoventral axis, which is

**Table 3**

Least squares regression equations relating measurements of opercle length (OP), cleithrum length (CL), and dentary length (DN) to total length (TL) and fork length (FL) for ten prey species in the Northwest Atlantic. All measurements are in millimeters. $s_b$ = standard error of the regression coefficient; $r^2$ = coefficient of determination; %PE = mean percent prediction error; $n$ = number of fish measured; Range = size range in total length. Fork lengths were not measured for red hake, silver hake, or Atlantic cod.

| | Total length | | | | Fork length | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Species | Equation | $s_b$ | $r^2$ | %PE | Equation | $s_b$ | $r^2$ | %PE | $n$ | Range |
| Alewife | $TL = 9.851OP - 1.119$ | 0.126 | 0.99 | 2.80 | $FL = 8.617OP + 0.307$ | 0.118 | 0.99 | 3.15 | 66 | 73–282 |
| | $TL = 7.115CL - 3.450$ | 0.097 | 0.99 | 2.80 | $FL = 6.217CL - 1.579$ | 0.097 | 0.98 | 3.22 | 66 | 73–282 |
| | $TL = 11.610DN - 23.205$ | 0.163 | 0.99 | 3.23 | $FL = 10.144DN - 18.824$ | 0.163 | 0.98 | 3.74 | 66 | 73–282 |
| Blueback herring | $TL = 10.014OP + 6.641$ | 0.547 | 0.90 | 3.07 | $FL = 9.198OP + 4.259$ | 0.555 | 0.88 | 3.46 | 38 | 83–134 |
| | $TL = 7.491CL + 0.161$ | 0.354 | 0.93 | 3.09 | $FL = 6.893CL - 1.863$ | 0.362 | 0.91 | 3.40 | 38 | 83–134 |
| | $TL = 11.743DN - 11.125$ | 0.653 | 0.90 | 2.96 | $FL = 10.871DN - 12.840$ | 0.621 | 0.90 | 3.04 | 38 | 83–134 |
| Atlantic herring | $TL = 11.732OP - 0.427$ | 0.168 | 0.99 | 2.30 | $FL = 10.405OP + 2.028$ | 0.168 | 0.98 | 2.65 | 71 | 97–269 |
| | $TL = 8.752CL - 10.804$ | 0.126 | 0.99 | 2.19 | $FL = 7.771CL - 7.353$ | 0.117 | 0.98 | 2.41 | 71 | 97–269 |
| | $TL = 10.692DN - 17.263$ | 0.180 | 0.98 | 3.02 | $FL = 9.495DN - 13.112$ | 0.164 | 0.98 | 3.10 | 71 | 97–269 |
| Atlantic mackerel | $TL = 11.114OP + 0.379$ | 0.179 | 0.99 | 2.01 | $FL = 9.867OP + 7.462$ | 0.163 | 0.99 | 2.06 | 44 | 158–330 |
| | $TL = 7.789CL - 6.990$ | 0.067 | 0.99 | 1.26 | $FL = 6.916CL + 0.889$ | 0.062 | 0.99 | 1.27 | 44 | 158–330 |
| | $TL = 12.564DN - 30.649$ | 0.212 | 0.99 | 2.53 | $FL = 11.148DN - 19.970$ | 0.201 | 0.99 | 2.44 | 44 | 158–330 |
| Butterfish | $TL = 7.956OP + 5.184$ | 0.299 | 0.92 | 7.64 | $FL = 6.598OP + 9.279$ | 0.266 | 0.91 | 8.48 | 63 | 54–193 |
| | $TL = 5.583CL - 27.802$ | 0.091 | 0.98 | 3.23 | $FL = 4.653CL - 18.698$ | 0.081 | 0.98 | 3.43 | 63 | 54–193 |
| | $TL = 13.643DN + 6.884$ | 0.484 | 0.93 | 7.49 | $FL = 11.309DN + 10.725$ | 0.436 | 0.92 | 8.25 | 63 | 54–193 |
| Sand lance | $TL = 18.903OP + 25.655$ | 1.042 | 0.82 | 5.46 | $FL = 18.352OP + 24.729$ | 1.044 | 0.81 | 5.60 | 75 | 109–209 |
| | $TL = 18.487CL - 1.156$ | 0.719 | 0.90 | 3.81 | $FL = 17.938CL - 1.228$ | 0.741 | 0.89 | 4.12 | 75 | 109–209 |
| | $TL = 20.785DN - 33.880$ | 0.772 | 0.91 | 3.89 | $FL = 20.300DN - 34.146$ | 0.752 | 0.91 | 3.92 | 75 | 109–209 |
| Red hake | $TL = 27.956OP - 4.679$ | 0.612 | 0.98 | 4.53 | | | | | 45 | 108–340 |
| | $TL = 9.061CL - 12.185$ | 0.123 | 0.99 | 2.81 | | | | | 45 | 108–340 |
| | $TL = 13.870DN - 11.769$ | 0.291 | 0.98 | 4.37 | | | | | 45 | 108–340 |
| Silver hake | $TL = 17.666OP - 11.964$ | 0.212 | 0.99 | 3.20 | | | | | 60 | 75–300 |
| | $TL = 7.875CL - 5.271$ | 0.071 | 0.99 | 2.57 | | | | | 60 | 75–300 |
| | $TL = 8.427DN - 5.149$ | 0.087 | 0.99 | 2.63 | | | | | 60 | 75–300 |
| Haddock | $TL = 23.040OP - 15.425$ | 1.053 | 0.91 | 5.52 | $FL = 22.351OP - 16.804$ | 0.984 | 0.92 | 4.78 | 47 | 79–202 |
| | $TL = 6.567CL - 2.688$ | 0.176 | 0.97 | 3.25 | $FL = 6.215CL - 1.202$ | 0.258 | 0.93 | 4.87 | 47 | 79–202 |
| | $TL = 12.348DN - 3.688$ | 0.496 | 0.93 | 5.07 | $FL = 11.680DN - 2.075$ | 0.606 | 0.89 | 6.29 | 47 | 79–202 |
| Atlantic cod | $TL = 19.019OP + 7.733$ | 0.705 | 0.96 | 5.43 | | | | | 31 | 52–140 |
| | $TL = 6.590CL + 1.118$ | 0.101 | 0.99 | 2.50 | | | | | 31 | 52–140 |
| | $TL = 10.458DN - 5.592$ | 0.181 | 0.99 | 2.29 | | | | | 31 | 52–140 |

unique among the fishes examined here (Fig. 2, E and F). The shape of the anterior process differs between the two genera of Clupeidae. In alewife, the anterior process is sickle-shaped, whereas in Atlantic herring, the anterior process is more symmetrical, resembling a mushroom. Additionally, the tip of the ventral process is distinctly sharper in the cleithrum of alewife than in the cleithrum of Atlantic herring. Atlantic mackerel cleithra are gently curved and relatively thin and one posterior process is located in the extreme dorsal region of the bone (Fig. 2G). The dorsal process of the Atlantic mackerel cleithrum is relatively small and rounded, whereas the ventral process is broad and does not end sharply as in the cleithra of the gadids. The cleithra of butterfish are only slightly curved along the dorsoventral axis and contain a broad, rounded posterior process. Butterfish cleithra can be distinguished among the families examined here by the presence of a distinctly sharp, thin dorsal process (Fig. 2H). The cleithra of sand lance have a general

**Table 4**

Independent variables included in stepwise multiple regression models estimating original fish length. Abbreviations for independent variables are those given in Tables 2 and 3. * indicates that forward and backward models were not identical.

| Species | Variables included in forward stepwise model | Variables included in backward stepwise model |
|---|---|---|
| Alewife | CP, PF, OP, CL | CP, PF, OP, CL |
| Blueback herring | PF, CL | PF, CL |
| Atlantic herring | BD, PF, OP, DN | BD, PF, OP, DN |
| Atlantic mackerel* | CL, DN | CL |
| Butterfish* | BD, CP, PF, CL | ED, CP, PF, CL |
| Sand Lance | CP, DN | CP, DN |
| Red hake | BD, ED, CL | BD, ED, CL |
| Silver hake* | OP, CL, DN | CL |
| Haddock | ED, CP, PF, CL | ED, CP, PF, CL |
| Atlantic cod | BD, PF, CL, DN | BD, PF, CL, DN |

**Table 5**

Least squares regression equations relating measurements (in millimeters) of body depth (BD), eye diameter (ED), caudal peduncle depth (CP), pectoral fin length (PF), opercle length (OP), cleithrum length (CL), and dentary length (DN) to total weight (W) in grams for ten prey species in the Northwest Atlantic. $s_b$ = standard error of the regression coefficient; $r^2$ = coefficient of determination; %PE = mean percent prediction error; $n$ = number of fish measured; Range = size range in total length.

| Species | Equation | $s_b$ | $r^2$ | %PE | $n$ | Range |
|---|---|---|---|---|---|---|
| Alewife | $W = 0.73 \times 10^{-3} BD^{2.940}$ | 0.041 | 0.97 | 10.74 | 137 | 73–282 |
| | $W = 2.62 \times 10^{-3} ED^{4.305}$ | 0.133 | 0.89 | 24.00 | 137 | 73–282 |
| | $W = 10.18 \times 10^{-3} CP^{3.194}$ | 0.037 | 0.98 | 8.87 | 137 | 73–282 |
| | $W = 1.25 \times 10^{-3} PF^{3.229}$ | 0.053 | 0.98 | 11.31 | 66 | 73–282 |
| | $W = 2.95 \times 10^{-3} OP^{3.331}$ | 0.052 | 0.98 | 11.73 | 66 | 73–282 |
| | $W = 0.81 \times 10^{-3} CL^{3.383}$ | 0.051 | 0.99 | 10.65 | 66 | 73–282 |
| | $W = 1.05 \times 10^{-3} DN^{3.739}$ | 0.055 | 0.99 | 10.66 | 66 | 73–282 |
| Blueback herring | $W = 0.64 \times 10^{-3} BD^{3.066}$ | 0.103 | 0.96 | 6.83 | 38 | 83–134 |
| | $W = 6.68 \times 10^{-3} ED^{4.049}$ | 0.340 | 0.80 | 15.73 | 38 | 83–134 |
| | $W = 13.80 \times 10^{-3} CP^{3.061}$ | 0.154 | 0.92 | 9.48 | 38 | 83–134 |
| | $W = 3.94 \times 10^{-3} PF^{2.903}$ | 0.158 | 0.90 | 9.88 | 38 | 83–134 |
| | $W = 10.40 \times 10^{-3} OP^{2.851}$ | 0.160 | 0.90 | 9.84 | 38 | 83–134 |
| | $W = 2.38 \times 10^{-3} CL^{3.027}$ | 0.139 | 0.93 | 8.15 | 38 | 83–134 |
| | $W = 3.00 \times 10^{-3} DN^{3.383}$ | 0.201 | 0.89 | 9.96 | 38 | 83–134 |
| Atlantic herring | $W = 2.96 \times 10^{-3} BD^{2.734}$ | 0.033 | 0.99 | 8.64 | 84 | 97–295 |
| | $W = 7.14 \times 10^{-3} ED^{4.012}$ | 0.092 | 0.96 | 16.58 | 84 | 97–295 |
| | $W = 7.96 \times 10^{-3} CP^{3.438}$ | 0.060 | 0.98 | 11.81 | 84 | 97–295 |
| | $W = 3.76 \times 10^{-3} PF^{2.935}$ | 0.065 | 0.97 | 12.06 | 84 | 97–295 |
| | $W = 10.53 \times 10^{-3} OP^{3.030}$ | 0.063 | 0.97 | 10.01 | 71 | 97–295 |
| | $W = 2.20 \times 10^{-3} CL^{3.193}$ | 0.069 | 0.97 | 10.01 | 71 | 97–295 |
| | $W = 3.52 \times 10^{-3} DN^{3.210}$ | 0.084 | 0.96 | 12.87 | 71 | 97–295 |
| Atlantic mackerel | $W = 2.79 \times 10^{-3} BD^{2.884}$ | 0.066 | 0.97 | 11.73 | 56 | 158–330 |
| | $W = 2.20 \times 10^{-3} ED^{4.762}$ | 0.377 | 0.75 | 39.17 | 56 | 158–330 |
| | $W = 247.52 \times 10^{-3} CP^{3.373}$ | 0.061 | 0.98 | 9.12 | 56 | 158–330 |
| | $W = 1.49 \times 10^{-3} PF^{3.399}$ | 0.078 | 0.97 | 12.07 | 56 | 158–330 |
| | $W = 3.90 \times 10^{-3} OP^{3.318}$ | 0.049 | 0.99 | 6.77 | 44 | 158–330 |

*continued*

butterfly shape that is clearly unique among the families examined here (Fig. 2I).

## Dentaries

The dentary is the largest bone of the lower jaw and bears teeth in many fishes. The posterior region of the dentary is attached directly to the angular and articular bones. The left and right dentaries are fused anteriorly at the mandibular symphysis. The dentaries of the fishes examined here can be differentiated by the presence or absence of teeth and by the relative lengths of the body of the dentary and the dorsal and ventral processes.

The dentaries of silver hake and red hake each possess a row of separate conical teeth extending slightly onto the dorsal process. Teeth are curved inwards and spaced relatively far apart (Fig. 3, A and B). The ratios of the lengths of the dorsal and ventral processes to the length of the body of the

**Table 5 (continued)**

| Species | Equation | $s_b$ | $r^2$ | %PE | $n$ | Range |
|---|---|---|---|---|---|---|
| Atlantic mackerel, continued | $W = 0.76 \times 10^{-3} CL^{3.419}$ | 0.048 | 0.99 | 5.97 | 44 | 158–330 |
| | $W = 0.99 \times 10^{-3} DN^{3.760}$ | 0.093 | 0.98 | 10.79 | 44 | 158–330 |
| Butterfish | $W = 0.18 \times 10^{-3} BD^{3.138}$ | 0.026 | 0.99 | 7.18 | 108 | 54–193 |
| | $W = 7.05 \times 10^{-3} ED^{4.076}$ | 0.113 | 0.92 | 24.59 | 108 | 54–193 |
| | $W = 94.11 \times 10^{-3} CP^{2.977}$ | 0.038 | 0.98 | 10.79 | 108 | 54–193 |
| | $W = 2.14 \times 10^{-3} PF^{2.795}$ | 0.039 | 0.99 | 10.55 | 63 | 54–193 |
| | $W = 3.94 \times 10^{-3} OP^{3.232}$ | 0.098 | 0.95 | 21.39 | 63 | 54–193 |
| | $W = 0.06 \times 10^{-3} CL^{3.905}$ | 0.056 | 0.99 | 10.83 | 63 | 54–193 |
| | $W = 25.57 \times 10^{-3} DN^{3.197}$ | 0.085 | 0.96 | 19.67 | 63 | 54–193 |
| Sand lance | $W = 35.99 \times 10^{-3} BD^{2.245}$ | 0.063 | 0.95 | 10.12 | 75 | 109–209 |
| | $W = 11.58 \times 10^{-3} ED^{4.925}$ | 0.372 | 0.71 | 20.83 | 75 | 109–209 |
| | $W = 95.52 \times 10^{-3} CP^{3.400}$ | 0.105 | 0.94 | 9.35 | 75 | 109–209 |
| | $W = 0.19 \times 10^{-3} PF^{4.366}$ | 0.274 | 0.78 | 20.26 | 75 | 109–209 |
| | $W = 34.61 \times 10^{-3} OP^{3.017}$ | 0.177 | 0.80 | 18.38 | 75 | 109–209 |
| | $W = 5.07 \times 10^{-3} CL^{3.618}$ | 0.111 | 0.94 | 9.84 | 75 | 109–209 |
| | $W = 0.93 \times 10^{-3} DN^{4.258}$ | 0.242 | 0.81 | 17.08 | 75 | 109–209 |
| Red hake | $W = 2.82 \times 10^{-3} BD^{2.865}$ | 0.129 | 0.92 | 23.72 | 45 | 108–340 |
| | $W = 1.26 \times 10^{-3} ED^{4.492}$ | 0.153 | 0.95 | 19.21 | 45 | 108–340 |
| | $W = 44.67 \times 10^{-3} CP^{3.286}$ | 0.091 | 0.97 | 15.93 | 45 | 108–340 |
| | $W = 1.23 \times 10^{-3} PF^{3.127}$ | 0.064 | 0.98 | 11.85 | 45 | 108–340 |
| | $W = 101.46 \times 10^{-3} OP^{3.073}$ | 0.077 | 0.97 | 13.48 | 45 | 108–340 |
| | $W = 1.58 \times 10^{-3} CL^{3.261}$ | 0.042 | 0.99 | 7.34 | 45 | 108–340 |
| | $W = 7.61 \times 10^{-3} DN^{3.193}$ | 0.080 | 0.97 | 13.75 | 45 | 108–340 |
| Silver hake | $W = 2.39 \times 10^{-3} BD^{2.971}$ | 0.053 | 0.97 | 18.47 | 95 | 75–300 |
| | $W = 3.11 \times 10^{-3} ED^{4.081}$ | 0.114 | 0.93 | 30.13 | 95 | 75–300 |
| | $W = 211.32 \times 10^{-3} CP^{2.647}$ | 0.037 | 0.98 | 13.88 | 95 | 75–300 |
| | $W = 2.47 \times 10^{-3} PF^{2.753}$ | 0.035 | 0.99 | 11.11 | 95 | 75–300 |
| | $W = 8.67 \times 10^{-3} OP^{3.458}$ | 0.044 | 0.99 | 11.54 | 95 | 75–300 |
| | $W = 0.84 \times 10^{-3} CL^{3.354}$ | 0.045 | 0.99 | 12.40 | 95 | 75–300 |
| | $W = 1.10 \times 10^{-3} DN^{3.343}$ | 0.043 | 0.99 | 11.61 | 95 | 75–300 |
| Haddock | $W = 2.60 \times 10^{-3} BD^{2.736}$ | 0.079 | 0.96 | 11.69 | 47 | 79–202 |
| | $W = 3.32 \times 10^{-3} ED^{4.078}$ | 0.289 | 0.82 | 25.98 | 47 | 79–202 |
| | $W = 103.33 \times 10^{-3} CP^{2.865}$ | 0.100 | 0.95 | 15.08 | 47 | 79–202 |
| | $W = 0.57 \times 10^{-3} PF^{3.523}$ | 0.123 | 0.95 | 14.97 | 47 | 79–202 |
| | $W = 23.77 \times 10^{-3} OP^{3.609}$ | 0.162 | 0.92 | 17.41 | 47 | 79–202 |
| | $W = 0.92 \times 10^{-3} CL^{3.296}$ | 0.085 | 0.97 | 11.11 | 47 | 79–202 |
| | $W = 7.16 \times 10^{-3} DN^{3.298}$ | 0.140 | 0.92 | 17.77 | 47 | 79–202 |
| Atlantic cod | $W = 4.89 \times 10^{-3} BD^{2.558}$ | 0.062 | 0.98 | 12.09 | 31 | 52–140 |
| | $W = 5.05 \times 10^{-3} ED^{4.042}$ | 0.233 | 0.91 | 25.68 | 31 | 52–140 |
| | $W = 67.74 \times 10^{-3} CP^{2.984}$ | 0.075 | 0.98 | 11.67 | 31 | 52–140 |
| | $W = 3.30 \times 10^{-3} PF^{2.987}$ | 0.078 | 0.98 | 12.21 | 31 | 52–140 |
| | $W = 73.85 \times 10^{-3} OP^{2.983}$ | 0.119 | 0.96 | 16.51 | 31 | 52–140 |
| | $W = 1.15 \times 10^{-3} CL^{3.273}$ | 0.052 | 0.99 | 6.96 | 31 | 52–140 |
| | $W = 2.48 \times 10^{-3} DN^{3.498}$ | 0.071 | 0.99 | 9.39 | 31 | 52–140 |

dentary of silver hake are much smaller relative to the same ratios for the red hake dentary. In addition, the teeth of red hake are much less prominent, and the ventral process of the dentary of red hake is considerably broader than that of silver hake. Similar to the dentaries of the hakes, the dentaries of Atlantic cod and haddock also possess a row of separate conical teeth that extend slightly farther onto the dorsal process (Fig. 3, C and D). The length of the dorsal process of the dentaries of Atlantic cod and haddock is much smaller than the length of the ventral process, which contrasts with the dentaries of the hakes. The dentaries of Atlantic cod and haddock can be distiguished by the teeth located just posterior to the mandibular symphysis; the teeth are longer in haddock than in Atlantic cod. Further, the ventral process is considerably broader in haddock than in Atlantic cod. The dentaries of alewife and Atlantic herring each consist of a long, slender ventral process that is considerably longer than the broadly expanded dorsal process, and are toothless (Fig. 3, E and F). The only noticeable difference between the dentaries of the alewife and Atlantic herring is a more gradual incline along the dorsal margin of the dorsal process and a slight hump located anteriorly in Atlantic herring. Similar to the dentaries of the gadids, Atlantic mackerel dentaries possess a row of separate conical teeth (Fig. 3G). However, the teeth of Atlantic mackerel extend well onto the dorsal process, are spaced relatively uniform distances apart, and are not curved inwards. The dentaries of butterfish possess a continuous row of separate teeth that are squared off at the tips, which is a unique feature among the fishes examined here (Fig. 3H). The ventral process of the butterfish dentary extends from the body of the dentary at a considerable angle. In sand lance, the dentaries have a long, thin ventral process that ends sharply and is much longer than the dorsal process, and are toothless (Fig. 3I). The dorsal process of the dentary of sand lance is curved along its margin, similar to the dorsal processes of the dentaries of alewife and Atlantic herring. However, the dorsal process of the dentary of sand lance is much less broad than that found in the dentaries of alewife and Atlantic herring.

**Table 6**

Independent variables included in stepwise multiple regression models estimating original fish weight. Abbreviations for independent variables are those given in Tables 2 and 3. * indicates that forward and backward models were not identical.

| Species | Variables included in forward stepwise model | Variables included in backward stepwise model |
|---|---|---|
| Alewife | BD, CP, CL | BD, CP, CL |
| Blueback herring | BD, CP, PF, CL | BD, CP, PF, CL |
| Atlantic herring | BD, CP, OP | BD, CP, OP |
| Atlantic mackerel | OP, CL | OP, CL |
| Butterfish | BD, CP, PF, CL | BD, CP, PF, CL |
| Sand Lance | BD, CP, CL, DN | BD, CP, CL, DN |
| Red hake | CP, PF, CL | CP, PF, CL |
| Silver hake* | BD, CP, PF, OP | BD, ED, CP, PF, OP, DN |
| Haddock | BD, CP, CL | BD, CP, CL |
| Atlantic cod | BD, CP, PF, CL | BD, CP, PF, CL |

**Table 7**

Least squares regression equations relating measurements (in millimeters) of total length (TL) and fork length (FL) to total weight (W) in grams for ten prey species in the Northwest Atlantic. $s_b$ = standard error of the regression coefficient; $r^2$ = coefficient of determination; %PE = mean percent prediction error; $n$ = number of fish measured; Range = size range in total length. Fork lengths were not measured for red hake, silver hake, or Atlantic cod.

| | Total length | | | | Fork length | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Species | Equation | $s_b$ | $r^2$ | %PE | Equation | $s_b$ | $r^2$ | %PE | $n$ | Range |
| Alewife | $W = 2.74 \times 10^{-6} TL^{3.213}$ | 0.031 | 0.99 | 7.12 | $W = 3.29 \times 10^{-6} FL^{3.254}$ | 0.035 | 0.99 | 7.82 | 137 | 73–282 |
| Blueback herring | $W = 6.24 \times 10^{-6} TL^{2.993}$ | 0.101 | 0.96 | 6.78 | $W = 13.78 \times 10^{-6} FL^{2.887}$ | 0.113 | 0.95 | 7.16 | 38 | 83–134 |
| Atlantic herring | $W = 4.10 \times 10^{-6} TL^{3.111}$ | 0.037 | 0.99 | 8.10 | $W = 4.53 \times 10^{-6} FL^{3.156}$ | 0.040 | 0.99 | 8.33 | 84 | 97–295 |
| Atlantic mackerel | $W = 1.09 \times 10^{-6} TL^{3.354}$ | 0.039 | 0.99 | 5.86 | $W = 0.85 \times 10^{-6} FL^{3.451}$ | 0.041 | 0.99 | 5.84 | 56 | 158–330 |
| Butterfish | $W = 8.14 \times 10^{-6} TL^{3.094}$ | 0.024 | 0.99 | 6.78 | $W = 8.43 \times 10^{-6} FL^{3.180}$ | 0.032 | 0.99 | 8.36 | 108 | 54–193 |
| Sand lance | $W = 0.32 \times 10^{-6} TL^{3.449}$ | 0.112 | 0.93 | 12.74 | $W = 0.41 \times 10^{-6} FL^{3.421}$ | 0.119 | 0.92 | 13.63 | 75 | 109–209 |
| Red hake | $W = 4.41 \times 10^{-6} TL^{3.053}$ | 0.034 | 0.99 | 5.75 | | | | | 45 | 108–340 |
| Silver hake | $W = 1.91 \times 10^{-6} TL^{3.213}$ | 0.027 | 0.99 | 8.96 | | | | | 95 | 75–300 |
| Haddock | $W = 3.44 \times 10^{-6} TL^{3.186}$ | 0.063 | 0.98 | 7.50 | $W = 3.78 \times 10^{-6} FL^{3.196}$ | 0.080 | 0.97 | 9.12 | 47 | 79–202 |
| Atlantic cod | $W = 1.99 \times 10^{-6} TL^{3.308}$ | 0.090 | 0.99 | 5.53 | | | | | 31 | 52–140 |

## Discussion

Each of the morphometric measurements, including those from diagnostic bones, were significantly related to total length, fork length, and weight. Measurements taken from diagnostic bones, especially cleithrum length, appear to be highly reliable predictors of original size for prey fish species in the Northwest Atlantic. Internal hard parts of fishes have historically proven accurate for estimating original sizes of prey fishes recovered from the stomachs of several freshwater piscivores (Knight et al., 1984; Trippel and Beamish, 1987; Hansel et al., 1988). Our results suggest that examination of diagnostic bones should also benefit diet analyses of marine piscivores.

The ability to estimate original length and weight of common prey fishes from a suite of morphometric measurements should result in a considerable increase in the amount of size-specific diet information for several predatory fishes in the Northwest Atlantic. Accurate information on the sizes of prey consumed across temporal and spatial scales is critical in order to calculate predator consumption rates and to determine predator impact on prey populations. Moreover, many piscivorous fishes feed selectively on specific sizes of prey (Juanes, 1994), suggesting that predatory impact may be greatest on a small range of prey sizes. Therefore, knowledge of prey sizes consumed is necessary in order to determine the extent of size-selective feeding patterns in Northwest Atlantic piscivores and their role in structuring marine fish populations. Finally, several authors have demonstrated the importance of body size in determining the outcome of predator-prey interactions among fishes (Werner and Gilliam, 1984, Miller et al., 1988, Stein et al., 1988). More complete information on predator-prey size relationships in the Northwest Atlantic may improve our understanding of the effects of body size on prey vulnerabilities to predation during various life history stages.

Clearly, the estimation of original prey sizes from diagnostic bone dimensions is not as susceptible to measurement error as estimates from external morphological features, where measurements are usually associated with soft tissues. Moreover, external morphology can often be altered during digestive processes, which may cause some or all external features to yield unreliable measurements. However, for recently consumed prey fishes, external morphological measurements may be highly reliable estimators of original prey size and represent a suitable alternative to diagnostic bones. For example, the linear relations of both eye diameter and caudal peduncle depth with total length were found to be reliable for reconstructing original prey lengths of six prey species consumed by juvenile bluefish (Scharf et al., 1997). Similarly, Serafy et al. (1996) found the linear relation between eye diameter and total length of red drum to be particularly useful in estimating the size of angled fish. In addition to cleithrum length, maximum body depth and caudal peduncle depth were consistent predictor variables for estimating original weight of prey fishes examined in this paper. Differences in fish condition factor may not be closely correlated with differences in other morphological measurements. Therefore, indices of fish girth, such as body depth and caudal peduncle depth, should be reliable indicators of condition factor and should be most closely related to body weight. Further, the reconstruction of original prey sizes from external morphological measurements has the advantage of being comparatively less labor intensive than dissection and removal of internal hard parts.

The reconstruction of original prey sizes from diagnostic bones or external morphological measurements does, however, have some important limitations. The potential effects of preservatives on bone dimensions need to be considered if stomach contents are stored in a chemical preservative. The fish used in this study were not exposed to preservatives but were frozen and thawed before measured. The use of boiling water to aid in the removal of soft tissue may cause shrinkage and deformation of extracted bones if sufficient time elapses between the boiling process and the completion of bone measurements. However, bone measurements for our analyses were completed immediately after dissection and removal. In addition to the potential effects of preservation, previous studies indicate that estimation of prey sizes from partial remains will likely underestimate the proportion of small prey fish in the diet, because bones and external features of larger prey fish should be more resistant to digestion and be recovered from piscivore stomachs more frequently (Trippel and Beamish, 1987; Hansel et al., 1988). Lastly, allometric relationships may not remain constant with changes in fish size. Therefore, regression equations should not be applied to fish outside the size range used for their generation.

The results of our study indicate that, for the families of fishes examined, the opercle, cleithrum, and dentary represent diagnostic tools that can potentially aid in the identification of prey fishes recovered from the stomachs of Northwest Atlantic piscivores. The diagnostic features unique to each of the three bones appear to perform equally well in distinguishing family taxa from one another. However, within the families Gadidae and Clupeidae, cleithra and dentaries are better suited to illustrate

differences between genera relative to opercles. Newsome (1977) and Hansel et al. (1988) revealed similar findings, demonstrating the limitations of opercles for identifying prey fishes beyond the family level. Moreover, Hansel et al. (1988) found that cleithra and dentaries were more resistant to digestion than opercles or pharyngeal arches, when examining several freshwater fishes, and concluded that, for young prey fish, the cleithrum may be the most reliable bone because of its large size and early development in relation to other diagnostic bones.

None of the three diagnostic bones appear useful for differentiating between the two species of the genus *Alosa* examined in this study. Similarly, Hansel et al. (1988) found that for certain congeneric freshwater fishes, identification was inconsistent and not dependable when opercles, cleithra, dentaries, and pharyngeal arches were used. The size range of fishes used in this study included juveniles and young adults (Table 1) and is typical of size ranges examined in previous studies (Trippel and Beamish, 1987; Hansel et al., 1988). Therefore, for these life stages, opercles, cleithra, and dentaries may be potentially useful as tools for identifying prey fishes to the family and, in some cases, the generic taxonomic level, but likely are not adequate for distinguishing between species of the same genus.

Our descriptions of the diagnostic bones provide a simple means to distinguish prey fishes based on general bone structure. Indeed, there have been more rigorous efforts directed at identifying the systematic relationships among several of the fishes examined in this paper. However, the bone descriptions in this paper were provided as a simple guide for field identification of prey fishes commonly recovered from piscivore stomachs, and thus centered on general overall shape and features that were common to all of the fishes. The differences among the taxa that are outlined here should be readily observable to a large range of workers with varying levels of fisheries training. Therefore, we suggest that the level of analysis and description presented here may compliment existing information and may be ideally suited for identification of prey fishes in field settings.

The bone descriptions and regressions presented in this paper clearly have the potential to increase the amount of dietary information obtainable from stomach contents analyses of Northwest Atlantic piscivores. Further, the generation of a series of regression equations relating measurements from both internal hard parts and external morphological features to original fish size may provide a means to cross reference prey size estimates, thus facilitating the identification of erroneous estimates.

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# Marine turtle populations on the west-central coast of Florida: results of tagging studies at the Cedar Keys, Florida, 1986–1995

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**Abstract.**—Large-mesh tangle nets were used to collect marine turtles in Waccasassa Bay, near the Cedar Keys, Florida, from June 1986 to October 1995. Tagging records were analyzed to determine the species composition, population structure, and seasonal occurrence of Kemp's ridley, *Lepidochelys kempii*, loggerhead, *Caretta caretta*, and green, *Chelonia mydas*, turtles. Additional information on local movements, morphometrics, growth, population estimation, and diet was provided for Kemp's ridley turtles. Subadult green turtles dominated the catch on the seagrass shoals of Waccasassa Reefs. Subadult Kemp's ridley turtles and, to a lesser degree, subadult and adult loggerhead turtles were primarily captured near the oyster bars of Corrigan Reef. Marine turtles were caught in these nearshore waters from April to November. Recaptures indicate that some Kemp's ridley turtles remain in the vicinity of Corrigan Reef during their seasonal occurrence and return to this foraging area annually. Seasonal and annual size distributions of Kemp's ridley turtles were investigated and regression equations were developed for carapace morphometrics. Carapace growth averaged 4–5 cm/yr for Kemp's ridley turtles, but growth analyses were confounded by the extrapolation of annual estimates from short-term recaptures. Population estimates for the Kemp's ridley mark-recapture data indicated a mean annual population size of 159 turtles at Corrigan Reef with presumably high rates of immigration and emigration by larger subadult turtles. Examination of fecal samples indicated that crabs were the primary food items of Kemp's ridley turtles captured near oyster bars.

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Historical information concerning marine turtles in the coastal waters of Florida is limited to landing statistics and observational data associated with the commercial turtle fishery (Ehrhart, 1983). During the late 1800s, large-mesh tangle nets were used to catch significant numbers of green turtles, *Chelonia mydas*, in the Indian River Lagoon and around the Cedar Keys (True, 1887; Brice, 1896). These turtles were exported to markets in the northeastern United States. Kemp's ridley, *Lepidochelys kempii*, and loggerhead turtles, *Caretta caretta*, were also captured and used as a food resource in local markets, but the landings of these species were not recorded in fisheries reports (Witzell, 1994a). The Florida fishery for marine turtles was greatly reduced by 1900 (Ingle and Smith, 1949). However, there are no quantitative data to demonstrate accurately that depletion had occurred as a result of overfishing (Caldwell and Carr, 1957). The lack of definitive data is further complicated by the fact that most of the fishery statistics reported for Florida after 1900 include green turtles imported from Costa Rica and Nicaragua by way of Key West, and no distinction was made between turtles caught in Florida and those imported from the Caribbean (Ingle and Smith, 1949; Caldwell and Carr, 1957; Witzell, 1994a, 1994b).

The first scientific investigations and conservation efforts for marine turtles were implemented fifty years after the reduction of the turtle fishery. Ingle and Smith (1949) and Carr (1952) outlined scientific data necessary for the protection and restoration of green turtles throughout their range. Carr and Caldwell (1956) conducted a one-year tagging study of green and Kemp's ridley turtles purchased from Cedar Key fish houses and provided the first details on size ranges, morphometrics, local movements, growth rates, and population estimates for these species. Florida enacted legislation in 1956 that prohibited the take of nesting female turtles and their eggs (Caldwell and Carr, 1957; Ehrhart, 1983).

Restrictions were imposed on the Florida turtle fishery in 1971, which consisted of closed seasons and size limits (Ingle, 1972). By 1978, all species of marine turtles were listed as threatened or endangered in the Endangered Species Act and protected under federal legislation.

Listing marine turtles in the Endangered Species Act outlawed their harvest and prompted surveys on nesting beaches and adjacent coastal waters in Florida (Carr et al., 1982). Entanglement nets, designed similarly to those formerly used in the turtle fishery, were employed to capture green and loggerhead turtles inhabiting the northern Indian River Lagoon System (Ehrhart and Yoder, 1978; Mendonça, 1981, 1983; Mendonça and Ehrhart, 1982; Ehrhart, 1983). These fishery-independent studies provided the first biological data on population size and structure, growth rates, and activity patterns for the previously exploited species of marine turtle in the lagoonal habitat. Trawls associated with the commercial shrimp fishery were used to collect turtles occurring in and around the Port Canaveral ship channel (Carr et al., 1980; Henwood, 1987; Henwood and Ogren, 1987). Information obtained from these fishery-dependent surveys includes size class distribution, seasonal occurrence, and migrations of loggerhead, Kemp's ridley, and green turtles.

In 1984, the National Marine Fisheries Service (NMFS) initiated long-term tagging studies of marine turtles occurring in the coastal waters of Florida, with emphasis placed on the critically endangered Kemp's ridley turtle (Ogren, 1989; Schmid and Ogren, 1990, 1992). Rudloe et al. (1991) reported on the size-class distribution, seasonal occurrence, and variations in carapace length by season and water depth for Kemp's ridley turtles incidentally captured in commercial fisheries of northwest Florida. Tagging records of turtles captured in the east-central Florida shrimp fishery provided additional data on species composition, size-class distribution, seasonal occurrence and migrations, morphometric relationships, and growth data for marine turtles along the Atlantic coast (Schmid, 1995). Fishery-independent capture techniques have also been used to collect marine turtles in the nearshore waters of west-central Florida and preliminary results of these efforts have been given by Schmid and Ogren (1990, 1992). The present paper analyzes tagging records collected near the Cedar Keys, Florida, from 1986 to 1995 in order to determine the species composition, population structure, and seasonal occurrence of Kemp's ridley, loggerhead, and green turtles. Additional information on local movements, morphometrics, growth, population estimation, and diet are provided for Kemp's ridley turtles.

## Materials and methods

### Study area

Marine turtles were collected east of the Cedar Keys in Waccasassa Bay, which is located on the west coast of Florida (Fig. 1). The northern and eastern boundaries of Waccasassa Bay are saltmarsh coastline inundated by numerous tidal creeks. The Waccasassa River flows into the northeast corner of the bay and is the main contributor of freshwater to the estuarine system (Wolfe, 1990). The western edge of the bay is semi-enclosed by the Cedar Keys, whereas the southern portion is open to tidal exchange with the Gulf of Mexico. Corrigan Reef, located in northwestern Waccasassa Bay, and Waccasassa Reefs, located in the eastern half of the bay, are the prominent geographic features of this shallow embayment.

Netting efforts were concentrated at three sites along Corrigan Reef (Fig. 1; site 1: 29°09'N, 82°58'W; site 2: 29°08'N, 82°58'W; and site 3: 29°07'N, 82°58'W), approximately 5 km east of the Cedar Keys. Corrigan Reef comprises a series of oyster (*Crassostera virginica*) beds in the northern region (site 1) and oyster shell bars in the southern region (sites 2 and 3). Limestone outcroppings occur among the mud and sand flats and in channels on the periphery of oyster bars. Netting was also conducted at the outer shoal of Waccasassa Reefs (29°06'N, 82°53'W), approximately 12 km east-southeast of the Cedar Keys. Waccasassa Reefs are composed of three seagrass shoals with a broad, deep-channel cutting midway through each shoal. The tides in both of these areas are mixed, with two highs and two lows of variable amplitude. Strong tidal currents flow through the channels, particularly during the new and full moon phases (spring tides).

### Data collection

Seasonal netting was conducted at Corrigan Reef from 1986 to 1991 and at Waccasassa Reefs from 1986 to 1988 (see Table 1 for effort and months fished each year). A full year of sampling was performed at Corrigan Reef in 1992 and 1993. Water temperatures were recorded sporadically from 1986 to 1991 and monthly for 1992 and 1993. Netting surveys were performed for 1–3 days every other week during the neap tides. One or two nylon mesh tangle nets (61- or 51-cm stretch mesh, 20 meshes deep, and 65 m length) were set across a channel at a given site and fished over a 6- to 12-hour tidal cycle. Nets were checked hourly or immediately after an entangled turtle had been sighted. Research efforts shifted from netting surveys to telemetric monitoring during 1994

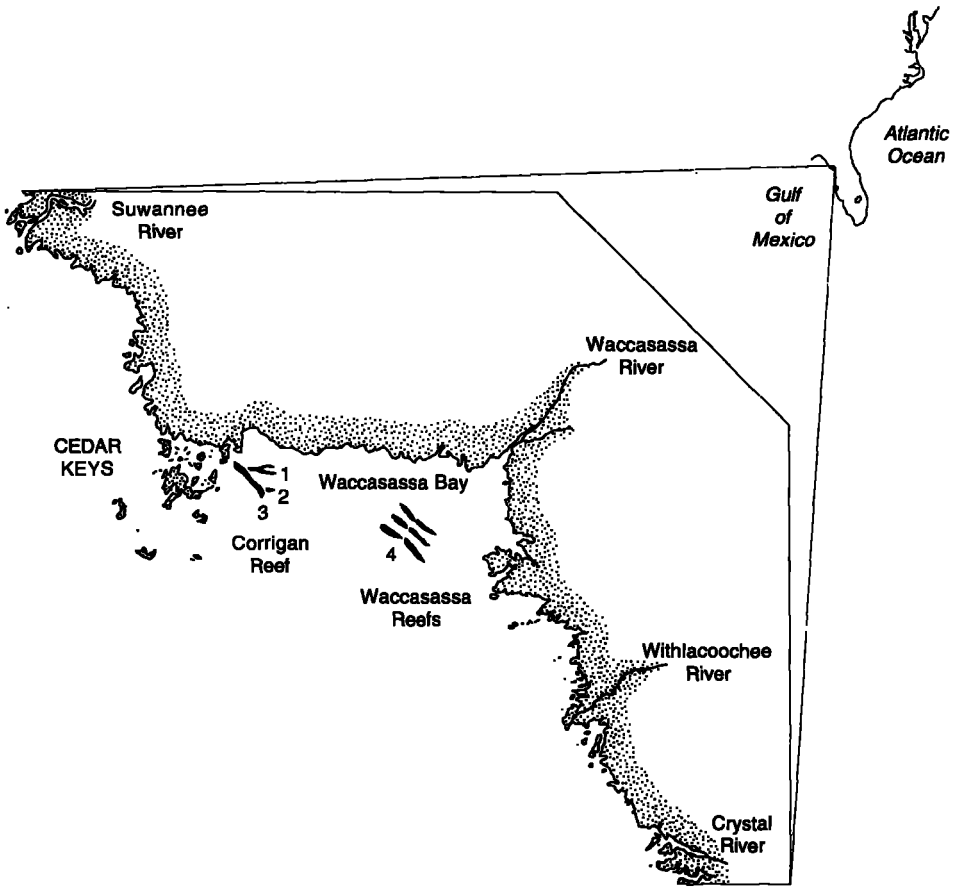


**Figure 1**

Map of the west-central coast of Florida showing the Cedar Keys study area. Numbers indicate the location of sampling sites described in the text.

**Table 1**

Annual effort (km-h) and CPUE (turtles/km-h) by species for Corrigan Reef and Waccasassa Reefs from 1986 to 1993. Lk=*Lepidochelys kempii*, Cc=*Caretta caretta*, and Cm=*Chelonia mydas*.

| Year (months) | Corrigan Reef | | | | Waccasassa Reefs | | | |
|---|---|---|---|---|---|---|---|---|
| | Effort | Lk/h | Cc/h | Cm/h | Effort | Lk/h | Cc/h | Cm/h |
| 1986 (Jun–Nov) | 153.9850 | 0.1104 | 0.0065 | 0.0000 | 9.3275 | 0.0000 | 0.0000 | 0.1072 |
| 1987 (May–Dec) | 236.0963 | 0.0720 | 0.0000 | 0.0042 | 19.6300 | 0.0000 | 0.0509 | 0.2547 |
| 1988 (May–Sep) | 142.3988 | 0.2388 | 0.0070 | 0.0000 | 1.2675 | 0.7890 | 0.0000 | 0.0000 |
| 1989 (Jun–Sep) | 177.4500 | 0.1634 | 0.0394 | 0.0113 | — | — | — | — |
| 1990 (Jun–Sep) | 233.4150 | 0.1499 | 0.0129 | 0.0000 | — | — | — | — |
| 1991 (Jun–Oct) | 152.5225 | 0.1246 | 0.0000 | 0.0000 | — | — | — | — |
| 1992 (May–Dec) | 461.5650 | 0.1148 | 0.0303 | 0.0022 | — | — | — | — |
| 1993 (Jan–Oct) | 124.8000 | 0.1923 | 0.0160 | 0.0000 | — | — | — | — |

and 1995, and tag data collected on these turtles were included in the analyses.

The following morphometric measurements (Pritchard et al., 1983) were recorded for each turtle: total straight-line carapace length (TSCL, anterior most edge of carapace to posterior margin of postcentral); standard straight-line carapace length (SSCL, nuchal notch to posterior margin of postcen-

tral); minimum straight-line carapace length (MSCL, nuchal notch to notch between postcentrals); minimum curved carapace length (MCCL, nuchal notch to notch between postcentrals); and straight-line carapace width (CW) at the widest point. Straight-line carapace lengths and width were measured to the nearest 0.1 inch with forester's calipers. Curved carapace length was measured to the nearest 0.1 cm with a flexible fiberglass measuring tape. Weight (WT) was measured to the nearest 0.25 lb with a spring scale. All measurements were performed by the author to avoid individual differences in measuring technique (Bjorndal and Bolten, 1988) and were converted to metric units for analysis. Notes on the condition of the turtle were recorded when the animal was injured or deformed (e.g. tag scars, carapace wounds, etc.).

Turtles were double tagged on the trailing edge of the fore flippers with no. 681 Inconel tags (June 1986 to May 1988; May 1994 to October 1995), with Jumbo Roto plastic tags (June 1988 to October 1991), or with both (May 1992 to September 1993). Beginning in 1988, two holes were drilled in specific marginal scutes of Kemp's ridley turtles in order to identify the year of capture (1988—left postcentral, 1989—right postcentral, 1990—left 12th marginal, 1991—right 12th marginal, 1992—left 11th marginal, 1993—right 11th marginal, 1994—left 10th marginal, and 1995—right 10th marginal). Passive integrated transponder (PIT) tags were applied to the left front flipper of Kemp's ridley turtles from June 1992 to October 1995. Turtles were immediately released after data collection approximately 100 m down-current from the netting site.

## Data analysis

Marine turtle life history stages were defined according developmental habitats and carapace lengths (Schmid, 1995). The term "juvenile" was reserved for immature turtles in the epipelagic stage of development. A turtle was considered "subadult" after recruiting to its respective coastal-benthic habitat and "adult" when sexually mature. Loggerhead turtles greater than 80 cm (Carr, 1986), green turtles greater than 83 cm (Witherington and Ehrhart, 1989), and Kemp's ridley turtles greater than 60 cm (Pritchard and Márquez M., 1973) were considered adult based on sizes of nesting females.

Capture records were analyzed to evaluate species composition within the Cedar Keys study area, length-frequency distribution of each species, and patterns of seasonal occurrence. Additional analyses of morphometrics, growth rates, population estimates, and dietary composition were performed for Kemp's ridley turtles. Standard straight-line carapace length was used in the analyses of size distribution and growth. Means are followed by ± one standard deviation unless noted otherwise. Turtle catch per unit of effort (CPUE) was standardized according to Shaver (1994) with the formula

$$E = \left(\frac{Nets \times Length}{1000}\right) Hrs,$$

where $E$ = the netting effort in hours fished by a 1-km tangle net;
$Nets$ = the number of tangle nets fished;
$Length$ = the length (m) of a net; and
$Hrs$ = the number of hours fished.

Kemp's ridley turtle morphometric relationships were investigated by regressing carapace width on length and log-transformed weight on length. Conversion formulae for Kemp's ridley turtle carapace lengths were calculated by regressing paired straight-line and curved carapace lengths. Turtles with carapace wounds or deformities were not included in regression equations.

Yearly growth rates for Kemp's ridley turtles were calculated with the formula

$$G = \left(\frac{\Delta Length}{Days}\right) 365,$$

where $G$ = the growth rate in cm/yr;
$\Delta\, Length$ = difference between the recapture length and the initial length; and
$Days$ = the number of days at large.

Growth rates were grouped and analyzed in terms of the recapture interval duration, recaptures between versus recaptures within netting seasons, and size classes of recaptured turtles. Growth rates were assigned to 10-cm size classes on the basis of mean of the initial and recapture carapace measurements (Bjorndal and Bolten, 1988). The von Bertalanffy growth interval equation was fitted to the recapture data with a nonlinear least-squares regression procedure (SAS Institute Inc., 1989). The von Bertalanffy growth interval equation (Fabens, 1965) for recapture data is:

$$CL_2 = a - (a - CL_1)e^{-kt},$$

where $CL_2$ = the carapace length at recapture;
$a$ = the asymptotic length;
$CL_1$ = the length at first capture;

$k$ = the intrinsic growth rate; and
$t$ = the time in years between captures.

Kemp's ridley turtle mark-recapture data for 1986–93 were tallied in a method B table (Krebs, 1989) and analyzed with the computer program JOLLY (Hines, 1988; Pollock et al., 1990). Summary statistics for the Jolly-Seber computer analysis include the total number of turtles captured and released each year ($n$), the number of marked ($m$) and unmarked ($u$) turtles captured each year, the number of turtles released each year that are captured again later ($r$), and the number of turtles captured before a given year and captured again later ($z$). The data were applied to a Jolly-Seber model that assumes that the population parameters survival rate ($\Phi$) and capture probability ($p$) are constant per unit time. Annual estimates of the number of marked turtles in the population ($M$), population size ($N$), and the number of individuals recruited to the population ($B$) were computed with the reduced parameter model.

Dietary analyses were conducted on Kemp's ridley fecal specimens fortuitously encountered during the tagging process. Fecal specimens were initially examined in the field and the contents were noted in tagging records. Additional examinations were performed from photographs and samples of feces. Components of the feces were identified to the lowest taxon possible and were analyzed to determine the percentage of specimens containing each component (Burke et al., 1994). Nomenclature of molluscs was identified by using the field guide of Abbott and Morris (1995).

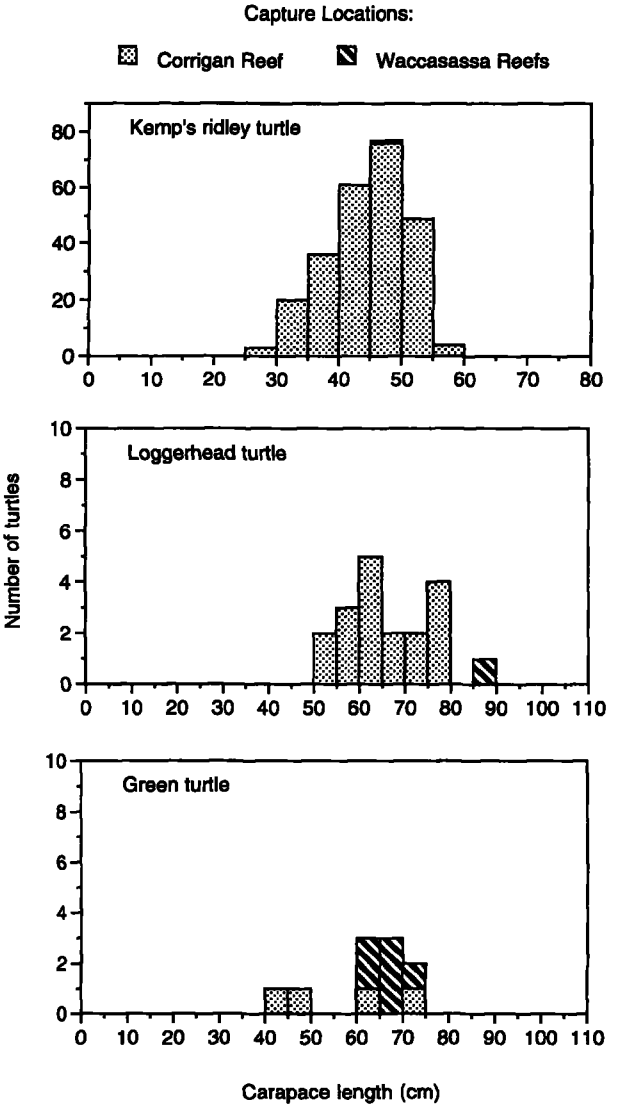


**Figure 2**

Length-frequency distributions for Kemp's ridley turtles, *Lepidochelys kempii*, loggerhead turtles, *Caretta caretta*, and green turtles, *Chelonia mydas*, collected in Waccasassa Bay, Florida, from 1986 to 1995. Note the different scale in y axis of upper graph.

## Results

### Marine turtle captures and effort

One (12.5%) Kemp's ridley, 1 (12.5%) loggerhead, and 6 (75%) green turtles were collected during 64.75 h of netting at Waccasassa Reefs. The Kemp's ridley turtle measured 47.6 cm SSCL, the loggerhead turtle measured 86.4 cm SSCL, and green turtles ranged from 63.0 to 73.9 cm SSCL (mean=68.0 ±3.9 cm; Fig. 2). Three of the green turtles captured at Waccasassa Reefs exhibited fibropapillomas (1–4 cm diameter), primarily in the axillary region of the flippers. Maximum CPUE for green turtles at Waccasassa Reefs was 0.255 turtles/km-h in 1987, and values of CPUE for loggerhead and Kemp's ridley turtles were 0.051 turtles/km-h in 1987 and 0.789 turtles/km-h in 1988, respectively (Table 1). Netting effort was conducted at this location from June through November and turtles were captured in July and August.

Two hundred and fifty-three (91.7%) Kemp's ridley, 19 (6.9%) loggerhead, and 4 (1.4%) green turtles were collected during 980.00 h of netting at Corrigan Reef. Kemp's ridley turtles ranged from 26.8 to 58.6 cm SSCL (mean=44.5 ±6.3 cm), loggerhead turtles ranged from 50.0 to 77.4 cm SSCL (mean=65.0 ±8.7 cm), and green turtles ranged from 42.9 to 70.9 cm SSCL (mean=56.8 ±12.9 cm; Fig. 2). Loggerhead turtles greater than 80 cm SSCL were caught at

Corrigan Reef but could not be landed for data collection. One such turtle was identified as a male because its tail extended considerably beyond the posterior marginal scutes. Fibropapillomas were not observed on green turtles captured at Corrigan Reef. Annual CPUE for Kemp's ridley turtles at Corrigan Reef ranged from 0.072 turtles/km-h in 1987 to 0.239 turtles/km-h in 1988 (Table 1). Maximum CPUE for loggerhead and green turtles at Corrigan Reef was 0.039 turtles/km-h and 0.011 turtles/km-h in 1989, respectively. Kemp's ridley and loggerhead turtles were captured in this area from April to November, whereas green turtles were captured from June to September.

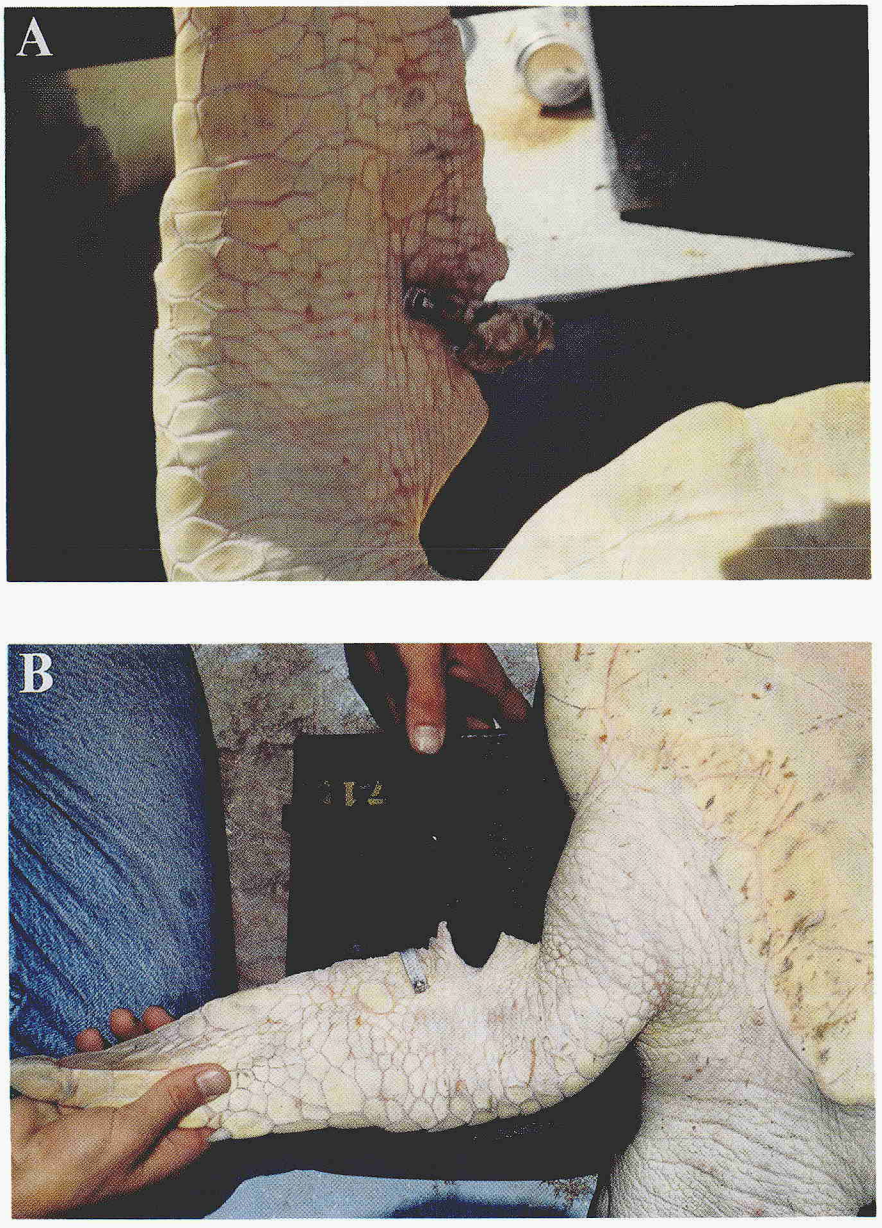


**Figure 3**

Photographs of recaptured Kemp's ridley turtles, *Lepidochelys kempii*, demonstrating (**A**) a barnacle-encrusted tag and (**B**) a flipper scar from tag loss.

## Recaptures and local movements

Thirty-four Kemp's ridley turtles (23 with tags and 11 with tag scars), five loggerhead turtles (3 with tags and 2 with tag scars), and one green turtle (with a tag scar) were identified as recaptures. All recaptured turtles with tags, with the exception of two NMFS Galveston laboratory headstart Kemp's ridleys, were initially captured and tagged at Corrigan Reef. Thirty-five percent of the recaptured turtles exhibited tag scars, which is indicative of moderate tag loss and may account for the lack of recaptures or recoveries in other areas. Schmid and Ogren (1992) identified barnacle fouling as a potential problem with the otherwise corrosion-resistant Inconel flipper tag. The increased drag and weight produced by the barnacle clusters and the necrosis of flipper tissue by the encrusted tag (Fig. 3A) resulted in the eventual shedding of the tags and the formation of a conspicuous notch in the trailing edge of the flippers (Fig. 3B). Barnacle growth was observed on both Inconel and plastic tags in as little as 14 days and tag loss was observed within 10 months after application. Similar retention times were noted for both types of tags, but a quantitative analysis of retention rates was not performed because of small sample sizes. The use of marginal markings allowed for the identification of tag-scarred turtles originally tagged at the Cedar Keys and the tabulation of recapture data by year classes. PIT tags were successfully used to identify tag-scarred Kemp's ridley turtles in the later part of the study.

Kemp's ridley recaptures ranged from 14 to 839 days and loggerhead recaptures ranged from 142 to 189 days. The two headstart Kemp's ridley turtles were recaptured approximately 3–4 years after their release in Texas waters as was determined from the location of the living tag in the carapace (Fontaine et al., 1993; Caillouet et al., 1995). Seven Kemp's ridley turtles with tag scars had marginal scute markings indicating the year of initial capture at Corrigan Reef. Four of these were at large for 1 year, one was at large for 2 years, and two were at large for 3 years. Four Kemp's ridley turtles had multiple recaptures in the vicinity of Corrigan Reef. One turtle was tagged at site 2 in September 1991 and recaptured at this site in October 1991 and May 1992 (0.7 year duration). Another turtle tagged at site 1 in July 1990 was recaptured at this site in June 1991 and June 1992 (1.9-year duration). A turtle tagged at site 2 in October 1991 was recaptured at this site in September 1992 and at site 3 in May 1994 (2.6-year duration). The fourth turtle had a 1991 marginal marking and was recaptured at site 2 in September 1993 and August 1995 (≈ 4-year duration).

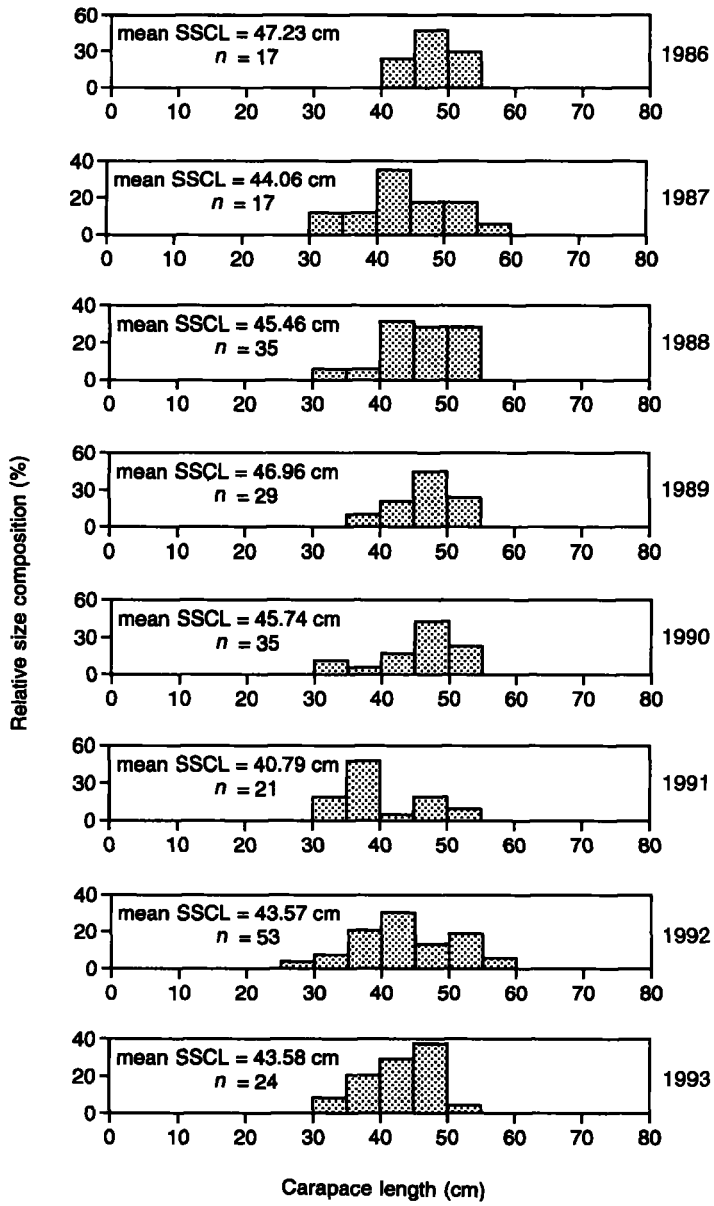


**Figure 4**

Annual relative size composition of Kemp's ridley turtles, *Lepidochelys kempii*, captured at Corrigan Reef from 1986 to 1993.

## Seasonal and annual size distributions

Mean water temperatures at Corrigan Reef were calculated by season (Table 2): winter (Dec–Feb), spring (Mar–May), summer (Jun–Aug), and fall (Sep–Nov). Turtles were captured in water temperatures greater than 20°C. Carapace lengths for Kemp's ridley turtles captured from 1986 to 1995 were pooled by season (spring, summer, or fall) according to the month of capture (Table 2). A significant difference ($F$=3.76, $P$=0.025) was detected between the mean SSCL of at least two seasons. Multiple comparisons with the Bonferroni procedure demonstrated no significant difference in mean SSCL between spring and summer, or spring and fall. However, mean SSCL in summer was significantly larger than that of fall.

Analysis of the annual relative composition of Kemp's ridley turtle carapace lengths from 1986 to 1993 indicated that the 40–50 cm size class dominated the catch during all years except 1991 (Fig. 4). The majority of turtles captured during 1991 were in the 30–40 cm size class. The carapace length distributions for 1986 through 1990 were not significantly different when compared with the Kolmogrov-Smirnov two-sample test. The distribution of carapace lengths for 1991 was significantly different from all years except 1987, and the distribution for 1992 was significantly different from all years except 1987 and 1988. The carapace length distribution for 1993

**Table 2**

Seasonal water temperatures and Kemp's ridley turtle, *Lepidochelys kempii*, carapace lengths at Corrigan Reef from 1986 to 1995 (standard deviations given in parentheses).

| Season | Mean water temperature | Mean carapace length | *n* | Size range |
|---|---|---|---|---|
| Spring | 22.5°C (3.0) | 44.1 cm (7.4) | 24 | 26.8–58.6 cm |
| Summer | 30.4°C (0.6) | 45.5 cm (5.9) | 142 | 28.2–54.4 cm |
| Fall | 22.9°C (4.2) | 43.1 cm (6.6) | 85 | 27.3–56.6 cm |
| Winter | 15.7°C (2.0) | — | 0 | — |

was not significantly different from the distributions of 1986 through 1990. The observed shift in size-class distribution for 1991 may have been caused by changes in fishing conditions that year. Beginning in July 1991, a smaller mesh (25.4-cm bar) net was deployed either singly or in combination with the larger mesh (30.5-cm bar) net that was used the previous years. The smaller mesh net may have resulted in the increased capture of 30–40 cm turtles in 1991, although the frequency of 40–50 cm turtles increased in the following years. Also, during August 1991, a massive influx of pelagic Sargassum occurred along the west coast of Florida and the majority of netting effort was conducted in the months following this unusual event. It is not known how this latter condition may have affected the relative frequency of carapace lengths, either by increasing the frequency of 30–40 cm turtles or decreasing the frequency of 40–50 cm turtles.

## Carapace regression equations

There was a strong correlation between carapace width and carapace length ($r$=0.9883, $n$=227) for Kemp's ridley turtles. Regression of width on length resulted in the equation

$$CW = -3.7415 + 1.0530\ (SSCL).$$

A strong correlation ($r$=0.9886, $n$=225) was calculated for the weight-to-length data transformed with the natural logarithm. Regression of these variables resulted in the equation

$$\ln WT = -8.1570 + 2.8128\ (\ln SSCL).$$

Conversion equations were computed between the straight-line and curved carapace length measurements (Table 3). These equations will allow for comparisons between studies with different measuring techniques.

**Table 3**

Formulae for converting between straight-line and curved carapace measurements of Kemp's ridley turtles, *Lepidochelys kempii*. TSCL = total straight-line carapace length, SSCL = standard straight-line carapace length, MSCL = minimum straight-line carapace length, and MCCL = minimum curved carapace length.

| Converted length | Conversion formula | *n* | $r^2$ |
|---|---|---|---|
| TSCL | 1.0118 SSCL + 0.0650 | 227 | 0.9990 |
| TSCL | 1.0214 MSCL + 0.3800 | 227 | 0.9982 |
| TSCL | 0.9720 MCCL + 0.2203 | 107 | 0.9920 |
| SSCL | 0.9874 TSCL – 0.0199 | 227 | 0.9990 |
| SSCL | 1.0094 MSCL + 0.3155 | 227 | 0.9990 |
| SSCL | 0.9598 MCCL + 0.1941 | 107 | 0.9929 |
| MSCL | 0.9773 TSCL – 0.2896 | 227 | 0.9982 |
| MSCL | 0.9897 SSCL – 0.2658 | 227 | 0.9990 |
| MSCL | 0.9495 MCCL – 0.0864 | 107 | 0.9933 |
| MCCL | 1.0205 TSCL + 0.1368 | 107 | 0.9920 |
| MCCL | 1.0345 SSCL + 0.1162 | 107 | 0.9929 |
| MCCL | 1.0462 MSCL + 0.3913 | 107 | 0.9933 |

## Growth analyses

Twenty-one Kemp's ridley turtles were recaptured a total of 24 times, yielding 24 annual growth rates. However, 83% of the recaptures occurred within a year of initial tagging and extrapolating annual growth rates from short-term recapture intervals will amplify any error associated with the measurements. The removal of short-term recaptures decreased the range of annual growth rates and increased the precision of the mean growth rate estimate (Table 4A). Subsequent analyses of growth by netting seasons and size classes were confounded by short-term recaptures. The mean growth rate of Kemp's ridley turtles recaptured within netting seasons (see Table 1 for months fished each year) was significantly larger ($\chi^2$=7.93, df=1, $P$=0.005) than that of turtles recaptured between netting seasons (Table 4B). However, the duration of all recaptures within netting seasons was less than 180 days (mean=49.6 ± 44.5 days) and the annual growth rates may have been overestimated owing to extrapolation error. Although mean growth rates did not vary significantly when compared by size class ($F$=0.753, $P$=0.484), Kemp's ridley turtles in the 40–50 cm size class appeared to have a higher mean growth rate than those in the 30–40 cm and the 50–60 cm size classes (Table 4C).

Deletion of data with recapture intervals less than 90 days reduced the mean growth rate of the 40–50 cm size class (4.7±3.0 cm/yr; $n$=9, range: 2.9–12.3 cm/yr).

The von Bertalanffy growth interval equation was fitted to each of the recapture interval data treatments. Estimates of asymptotic length ranged from 77.3 to 91.4 cm and estimates of intrinsic growth rate ranged from 0.0852 to 0.1167 (Table 5). The growth interval equation for all Kemp's ridley turtles recaptured at Cedar Key had the lowest residual mean square, a standard that has been used to select the best fit growth model (Dunham, 1978). However, the estimated asymptotic length for this model ($a$=91.4 cm) is considerably larger than the average carapace length reported for nesting females (65 cm; Márquez M., 1994) and should therefore be considered biologically unrealistic (Frazer et al., 1990). The estimated asymptotic length for recapture intervals greater than 180 days ($a$=77.3 cm) would be more appropriate if this latter criterion is used. This model has the least amount of error from short-term recaptures, but suffers from a reduced sample size and a truncated range of carapace lengths.

## Population estimations

The computer program JOLLY computed a survival rate of 0.41 (± 0.07 SE) and a capture probability of 0.18 (±0.05 SE) for Kemp's ridley turtles at Corrigan Reef. Population estimates ranged from 98.05 turtles in 1987 to 262.79 turtles in 1992 (Table 6). For 1987 through 1993, the mean annual population size was 158.50 (±112.40 SE) turtles and there was a mean of 15.35 (±11.58 SE) marked turtles in the population (10% of the estimated mean population size). For 1987 through 1992, there was a mean annual recruitment of 102.71 (±48.23 SE) turtles (65% of the estimated mean population size).

## Food

Fecal specimens from 12 Kemp's ridley turtles were examined during the course of this study. Crab components were identified in all specimens. In addition, two (17%) of the fecal specimens contained mollusc shells and two (17%) specimens contained a portion of undigested seagrass (*Halodule wrightii* in one and *Halophila engelmannii* in the other). Seven (58%) of the fecal specimens contained unidentified crab fragments. Five (42%) of the turtles had consumed chelipeds of stone crab, *Menippe* spp., and three (25%) had consumed chelipeds of blue crab, *Callinectes sapidus*. Two (17%) Kemp's ridley turtles had consumed shark eye shells (*Polinices duplicata*), one of which also consumed a common eastern nassa shell (*Nassarius vibex*), that contained hermit crabs (Paguridae). The two turtles that consumed hermit crabs also ingested mollusc components. Cancellate cantharus shells (*Cantharus cancellarius*) and oys-

**Table 4**

Mean annual growth rates of Kemp's ridley turtles, *Lepidochelys kempii*, by recapture interval, netting season, and size class (standard deviations given in parentheses). Turtles were assigned to size classes by mean of initial and recapture SSCL.

| Data treatments | $n$ | Mean SSCL growth rate (cm/yr) | Range of growth rates (cm/yr) |
|---|---|---|---|
| Recapture interval | | | |
| All recaptures | 24 | 5.4 (3.3) | 1.2–13.0 |
| Recaptures > 90 days | 16 | 4.5 (2.6) | 1.2–12.3 |
| Recaptures > 180 days | 13 | 3.6 (1.2) | 1.2–5.4 |
| Netting season | | | |
| Within season | 10 | 7.7 (3.6) | 1.7–13.0 |
| Between seasons | 11 | 3.3 (1.1) | 1.2–4.7 |
| Size class | | | |
| 30–40 cm | 7 | 4.6 (2.8) | 1.2–9.4 |
| 40–50 cm | 13 | 6.2 (3.7) | 2.9–13.0 |
| 50–60 cm | 4 | 4.6 (2.5) | 2.2–7.9 |

**Table 5**

Estimated values of asymptotic length ($a$) and intrinsic growth rate ($k$) from nonlinear regression of von Bertalanffy growth interval equation for Kemp's ridley turtles, *Lepidochelys kempii* (one asymptotic standard error in parentheses).

| Data treatment | $n$ | $a$ | $k$ |
|---|---|---|---|
| All recaptures | 24 | 91.4 cm (41.9) | 0.0852 (0.0720) |
| Residual mean square error = 1.3872 | | | |
| All recaptures > 90 days | 16 | 90.9 cm (51.1) | 0.0858 (0.0892) |
| Residual mean square error = 2.1179 | | | |
| All recaptures > 180 days | 13 | 77.3 cm (29.2) | 0.1167 (0.0957) |
| Residual mean square error = 2.0085 | | | |

**Table 6**

Summary statistics and estimated parameters for the Jolly-Seber analysis of Kemp's ridley turtle, *Lepidochelys kempii*, mark-recapture data (standard errors given in parentheses). Descriptions of the notation are as follows: $n$ = total number of turtles captured and released each year; $m$ = number of marked turtles captured each year; $u$ = number of unmarked turtles captured each year; $r$ = number of turtles released each year that were captured again later; $z$ = number of turtles captured before a given year and captured again later; $M$ = annual estimate of the number of marked turtles in the population; $N$ = annual estimate of population size; and $B$ = annual estimate of the number of individuals recruited to the population.

| | Summary statistics | | | | | Estimated parameters | | |
|---|---|---|---|---|---|---|---|---|
| Year | $n$ | $u$ | $m$ | $r$ | $z$ | $M$ | $N$ | $B$ |
| 1986 | 17 | 17 | 0 | 3 | — | — | — | — |
| 1987 | 17 | 16 | 1 | 3 | 2 | 10.91 (5.49) | 98.05 (32.11) | 139.87 (42.90) |
| 1988 | 35 | 31 | 4 | 1 | 1 | 18.20 (7.41) | 187.03 (55.83) | 96.38 (32.86) |
| 1989 | 29 | 28 | 1 | 3 | 1 | 7.30 (4.70) | 159.79 (50.22) | 107.25 (34.87) |
| 1990 | 32 | 29 | 3 | 2 | 1 | 14.17 (6.72) | 172.66 (52.53) | 45.54 (24.72) |
| 1991 | 20 | 18 | 2 | 6 | 1 | 11.32 (6.05) | 109.35 (35.92) | 201.60 (58.21) |
| 1992 | 49 | 43 | 6 | 2 | 1 | 28.61 (10.55) | 262.79 (75.59) | 25.64 (28.35) |
| 1993 | 22 | 19 | 3 | — | — | 16.34 (9.53) | 119.81 (39.34) | — |

ter shell fragments were identified in both of the fecal specimens. Furthermore, one of these specimens contained hooked mussels (*Ischadium recurvus*) attached to an oyster shell fragment.

## Discussion

The results of this study indicate the importance of seagrass beds and oyster reefs as developmental habitats for Kemp's ridley, loggerhead, and green turtles. Furthermore, these species may be preferentially utilizing the two habitat types on the basis of their respective feeding strategies. The extensive seagrass flats along the west coast of Florida have been identified as foraging habitat for the herbivorous green turtle (True, 1887; Carr and Caldwell, 1956; Caldwell and Carr, 1957). Netting effort at the seagrass shoals of Waccasassa Reefs resulted in captures of mid- to late subadult green turtles, comparable to the size class of green turtles reported by Carr and Caldwell (1956). The Kemp's ridley turtle is primarily cancivorous (Shaver, 1991; Burke et al., 1994), and the distribution of this species can be correlated to areas with abundant crab populations (Ogren, 1989). Intertidal oyster bars provide refuge for stone crabs (McRae, 1950; Bender, 1971; Wilber and Herrnkind, 1986), whereas the mud bottom adjacent to these bars is the preferred substrate of blue crabs (Evink, 1976; Wolfe, 1990). Subadult Kemp's ridley turtles dominated the aggregation of marine turtles captured in the vicinity of Corrigan Reef and the food items for these turtles were typical of the macroinvertebrate fauna inhabiting nearshore oyster bars. Subadult and adult loggerhead turtles were also captured at Corrigan Reef; this species also feeds on benthic invertebrates, particularly molluscs (Dodd, 1988). The possibility of competition for food resources between loggerhead and Kemp's ridley turtles is unknown and could be investigated by comparing fecal specimens of both turtles captured in the same location.

Tagging studies of Kemp's ridley turtles have revealed reproductive migrations of females in the Gulf of Mexico (Pritchard and Márquez M., 1973), seasonal migrations of subadults along the Atlantic coast (Henwood and Ogren, 1987; Schmid, 1995), and an east–west movement of subadults in the northern Gulf (Ogren, 1989). However, there are no mark-recapture data to indicate a seasonal migration of subadult turtles in the eastern Gulf of Mexico. As stated by Carr (1980) and observed in the present study, turtles apparently immigrate to the nearshore waters of the Cedar Keys in April and emigrate to some

unknown locality in November, presumably in response to changes in water temperature. Ogren (1989) suggested a seasonal offshore movement of Kemp's ridley turtles in the northern Gulf on the basis of capture of subadult turtles in deeper waters off Apalachicola Bay during the winter (Rudloe et al., 1991). Satellite telemetry has demonstrated that Kemp's ridley turtles on the Atlantic coast respond to a decrease in water temperature by moving to warmer waters southward or offshore (Renaud, 1995). Marine turtles in the Cedar Keys area could be moving westward to deeper waters offshore or southward within the shallow coastal waters. Alternatively, some Cedar Key fishermen believe that turtles overwinter in the remote coastal waters by "burying up" in mud bottom holes (Carr and Caldwell, 1956; Schmid and Ogren, 1990). Loggerhead turtles have exhibited this behavior in the Port Canaveral ship channel at water temperatures below 15°C (Carr et al., 1980; Ogren and McVea, 1982). Water temperatures as low as 12–14°C were recorded at the Cedar Keys study area from December to February. The possibility of winter dormancy or migration (or both) by west coast turtles requires additional information (Ogren and McVea, 1982) and could be investigated by attaching satellite transmitters to turtles during the fall.

Recaptures of Kemp's ridley turtles tagged and released in the northeastern Gulf of Mexico have provided information on their use of coastal foraging grounds. Carr and Caldwell (1956) observed that Kemp's ridley and green turtles released from Cedar Key returned to the Withlacoochee-Crystal River fishing grounds within a short period of time. The authors implied that the turtles may be exhibiting a homing behavior and maintaining home ranges at the site of initial capture. Schmid and Ogren (1990) suggested that Kemp's ridley turtles in the Florida panhandle region were transitory because of the lack of long-term recaptures (Rudloe et al., 1991). By comparison, recaptures in the Cedar Keys area were indicative of a more residential aggregation. Although the majority of Kemp's ridley turtles tagged near the Cedar Keys were recaptured within a year of initial capture, almost equal numbers of turtles were recaptured within netting seasons and between netting seasons. Recaptures within a netting season suggest that some turtles remain in the vicinity of Corrigan Reef during their seasonal occurrence in this region. Recaptures between netting seasons indicate that some turtles return to the previously utilized oyster bar habitat annually and may do so for up to four years. Efforts are currently underway to determine the activity patterns and habitat associations of Kemp's ridley turtles in the Cedar Keys area (Schmid, 1994).

Kemp's ridley turtles were numerous in the coastal waters of Florida prior to the 1950s (Carr, 1980). Data provided by Carr and Caldwell (1956; p. 21, Fig. 3) indicated that approximately 1% of the Kemp's ridley turtles captured at the Withlacoochee-Crystal River fishing grounds were early to mid-subadults (20–40 cm), 88% were mid- to late subadults (40–60 cm), and 11% were adult (60+ cm). There was also an unconfirmed report of a vitellogenic female weighing 42 kg with an estimated length of 75 cm. The presence of adult turtles in this 1955 survey corresponds to a period when there were relatively large, though declining, nesting aggregations of Kemp's ridley turtles (U.S. Fish and Wildlife Service and National Marine Fisheries Service, 1992). The lack of 20–40 cm turtles may be indicative of lower subadult recruitment resulting from the intensive egg harvesting that was occurring at this time (Hildebrand, 1982). In contrast, the catch at the Cedar Keys from 1986 to 1995 comprised 24% early to mid-subadults and 76% mid- to late subadults. Observations and captures of adult Kemp's ridley turtles at sea have become extremely rare owing to the greatly reduced nesting population, whereas the higher frequency of 20–40 cm turtles may suggest higher subadult recruitment as a result of nesting beach protection (Ogren, 1989).

Carr and Caldwell (1956) also described an apparent, though not statistically significant, seasonal shift in the mean carapace length of Kemp's ridley turtles taken in the commercial turtle fishery. Larger turtles (mean=54.9 cm) were captured early in the April to November fishing season, whereas smaller turtles predominated the mid- and late season catch (mean=50.3 cm and 52.1 cm, respectively). The seasonal mean carapace lengths reported in this earlier study were 5–10 cm greater than those recently recorded at the Cedar Keys. The authors' description of their measurement technique (". . . from the center of the anterior end of the carapace and the greatest posterior projection of the carapace.") corresponds to the standard straight-line carapace length. Furthermore, the entanglement nets used in the present study were the same mesh size as those used in the commercial turtle fishery. The perceived difference could be due to preference by the former turtle fishermen for larger, higher-priced turtles. Alternatively, the smaller mean carapace lengths of the present study may be indicative of an increased aggregate of smaller Kemp's ridley turtles along the west coast of Florida.

Despite numerous tagging studies, there is very little information available on the growth rates of wild Kemp's ridley turtles (Márquez M., 1994). The data treatments used to analyze Kemp's ridley turtle

growth at the Cedar Keys indicated an average increase of 4–5 cm/yr in carapace length. Growth rates of 6–9 cm/yr were obtained for Kemp's ridley turtles at Cape Canaveral with the same data treatments (Schmid, 1995). The higher growth rates observed for east coast turtles are possibly due to measurement errors identified in the Cape Canaveral study. Error was minimized in the Cedar Key study because all measurements were determined by the author using the same equipment and techniques. Assuming a constant growth rate of 4–5 cm/yr, a Kemp's ridley turtle would require 8–10 years to grow from a 20-cm postpelagic subadult (Ogren, 1989) to a 60-cm adult. An estimate of 10–12 years to maturity is calculated by combining the duration of the subadult stage with the estimated 2-year pelagic juvenile stage (Schmid and Ogren, 1990). This calculated age to sexual maturity is in agreement with Kemp's ridley growth models computed from skeletochronological age estimates (Zug and Kalb, 1989; Zug, 1990) and the combination of recapture data for Cape Canaveral and Cedar Keys (Schmid and Witzell, 1997).

The Kemp's ridley turtle aggregation at the Cedar Keys was considered an open "population" with recruitment in terms of postpelagic turtles and subadult immigrants from other locations and with losses in terms of death and permanent emigration to other subadult or adult aggregations. Annual estimates from the Jolly-Seber analysis were indicative of the catchable turtle population at Corrigan Reef within the months fished, which may or may not be representative of the entire aggregation in this area (Krebs, 1989). The relatively low number of recaptures, and corresponding low estimated capture probability, reduced the precision of the population estimates as evidenced by their high standard errors (Pollock et al., 1990). Nonetheless, general comments can be made concerning the estimates of recruitment and survival of Kemp's ridley turtles in the Cedar Keys area. The majority of turtles captured in this locality were mid- to late subadults; there were very few captures of postpelagic turtles. Therefore, provided that sampling bias due to the large-mesh nets was minimal, the high level of recruitment estimated from the Jolly-Seber analysis was presumably a result of immigration by larger subadult turtles. The low estimated survival rate was probably a function of emigration rather than high turtle mortality. However, there were no recaptures of turtles tagged at Cedar Key to indicate emigration to other localities and there was no systematic sampling of turtle strandings to demonstrate the extent of mortality in this region.

In conclusion, tagging studies conducted at the Cedar Keys are models for characterizing foraging populations of marine turtles and these efforts must be expanded to include regions not yet sampled in order to accurately manage these threatened and endangered species (Magnuson et al., 1990; Thompson et al., 1990; U.S. Fish and Wildlife Service and National Marine Fisheries Service, 1992). Areas where marine turtle congregate need to be identified through anecdotal information, historical records, incidental captures, and stranding data. In-water sampling programs should be conducted over an extended period of time to establish the distribution and abundance of turtles in areas of aggregation. After implementing a mark-recapture study, supplementary research activities may include the following: holding turtles for fecal sample collection; sampling blood for stress response, sex determination, and genetic analyses; monitoring local movements via radio and sonic telemetry; discerning migrations via satellite telemetry; and developing GIS models for marine turtle habitat associations.

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# Effects of hypoxia and temperature on survival, growth, and respiration of juvenile Atlantic sturgeon, *Acipenser oxyrinchus**

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**Abstract.**—Hypoxia in Chesapeake Bay has increased during the past century, coincident with the disappearance of Atlantic sturgeon spawning stocks. We hypothesized that Atlantic sturgeon young-of-the-year (YOY) might be more susceptible than other estuarine fishes to high temperature and low oxygen conditions, now prevalent in Chesapeake Bay. Atlantic sturgeon (10–70 g) were reared under conditions of hypoxia (2–3 mg/L dissolved oxygen) and normoxia (6–7 mg/L) at 19°C and 26°C for 10 days. High-temperature hypoxia resulted in lower survival (mean=6.3%) and respiration rate (mean=0.136 mg $O_2$/(g·h)). Low-temperature hypoxia resulted in a mean survival of 78% and mean respiration rate of 0.212 mg/(g·h). Under hypoxia, mean weight-specific growth rate was 1.27%/d, ca. threefold less than growth under normoxia. Temperature alone did not significantly affect growth rates. When sturgeon were denied access to the surface, growth rates were significantly diminished in both normoxic and hypoxic treatments. At low ambient oxygen levels and high temperature, denial of surface access was fully lethal within 30 hours. We conclude that increased incidence of summertime hypoxia during this century has degraded sturgeon nursery habitats in Chesapeake Bay.

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An economically important population of Atlantic sturgeon, *Acipenser oxyrinchus*, once inhabited Chesapeake Bay. During the late nineteenth century, Chesapeake Bay supported the second greatest caviar fishery in the eastern United States (Murawski and Pacheco, 1977). In the early 1900s, the population collapsed. In Maryland, fishery landings declined from 74,500 kg, in 1904, to 320 kg in 1920 (Hildebrand and Schroeder, 1928). Atlantic sturgeon have not recovered in Chesapeake Bay (Spier and O'Connell, 1996). The last fish legally harvested in Chesapeake Bay, a mature female, was captured in 1970 from the Potomac River. The spawning population of Atlantic sturgeon may have been extirpated from Chesapeake Bay (Speir and O'Connell, 1996; Grogan and Boreman[1]).

State, federal, academic, and nonprofit organizations have begun to mobilize public interest and support for an aquaculture-based restoration program for Atlantic sturgeon in Chesapeake Bay. A principal assumption for Atlantic sturgeon restoration is that deleterious conditions that led to the extirpation of the population (e.g. loss of habitat or over fishing) are now abated. Therefore, it is critical to evaluate possible causes for Atlantic sturgeon extirpation from Chesapeake Bay before state and federal agencies move forward with a large-scale aquaculture-based restoration program.

We hypothesize that increased hypoxia in Chesapeake Bay resulted in reduced habitat for Atlantic sturgeon and contributed to their decline. During this century, periodic increases (albeit small) in Atlantic sturgeon abundances have occurred in the southern and northern extent of the species' range (Murawski and Pacheco, 1977). However, no evidence exists for periodic recoveries of Atlantic sturgeon in Chesapeake Bay. The period of population decline and low abundance in Chesapeake Bay corresponds to a period of poor water quality, from 1950 to present, caused by increased nutrient loading and increased spatial and temporal frequency of hypoxia (Officer et al., 1984; Mackiernan, 1987; Jordan et al., 1992; Kemp et al., 1992; Cooper and Brush, 1993).

* Contribution 3060 of the Chesapeake Biological Laboratory, Center for Environmental Science, University of Maryland, Solomons, MD 20688-0038.

[1] Grogan, C. S., and J. Boreman 1997. Determining the probability that historical populations of fish species are now extirpated. Unpubl. manuscr., U. Mass. Amherst, MA, 25 p.

The goal of the study was to investigate the effects of dissolved oxygen and temperature on growth, survival, and respiration of juvenile (young-of-the-year) Atlantic sturgeon. High temperatures are known to amplify negative effects of hypoxia on growth and survival of estuarine fishes (Coutant, 1985). Habitats in Chesapeake Bay that satisfy both temperature and dissolved oxygen (DO) preferences of Atlantic sturgeon may be limiting during the summer as have been demonstrated for striped bass (Coutant and Benson, 1990; Brandt and Kirsch, 1993). In this study we define hypoxia as oxygen concentrations <4.0 mg/L. Hypoxia has been defined previously as <2 mg/L for Chesapeake Bay (Phil et al., 1991; Harding et al., 1992), an ambient oxygen level that is detrimental to benthic infaunal production. This definition, however, may be too stringent for fishes because oxygen concentrations at this level are often lethal (Brett, 1970; Jordan et al., 1992).

A nested-multifactorial experiment was designed to investigate the effects of temperature and dissolved oxygen on growth, respiration, and survival of young-of-the-year Atlantic sturgeon. During the course of our experiments we observed that fish in hypoxic conditions frequently surfaced, often breaking the surface of the water with their snout. Therefore we included surface access as a third factor in our investigation—whether this behavior might benefit growth and survival under conditions of oxygen stress.

## Methods

### Experimental material

Juvenile Atlantic sturgeon were obtained from the U.S. Fish and Wildlife Service, Northeast Fishery Center, Lamar, Pennsylvania (Hendrix, 1995). During June 1995, Center personnel collected a large female (2.4-m total length) and three male Atlantic sturgeon from the Hudson River near Hyde Park (River km 135). Fish were transported to the Center for artificial spawning and for larval rearing. Larvae and early juveniles were reared at the Center at 17°C and 1 ppt salinity. A failure in the water heating system at the Center caused juveniles, age 45 to 60 days after hatching, to experience low water temperatures, ca. 10°C. At 60 days after hatching, 500 juveniles (0.3–2.0 g wet weight) were transported in an oxygenated container to Chesapeake Biological Laboratory and acclimated to 19°C and 2 ppt salinity over a 10-d period. Juveniles were reared in sixteen 40-liter tanks and fed Biokyowa© fry feed (700–2000 μm diameter) ad libitum until they were ca. 5 grams wet weight (>10 cm total length) and large enough to be handled with little or no stress for scute-clips (see below).

### Nested growth and survival experiments

A nested multivariate experiment (Fig. 1) evaluated survival and growth rates in relation to access to surficial water (sealed or unsealed tank), temperature (~20°C and ~26°C), dissolved oxygen (~3 mg/L or ~7 mg/L), and tank replication. The nested design directed the analysis of variance to occur in hierarchical order at four levels. The model of the nested design for growth rate was

$$y_{ijklm} = \mu + \tau_i + \beta_{j(i)} + \gamma_{k(ij)} + \theta_{\lambda(ijk)} + \varepsilon_{(ijkl)m},$$

where $y_{ijklm}$ = the growth rate response by individual juveniles;
$\mu$ = overall mean;
$\tau_i$ = the effect of the $i$th surface access category;
$\beta_{j(i)}$ = the effect of the $j$th temperature;
$\gamma_{k(ij)}$ = the effect of the $k$th oxygen level;
$\theta_{l(ijk)}$ = the effect of the $l$th tank (replicate); and
$\varepsilon_{(ijkl)m}$ = the random error component.

The model of the nested design for survival rate was

$$S_{ijkl} = \mu + \tau_i + \beta_{j(i)} + \gamma_{k(ij)} + \varepsilon_{l(ijk)},$$

where $S_{ijkl}$ = the arcsine-transformed survival rate for each replicate.

Statistical significance for factors was accepted at $\alpha = 0.05$ (type-I sum of squares for type-I error). To remove possible effects due to differences in fish size among experiments and experimental levels, initial fish weight was included in ANOVAs as a covariate. Calculations of variances and significance tests were performed by using PC-SAS, PROC NESTED (SAS, 1982). Survival data were arcsine transformed to meet assumptions of normally distributed error.

Four 10-day experiments were conducted under the four combinations of surface access, temperature, and dissolved oxygen, each replicated twice. In the high-temperature hypoxia treatments, high mortality was observed. Because we wished to have greater confidence in associating low survival with high-temperature hypoxia, we repeated the treatments with surface access and high temperature (at both low and high DO levels) for a total of four replicates (Fig. 1).

Experimental tank dimensions were 78-cm diameter, 46-cm height, and 220-liter volume. External

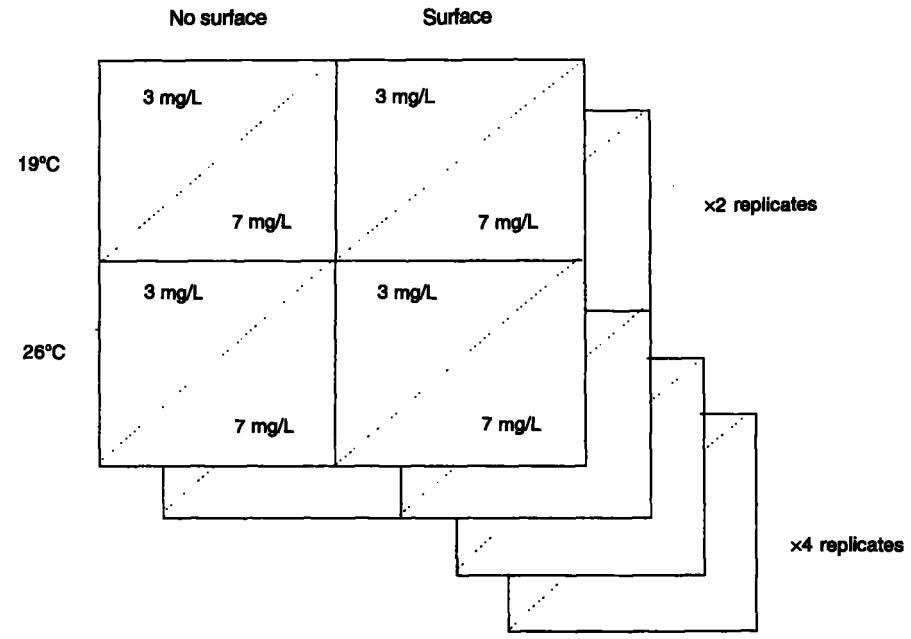


**Figure 1**

Nested experimental design. Replicates are presented as layers. Dissolved oxygen rates (3 or 7 mg/L) were nested within temperature and surface access levels.

stand-pipes for flow-through water allowed sturgeon to use the entire bottom surface. During the experiments clear plexiglass lids were attached to the tanks with clamps and duct tape. A large hole (5-cm diameter) in each lid, fitted with a stopper, permitted access to the tank for feeding of fish, for periodic checks of water quality, and for removal of dead individuals. Hoses for air and water supply also passed through the lid. In the tanks that permitted access to the air-water interface, water level was maintained at 5 cm below the lid. In treatments designed to limit access to the surface, lids were sealed to the tank and tanks were filled completely. Two head tanks delivered water at either 19°C or 26°C to experimental tanks, each maintained at a rate of 1.2 –1.5 L of flow-through water/min. Dissolved oxygen was controlled by maintaining hypoxic conditions in head-tanks and by adding aeration directly to normoxic treatment tanks. Hypoxic levels (2.5–3.0 mg/L) were maintained in head-tanks by mixing hypoxic well water (<2 mg/L) with oxygenated Patuxent estuary water (6 mg/L). Thus, salinity varied slightly between experiments but was always within the range 1.5–3 ppt. When necessary, water was aerated to bring oxygen levels to 2.5 mg/L in the head-tank. Normoxic treatment water was a mixture of well water and Patuxent estuary water. Dissolved oxygen levels were well mixed (homogenous) in the tanks owing to their shallow design, flow-through water, and constant swimming of YOY sturgeon. Lighting was provided on a 12:12 h light:dark cycle.

With the exception of the 26°C and no-surface-access treatment, temperature and oxygen concentrations were maintained within 10% of their prescribed levels (19 or 26°C, 3 or 7 mg/L). In the 26°C sealed experiment, aeration supplied to the head-tank was insufficient to attain oxygen conditions close to 7 mg/L for the normoxic treatment (mean replicate dissolved oxygen concentrations were 5.10 and 5.25 mg/L). In the hypoxic sealed treatment (mean replicate dissolved oxygen concentrations were 3.76 and 4.44 mg/L), dissolved oxygen was deliberately held above 3 mg/L because this level with high temperature had been observed previously to be lethal in unsealed tanks. Despite these elevated "hypoxic" conditions, the combination of high temperature and low oxygen was fully lethal in the sealed tanks (see below).

Juveniles (8 to 30 grams wet weight) were acclimated to experimental conditions over a 4-d period. On day 0 of each experiment, lengths and wet weights (juveniles weighed in water on a top-loading balance) were recorded and a dorsal scute(s) clipped to identify each individual. In preliminary trials, we found that scute clips did not significantly affect growth

rate. Regeneration of the scute did not obscure the clip during the 10-d experiments. Six to eight juveniles were placed in each experimental tank and fed the formulated diet (2-mm pellets) at 2.5% body weight per day. Fish were fed at 06:00, 10:00, 14:00, 18:00, and 20:00 h. Water quality was checked during feeding times and any remaining food or feces were siphoned prior to feeding. Food amounts were adjusted when mortalities occurred. On day 10 of the experiment, individual weights and lengths were recorded. Weight-specific absolute and instantaneous growth rates were determined for the experimental period according to Ricker (1975). In instances where juveniles died before the end of the experiment, individuals surviving >3 days of experimental conditions were included in the analysis of treatment effects on growth.

### Respiration experiment

Respiration was estimated over a 42-h period for four combinations of temperature (19 or 26°C) and dissolved oxygen (~3 or ~7 mg/L) each replicated once. Juveniles were acclimated for a 4-day period and starved 12 h prior to the start of respiration measures. Seven juveniles were weighed (in water) and placed in each tank "respirometer." The tanks were sealed (no air gap). Oxygen levels were maintained by aerating the head-tanks, rather than each experimental tank. There was no feeding during the 42-h experiments. Inflow and outflow temperature, salinity, oxygen content, and flow rate were measured in experimental and control "blank" tanks (Cech, 1990) at 06:00, 10:00, 14:00, 18:00 and 22:00.

Experimental conditions of temperature were maintained within 1°C of the prescribed treatment level (19 or 26°C) (Table 1). Oxygen levels varied substantially from the prescribed levels between temperatures. For the hypoxic treatments, oxygen was provided at significantly higher levels ($P$=0.001) at 26°C (4.09 ±0.07 mg/L) than at 19°C (2.51 ±0.05 mg/L). This was intentional because survival and growth experiments had shown that DO levels <3.5 mg/L in concert with high temperature were lethal. Despite this precaution, all fish at 26°C and at low oxygen level perished within 24 hours. At the high-level DO treatments, oxygen conditions were ca. 1 mg/L higher at 19°C than at 26°C. Total biomass of the 7 fish per tank ranged from 157.6 to 248.2 grams (Table 1).

Respiration (i.e. oxygen uptake) was estimated (Cech, 1990) as

$$R = (M_E - M_C)/B$$
$$M_{E,C} = \left((C_I - C_O\right)V$$

where $R$ = weight-specific $O_2$ consumption rate (mg $O_2$/(g·h);
$M_{E,C}$ = $O_2$ consumption rate in experimental $E$ or control $C$ tanks (mg $O_2$/h);
$B$ = combined wet weight (biomass) of sturgeon juveniles (g);
$C_I$ = $O_2$ concentration in inflowing water (mg $O_2$/L);
$C_O$ = $O_2$ concentration in outflowing water (mg $O_2$/L); and
$V$ = water flow rate (L/h).

## Results

### Survival

Deaths were observed only in hypoxic treatments (Table 2). At hypoxic level, survival was substantially lower at 26°C (mean=6.3% survival) than at 19°C

**Table 1**

Replicate tank environmental conditions and respiration rates (mean ± standard error) for respiration experiment. Dissolved oxygen (DO) levels, low or high, refer to prescribed levels of 3 mg/L and 7 mg/L, respectively. Inflow oxygen and tank temperature refer to actual conditions provided to tanks. Biomass is the total initial weight of the seven sturgeon used in each replicate.

| Temperature level | DO level | Inflow oxygen mg/L | Tank temperature | Biomass (g) | Respiration rate mg $O_2$/g·h |
|---|---|---|---|---|---|
| 26°C | Low | 3.762 ± 0.163 | 25.20 ± 0.04 | 216.6 | 0.175 ± 0.042 |
| | | 4.436 ± 0.209 | 25.34 ± 0.02 | 181.3 | 0.103 ± 0.030 |
| | High | 6.310 ± 0.075 | 25.54 ± 0.02 | 188.1 | 0.245 ± 0.028 |
| | | 6.259 ± 0.088 | 25.47 ± 0.02 | 179.6 | 0.307 ± 0.020 |
| 19°C | Low | 2.536 ± 0.029 | 19.51 ± 0.02 | 196.3 | 0.202 ± 0.028 |
| | | 2.495 ± 0.020 | 19.43 ± 0.02 | 157.6 | 0.214 ± 0.022 |
| | High | 7.361 ± 0.060 | 19.73 ± 0.06 | 189.5 | 0.228 ± 0.028 |
| | | 7.273 ± 0.058 | 19.67 ± 0.04 | 249.2 | 0.207 ± 0.020 |

**Table 2**

Replicate tank deaths during the nested survival and growth experiment. Experiments are labeled according to the temperature treatment and whether tanks were sealed or unsealed (unsealed tanks permitted access by sturgeon to surface water). Dissolved oxygen (DO) levels, low and high, refer to prescribed levels of 3 mg/L and 7 mg/L, respectively. Rep. = replicate(s).

| Experiment | DO level | Rep. | Experimental day | | | | | | | | | | Survival (%) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | |
| 26°C unsealed 1 | Low | 1 | | | 6 | 1 | 1 | | | | | | 0 |
| | | 2 | | | 2 | | 4 | | | | | 2 | 0 |
| | | 3 | | 4 | | | 1 | 2 | 1 | | | | 0 |
| | | 4 | | | | 1 | | 1 | | 1 | 1 | | 50 |
| 26°C unsealed 2 | High | 1 | | | | | | | | | | | 100 |
| | | 2 | | | | | | | | | | | 100 |
| | | 3 | | | | | | | | | | | 100 |
| | | 4 | | | | | | | | | | | 100 |
| 26°C sealed | Low | 1 | 8 | | | | | | | | | | 0 |
| | | 2 | 7 | 1 | | | | | | | | | 0 |
| | High | 1 | | | | | | | | | | | 100 |
| | | 2 | | | | | | | | | | | 100 |
| 19°C unsealed | Low | 1 | | | 1 | | 1 | | | | | | 75 |
| | | 2 | | | 1 | | | 1 | | | | | 75 |
| | High | 1 | | | | | | | | | | | 100 |
| | | 2 | | | | | | | | | | | 100 |
| 19°C sealed | Low | 1 | | | | | | | 1 | | | | 88 |
| | | 2 | | | | | | 1 | 1 | | | | 75 |
| | High | 1 | | | | | | | | | | | 100 |
| | | 2 | | | | | | | | | | | 100 |

(mean=78.3% survival). No significant difference was found in overall survival rate between sealed and unsealed tanks ($P$=0.54). In unsealed tanks, deaths were distributed throughout the 10-d experimental period. In the 26°C sealed-hypoxic level tanks, all individuals succumbed within the first 30 hours of the experiment. Moribund sturgeon were observed at the air-water interface in unsealed tanks, or just below the lid in sealed tanks. Fin margins of dead individuals were perfused with blood, an indicator of oxygen deprivation (Jobling, 1995).

## Growth

Across replicates, growth rates ranged in weight from 0.3% to 5.1% per day (Table 3). Sturgeon experienced positive growth in weight and length under all experimental conditions. Initial mean weights and lengths varied substantially among experiments; range was 10.94 to 69.20 g in weight and 14.59 to 26.60 cm in length. Absolute growth in weight was positively related to initial size (regression analysis; $P$<0.01); tanks with fish having initial mean weights greater than 50 g showed the highest absolute growth rates (>1.0 mg/d). Because initial size covaried with growth rate, initial weight was used as a covariate in statistical analyses of treatment effects.

Analysis of variance of instantaneous growth rate showed significant effects due to surface access and oxygen level (Table 4); temperature, replicate, and individual fish did not explain significant variance, although at 7 mg/L DO there was a trend for lower growth rates at 26°C than at 19°C (Fig. 2, Table 3). Mean growth rates were 2.9 times less at 3 mg/L (1.27%/d) than at 7 mg/L (3.62%/d). Sealed tanks showed consistently lower growth rates than those with surface access. The effect was greatest at 3 mg/L oxygen. Only 0.3%/d weight-specific growth was observed in the 19°C sealed tanks, and all fish perished before growth determinations could be made in the 26°C sealed tanks. Absolute growth in weight was significantly affected by surface access, temperature, surface access in combination with temperature interaction, and by oxygen level. Absolute growth rate was higher when surface access was allowed and at the higher DO level; absolute growth rate was inversely related to temperature.

## Respiration

Respiration rates measured over the entire experiment ranged from 0.05 to 0.55 mg $O_2$/(g·h) (Fig. 3). Respiration rates were normally distributed for the high oxygen treatment with a mean of 0.245 ± 0.013

## Table 3

Growth rates (mean ± standard error) of Atlantic sturgeon during the laboratory experiment. Growth rates in weight and length are instantaneous rates. Absolute growth rates in weight is presented under the heading mg/d. Experiments are labeled according to the temperature level and whether tanks were sealed or unsealed (unsealed tanks permitted access by sturgeon to surface water). Dissolved oxygen (DO) levels, low and high, refer to prescribed levels of 3 mg/L and 7 mg/L, respectively. *n* = number of individuals in each tank. Rep. = replicate(s).

| Experiment | DO level | Rep. | Growth rate in weight (per day) | mg/d | Growth rate in length (per day) | *n* |
|---|---|---|---|---|---|---|
| 26°C unsealed | Low | 1 | 0.023 ± .006 | 0.345 ± 0.094 | ~0 | 2 |
| | | 2 | 0.013 ± 0.003 | 0.202 ± 0.056 | ~0 | 6 |
| | | 3 | 0.006 ± 0.005 | 0.093 ± 0.062 | 0.003 ± 0.001 | 4 |
| | | 4 | 0.029 ± 0.019 | 0.324 ± 0.192 | 0.003 ± 0.001 | 8 |
| | High | 1 | 0.037 ± 0.004 | 0.524 ± 0.076 | 0.010 ± 0.001 | 8 |
| | | 2 | 0.037 ± 0.006 | 0.643 ± 0.116 | 0.012 ± 0.002 | 8 |
| | | 3 | 0.036 ± 0.007 | 0.587 ± 0.112 | 0.012 ± 0.002 | 8 |
| | | 4 | 0.036 ± 0.004 | 0.789 ± 0.117 | 0.015 ± 0.001 | 8 |
| 26°C sealed | Low | 1 | Lethal | | | 0 |
| | | 2 | Lethal | | | 0 |
| | High | 1 | 0.029 ± 0.001 | 2.220 ± 0.059 | 0.006 ± 0.001 | 6 |
| | | 2 | 0.025 ± 0.001 | 2.015 ± 0.178 | 0.007 ± 0.001 | 6 |
| 19°C unsealed | Low | 1 | 0.013 ± 0.002 | 0.185 ± 0.029 | 0.005 ± 0.001 | 7 |
| | | 2 | 0.011 ± 0.003 | 0.129 ± 0.037 | 0.005 ± 0.001 | 7 |
| | High | 1 | 0.050 ± 0.005 | 0.721 ± 0.057 | 0.014 ± 0.001 | 8 |
| | | 2 | 0.045 ± 0.002 | 0.719 ± 0.044 | 0.015 ± 0.001 | 8 |
| 19°C sealed | Low | 1 | 0.003 ± 0.001 | 0.072 ± 0.030 | 0.004 ± 0.001 | 8 |
| | | 2 | 0.003 ± 0.001 | 0.071 ± 0.031 | 0.004 ± 0.001 | 8 |
| | High | 1 | 0.028 ± 0.003 | 1.887 ± 0.253 | 0.009 ± 0.001 | 6 |
| | | 2 | 0.031 ± 0.002 | 2.270 ± 0.197 | 0.008 ± 0.001 | 6 |

## Table 4

Nested analysis of variance of surface access, temperature, oxygen level, replicate and individual effects on growth rate. Initial weight was used as a covariate in the analyses. Sealed refers to whether tanks were sealed or unsealed (unsealed tanks permitted access by sturgeon to surface water). Designated temperature and oxygen levels were 19°C and 26°C, and 3 mg/L and 7 mg/L, respectively. Factors in parentheses indicate the nesting procedure. For example "Oxygen (Sealed-Temperature)" refers to variance explained by oxygen level nested within combinations of surface access and temperature.

| Type of variable | Variable | df | Sum of squares | Significance level (*P*) |
|---|---|---|---|---|
| Instantaneous growth rate in weight | | | | |
| Covariate | Initial weight | 1 | 0.3892 | 0.0001 |
| Class variables | Sealed | 1 | 0.0392 | 0.019 |
| | Temperature (sealed) | 2 | 0.0086 | 0.54 |
| | Oxygen (sealed-temperature) | 3 | 0.0981 | 0.0039 |
| | Tank (sealed-temperature-oxygen) | 7 | 0.0097 | 0.99 |
| | Individual (sealed-temperature-oxygen-tank) | 14 | 0.0077 | 0.99 |
| Absolute growth rate in weight | | | | |
| Covariate | Initial weight | 1 | 0.0839 | 0.0001 |
| Class variables | Sealed | 1 | 0.0445 | 0.0001 |
| | Temperature (sealed) | 2 | 0.0523 | 0.0002 |
| | Oxygen (sealed-temperature) | 3 | 0.7734 | 0.0001 |
| | Tank (sealed-temperature-oxygen) | 7 | 0.0293 | 0.17 |
| | Individual (sealed-temperature-oxygen-tank) | 14 | 0.0194 | 0.92 |

mg $O_2$/(g·h). In relation to the high oxygen treatment, hypoxic oxygen treatment respiration rates were skewed towards lower rates with a mean of 0.174 ±0.016 mg $O_2$/(g·h). Two individual tank respiration rates for the hypoxic treatment were exceptionally high (Fig. 3). These data were measured at 0 hours from tanks at 19°C and 26°C and may have reflected an insufficiently long period of acclimation prior to the experiments. Therefore, we chose to exclude measures taken at 0 hours in the analysis of variance on respiration rates.

Respiration rates were significantly influenced by oxygen level ($P$=0.001), by the interactions between temperature and oxygen ($P$=0.04), and by the interaction among temperature, oxygen, and replicate ($P$=0.04). Mean respiration rates were 0.187 ± 0.012 and 0.247 ± 0.015 mg $O_2$/(g·h) under hypoxia and normoxia, respectively (Table 1). At high oxygen levels, 26°C respiration rates (mean=0.281 ±0.023 mg $O_2$/(g·h)) tended to be higher than 19°C respiration rates (mean=0.210 ±0.021 mg $O_2$/(g·h)). However, the converse was true at hypoxic levels; mean respiration rate at 26°C (0.136 ±0.027 mg $O_2$/(g·h)) was significantly lower than at 19°C (0.212 ±0.021 mg $O_2$/(g·h)). For all but the 26°C and hypoxic-level combination, replicate rates were similar. Respiration for the second replicate for the 26°C and hypoxic-level combination was substantially lower than other replicates that may have produced the significant interaction among temperature, oxygen, and replicate factors in the analysis of variance. In a procedure to reduce bias associated with deviations of actual inflow DO levels from those prescribed, an analysis of variance was conducted for which the inflow oxygen concentration was a covariate. After viariance associated with individual tank DO conditions was removed, the effect of oxygen level (high or low) remained significant ($P$=0.04).

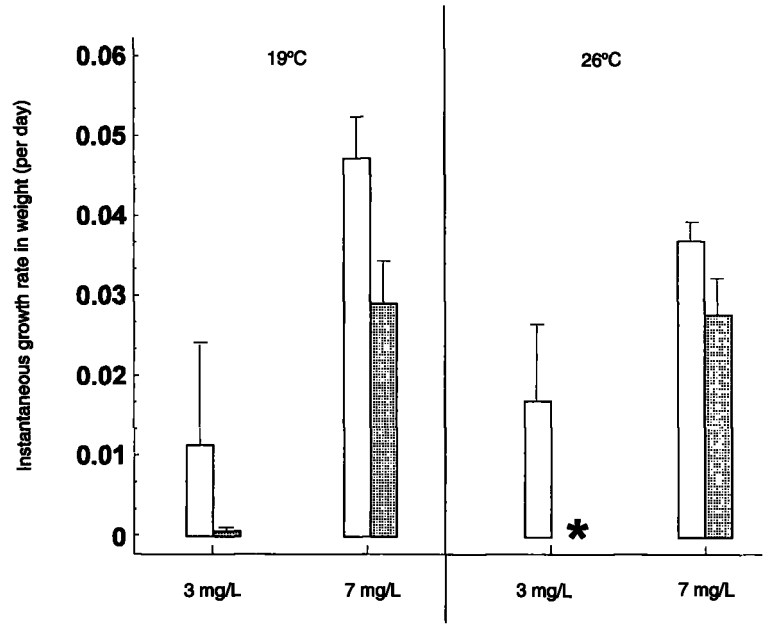


**Figure 2**

Effects of dissolved oxygen concentration on instantaneous growth rates in weight (per day) (mean ± 95% confidence interval) of young-of-the-year Atlantic sturgeon at two temperatures and different tank configurations. Stippled bars indicate treatments denying surface access. Replicate tanks were combined for each treatment level comination. The asterisk indicates that complete mortality occurred for that treatment.

## Discussion

Juvenile Atlantic sturgeon were vulnerable to conditions of high temperature and low oxygen. In five out of six replicates (sealed and unsealed tanks combined) at 26°C and ~3 mg/L DO, all juveniles died. All sturgeon that died showed a perfusion of blood along the margins of their fins, indicative of oxygen deprivation (Jobling, 1995). Reduced oxygen levels resulted in a threefold reduction in growth rate and a 50% reduction in routine respiration rate. At 19°C, respiration rates were similar between hypoxic and normoxic treatments. But, at the 26°C hypoxic treatment, mean respiration rates dropped below 2 mg $O_2$/(g·h) and all sturgeon died. We speculate that these fish were unable to supply sufficient oxygen to their tissues at this level of reduced respiration.

Despite reduced survival and respiration in conditions of low dissolved oxygen, feeding continued and fish grew. Apparently, Atlantic sturgeon were able to reduce activity but still feed and allocate some energy to growth. In unsealed tanks, weight gain ranged from 1.1% to 2.9%, and from 3.6% to 5.0% body weight per day, at ~3 and ~7 mg $O_2$/L, respectively. Cech et al. (1984) also observed continued growth by juvenile white sturgeon (*Acipenser transmontanus*) (ca. 0.5 to 5 g) under conditions of hypoxia. Daily weight-specific growth rates of white sturgeon varied between 1.6% (15°C) and 2.9% (25°C) under normoxic conditions and between 0.6% (15°C) and 2.3% (25°C) under hypoxic conditions. Growth rates measured by Cech et al. (1984) under hypoxia were substantially higher than those that we ob-

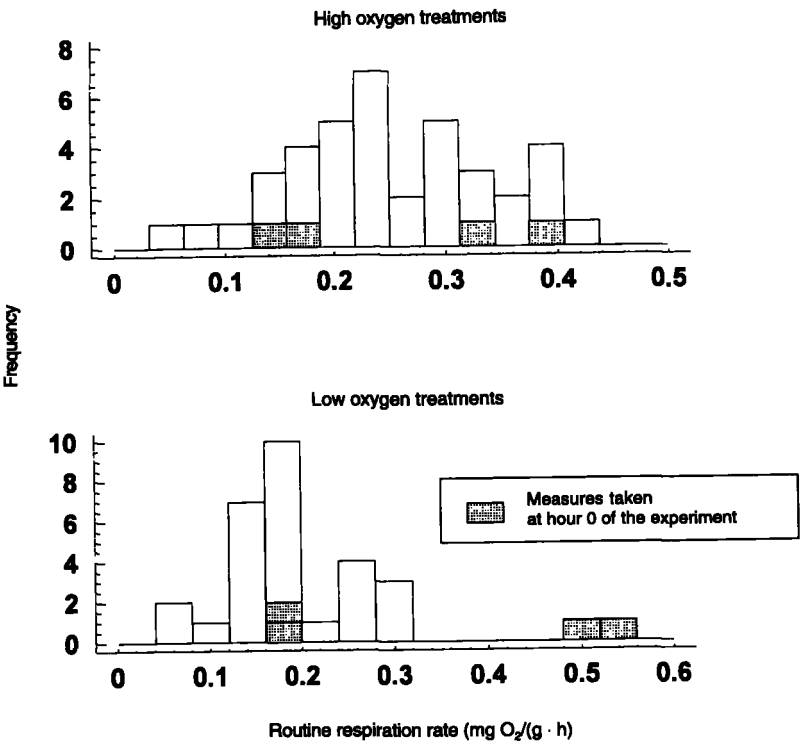


**Figure 3**

Frequency histogram of respiration rates for young-of-the-year Atlantic sturgeon exposed to either high (7 mg/L) or low levels (3 mg/L) of dissolved oxygen. Measures taken at the initiation of the experiment (hour 0) are stippled.

served. This may be attributable to a higher designated oxygen level for hypoxic treatments (<5 mg/L), differences between the two species, or an ontogenetic effect. Juvenile white sturgeon were substantially smaller (initial weight 0.5 grams) than those used in our study (mean initial weight=23.7 grams).

Our study was unique in examining the effects of long-term hypoxia on routine metabolism. Other studies have examined the effects of hypoxia on sturgeon respiration in short-term respirometry studies (Table 5). Investigations on white sturgeon and Siberian sturgeon (*Acipenser baeri*) have indicated reduced rates of respiration under hypoxic conditions. An ontogenetic trend of decreasing routine metabolic rates with increased mass, which is typical in fishes, was also suggested in the comparison of studies. Metabolic rates under normoxic conditions ranged from 0.9 mg $O_2$/(g·h) (1–2 g fish) to 0.055 mg $O_2$/(g·h) (1800-g fish). Metabolic rates (0.2

**Table 5**

Summary of studies on hypoxia and routine metabolism for sturgeons. Oxygen concentrations and consumption rates have been converted to common units (mg $O_2$/L or mg $O_2$/(g·h) from reported units (e.g. mm Hg or µmol $O_2$/kg(g·h) for several of the studies. Wt = wet weight; Hyp = hypoxia treatment; Norm = normoxia treatment; Swim = velocities were provided in respirometer to induce swimming velocities; S = salinity; and T = temperature.

| Species | Wt (g) | Treatments | Routine metabolism mg/(g·h) | S (ppt) | T (°C) | Study duration | Reference |
|---|---|---|---|---|---|---|---|
| *Acipenser transmontanus* | 0.5–5 | Hyp: 4.7 - 5.7 mg/L<br>Norm: 6.8 - 8.2 mg/L | Not measured | 0 | 15, 20, 25 | 30 d | Cech et al., 1984 |
| *A. baeri* | 1–2 | High density<br>Low density | 0.3 to 0.5<br>0.4 to 0.9 | 0 | 22–24 | 2–12 h | Khakimullin, 1987 |
| *A. baeri* | 3–7 | Routine<br>Swim: 5–30 cm/sec | 0.3 to 0.7<br>0.4 to 3.6 | 0 | 22–24 | 3 h | Khakimullin, 1988 |
| *A. oxyrinchus* | 12–69 | Hyp: 2.5–4.4 mg/L<br>Norm: 6.3–7.4 mg/L | 0.1 to 0.2<br>0.2 to 0.3 | 1.8–2.5 | 19, 26 | 10 d | This study |
| *A. transmontanus* | 950 | Hyp: 1.7–6.3 mg/L<br>Norm: 9.8 mg/L | ~0 to 0.015<br>0.079 | 0 | 15 | 4.5 h | Burggren and Randall, 1978 |
| *A. baeri* | 1800 | Hyp: 1.3–3.8 mg/L<br>Norm: 8.2 mg/L | 0.023<br>0.055 | 0 | 15 | 3.5 h | Nonnotte et al., 1993 |
| *A. transmontanus* | 2000 | Hyp: 4.7–5.9 mg/L<br>Norm: 7.7–8.9mg/L | 0.090<br>0.098 | 0<br>0 | 18 | 24 h | Ruer et al., 1987 |

to 0.3 mg $O_2$/(g·h) and fish sizes (12 to 69 g) in our experiments were both intermediate within this range.

### Surface behavior

In the nested growth and survival experiment, surface access influenced both growth and survival rates. Eliminating surface accesses in tanks reduced growth rates by ca. 35%, and fivefold at high and low levels of DO, respectively. The effects of denying surface access under "hypoxia" at 26°C was fully lethal within a 30-h period. In the 26°C hypoxic treatments that allowed surface access, the majority of juveniles survived the first 5 days of exposure, although they too eventually died.

Many fishes surface in hypoxic environments to convey relatively oxygen-rich water, located at the air-water interface, across their gills. In laboratory experiment, access to surface waters may have increased the effective level of DO above nominal levels, resulting in improved growth and survival. Alternatively, aerial respiration cannot be ruled out for sturgeon that are physostomous. Histological studies should be undertaken to investigate whether the swim bladder of Atlantic sturgeon contains a vascular structure, apart from the gas gland, which meets the criteria for an aerial respiratory organ. No such structure has been identified in any sturgeon species.

### Reasons for decline of Atlantic sturgeon in Chesapeake Bay

We conclude that increased frequency of hypoxia in Chesapeake Bay during this century (Officer et al., 1984; Cooper and Brush, 1993) was detrimental to Atlantic sturgeon production. Recent water quality monitoring has shown that during summer months (mid-June through mid-September), temperatures >25°C and DO levels <4.0 mg $O_2$/L are prevalent in Chesapeake Bay benthic habitats (Breitburg, 1990, 1992; Phil et al., 1991). Our laboratory experiments showed that juvenile Atlantic sturgeon were less tolerant of summertime hypoxia than were other juvenile estuarine species. Young-of-the-year spot, *Leiostomus xanthurus* (total length 10–20 cm), survived long-term (>1 week) experimental exposure of 2.4–3.0 mg/L at 25°C, but 0.8–1.0 mg/L DO was fully lethal (Phil et al., 1991). Juvenile and adult hogchokers, *Trinectes maculatus* (Phil et al., 1991), and naked gobies, *Gobiosoma bosc* (Brietburg, 1992), can tolerate several-day periods of 0.5–1.0 mg/L DO.

Our laboratory experiments did not consider behaviors that can 1) reduce exposure to hypoxic waters and 2) compensate for reduced dissolved oxygen levels. Phil et al. (1991) and Brietburg (1992) have provided field evidence that fish will escape hypoxic conditions through local migrations. These include vertical or shoalward emigrations from hypoxic or anoxic bottom habitats. Following hypoxic events, bottom habitats are recolonized. Further, short-term episodic hypoxia may benefit bottom-feeding fish. Burrowing macrobenthic prey will emerge at DO levels <2 mg/L, increasing their vulnerability to predation by fish that can tolerate short-term excursions into hypoxic waters (Phil et al., 1992). If unable to escape hypoxic conditions, sturgeon may be able to compensate by either surfacing to exploit higher oxygen concentrations in surficial water or in the atmosphere or by adjusting their metabolic rate (e.g. through reduced swimming [Cech et al., 1984]).

Hudson River "strain" Atlantic sturgeon, used in our experiment, might have exhibited a different response to hypoxia than a strain native to Chesapeake Bay. The Hudson River rarely becomes hypoxic (Cooper et al., 1988). Therefore, Hudson River Atlantic sturgeon may not have been adapted to hypoxic conditions. An aquaculture study by Serov et al. (1988) on stellate sturgeon (*A. stellatus*) showed that heterozygosity in the LDH gene conferred survival advantages to hypoxia and high temperature. Therefore, it is conceivable that selection of Chesapeake Bay Atlantic sturgeon to hypoxic conditions could have occurred over several generations. However, because generation time is extremely high in Atlantic sturgeon (c.a. 29 years [Stevenson and Secor, 1996]) and because hypoxia increased rapidly during this century in the Chesapeake Bay, Chesapeake Bay Atlantic sturgeon may not have been able to recoup historical abundances by dint of selection to low-oxygen conditions. In addition, Hudson River Atlantic sturgeon juveniles >80 cm TL are known to visit Chesapeake Bay during summer months (Dovel and Berggren, 1983). Presumably, these fish could have adapted to Chesapeake Bay conditions. Serov et al.'s (1988) observation that water quality experienced by juveniles in culture influences genotypic frequencies has important implications for the use of hatchery-produced sturgeon in restoration programs and merits additional research.

Scientists and managers are now considering a restoration program for Atlantic sturgeon in Chesapeake Bay and elsewhere (St. Pierre, 1994; Secor, 1995). The feasibility of a sturgeon restoration program must address the same issues that led to the sturgeon's decline. If these conditions persist in Chesapeake Bay, a restoration program cannot be easily justified. Necessary conditions for population recovery must include increased population abundance, and improvement in the quality and size and number of essential habitats. Population abundance

can be increased by deliberately releasing artificially produced progeny (parentage from an outside population like the Hudson River population), by imposing a moratorium on sturgeon harvests, and by making efforts to reduce sturgeon taken as bycatch in other fisheries.

A critical and unresolved question is whether habitat quality remains sufficient at present in the Chesapeake Bay to support Atlantic sturgeon growth, survival, and reproduction. An encouraging finding has been a trend in improved water quality and macrobenthic production in Chesapeake Bay tributary nursery habitats, the apparent result of nutrient abatement programs (Dauer, 1995).

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# Multiple population bottlenecks and DNA diversity in populations of wild striped bass, *Morone saxatilis*

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**Abstract.**—Striped bass, *Morone saxatilis*, in the Coos River, Oregon, are derived from natural colonists from San Francisco Bay, which in turn were intentionally transplanted from the Hudson River. Because of founder effects, this unusually well-documented colonization sequence should have resulted in diminished genetic variability in the penultimate and ultimate populations, which may have been further compounded in the Coos River population by subsequent drastic reductions in its abundance. To test whether these sequential bottlenecks reduced genetic diversity we surveyed both nuclear DNA (nDNA) and mitochondrial DNA (mtDNA) variation in the Coos River population and in both populations along the historical pathway that led to its founding. There was no evidence of reduced nDNA diversity among these populations at the three loci examined. However, the number of mtDNA haplotypes revealed decreased from 8 in the original Hudson River population, to 5 in the San Francisco Bay population, to only 1 in the Coos River population. This pattern of conserved nDNA diversity and reduced mtDNA diversity is consistent with a recent population bottleneck. Coos River striped bass have shown increasing levels of pathological hermaphroditism. We speculate that the reduced genetic diversity of the Coos River striped bass population may have led to a depensatory cascade involving hermaphroditism that inhibited reproduction and recruitment, followed by increased levels of inbreeding as the population declined.

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Population bottlenecks are often invoked to explain lower than expected levels of genetic diversity in wild populations of fishes (e.g. Bernatchez et al., 1989; Brown et al., 1992; Richardson and Gold, 1997), but rarely is there detailed information available on the degree and duration of the bottlenecks. Striped bass (*Morone saxatilis*) offer an exception because sequentially established populations (Fig. 1) in historical times have experienced unusually well documented bottlenecks.

Striped bass were introduced to the Pacific coast at San Francisco Bay in 1879 and 1882 (Stevens et al., 1987). The two plantings totaled approximately 430 individuals (132 in 1879; approximately 300 in 1882). All were yearlings collected in the Navesink and Shrewsbury rivers, New Jersey. The Navesink and Shrewsbury rivers are minor systems that do not support reproduction by striped bass and that are located near the mouth of the Hudson River; the transplants were almost certainly part of the proximal Hudson River striped bass population. The transplanted yearlings rapidly established a population in San Francisco Bay which reproduced in its two main tributaries: the Sacramento and San Joaquin rivers. The introduction of striped bass to San Francisco Bay has been viewed as one of the few highly successful introductions of non-native fishes (Raney, 1952); within 10 years of the original introduction striped bass were available in commercial quantities in California waters.

The first striped bass captured in Oregon waters were two adults taken in Coos Bay in 1914 (Morgan and Gerlach[1]). These fish were vagrants (or less likely, the offspring of vagrants) from the San Francisco Bay population, the only possible source along the Pacific coast. Since 1914, reproducing populations of striped bass became established in Oregon in the Coos, Coquille, Umpqua, Smith, and Siuslaw estuaries. Of these, the Coos River population was the largest and most studied.

[1] Morgan, A. R., and A. R. Gerlach. 1950. Striped bass studies on Coos Bay, Oregon in 1949 and 1950. Oregon Fish Commission Contribution 14, 31 p.

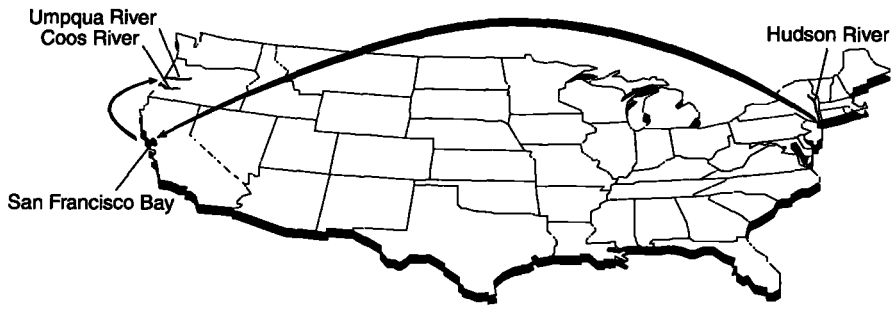


**Figure 1**
Colonization pathway of striped bass populations surveyed.

By the mid-1920s, striped bass were being commercially harvested in Coos Bay, and in 1945, annual landings from Coos Bay reached a high of 231,000 lb. The adult population also appeared to peak in 1945 at about 69,000 individuals (≥age-3), based on catch-per-unit-of-effort sampling. Pathological hermaphroditism was noted, but it was rare among Coos River striped bass during this period; Morgan and Gerlach[1] reported a 3% ($n$=124) incidence in 1950.

Since 1945, the Coos River striped bass population has crashed, whereas the incidence of hermaphroditism has increased dramatically. Between 1950 and 1975, population estimates of adults ranged from as many as 43,000 in 1963 to as few as 7800 in 1973. No adult population estimate is available for 1980, but in that year Moser et al. (1983) found 11 of 42 (26%) wild fish to be hermaphrodites. Population size of Coos River adult striped bass was not evaluated again until 1988 and 1989, when estimates of between 1000 and 3000 for both years were obtained. Estimates to date for the 1990s are of an adult population size under 1000. Furthermore, virtually no natural recruitment appears to be occurring (but supplemention is occurring through stocking of hatchery-produced offspring of San Francisco Bay broodstock). A standardized seine-haul survey of juvenile production begun in 1978 showed a decline in catch-per-unit-of-effort from 2.9 in 1978 to between 0.3 and 0.1 until 1986, and then only infinitesimal levels or zero through 1995. Recent estimates are that hermaphrodites make up 30% of the naturally produced adult population in the Coos River system (Reimers et al.[2]). Additionally, during 1993, an angling guide captured a hermaphroditic striped bass from the Umpqua River, the first reported from that system.

We hypothesized that Coos River striped bass would show reduced genetic diversity because both the history of the population's establishment and its subsequent demographics favored inbreeding. To test this hypothesis, we surveyed both nuclear DNA (nDNA) and mitochondrial DNA (mtDNA) variation in the Coos River population, the similarly non-native San Francisco Bay population (the source of the Oregon populations), and the source for the San Francisco Bay population, the Hudson River, New York. We also examined mtDNA variation in a second Oregon population (Umpqua River).

## Methods

Coos River striped bass (both wild fish and fish that were originally hatchery-cultured) were captured in gill nets during spring 1993. These fish were distinguished on the basis of size; significant stocking of hatchery-cultured striped bass (age-0 only) did not begin until 1989. Only wild Oregon striped bass were used as broodstock until 1991, when broodstock from California were used. Umpqua River specimens were collected in 1992 by angling. San Francisco Bay samples were collected by means of gillnetting in the lower Sacramento and San Joaquin rivers during 1991 and 1992. Collections of striped bass from the Hudson River are described in Wirgin et al. (1990, 1993).

Total DNA was isolated from livers or blood by the CTAB method (Saghai-Maroof et al., 1984; Wirgin et al., 1990), phenol-chloroform extractions, and ethanol precipitations. To determine mtDNA haplotypes, DNAs were digested with *Acc* I, *Hind* III, and *Rsa* I, electrophoretically separated in 1.2% agarose gels, and visualized in Southern blot analyses by using $^{32}P$

[2] Reimers, P. E., R. E. Bender, J. A. Johnson, T. Rumreich, D. J. Van Dyke, T. A. Confer, R. C. Smith, J. A. Hutado, and R. S. Boots. 1990. Tenmile-Coos-Coquille Fish District: a review of stocks of concern. State conservation department report, Oregon Department of Fish and Wildlife, 41 p.

**Table 1**

Genotypic frequencies for three single copy, nuclear DNA loci. Heterozygosity values in parentheses.

| | Locus 25 *Dra* I | | | | Locus 27 *Eco*R V | | | | Locus 22 *Hinf* I | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Population | *N* | AA | AB | BB | *N* | AA | AB | BB | *N* | AA | AB | BB |
| Hudson River | 35 | 0 | 11 (0.314) | 24 | 123 | 6 | 42 (0.342) | 75 | 80 | 47 | 24 (0.300) | 9 |
| San Francisco Bay | 64 | 6 | 23 (0.359) | 35 | 49 | 3 | 22 (0.449) | 24 | 65 | 41 | 20 (0.308) | 4 |
| Coos River (wild) | 27 | 1 | 12 (0.444) | 14 | 32 | 3 | 14 (0.438) | 15 | 34 | 11 | 9 (0.265) | 14 |
| Coos River (hatchery) | 23 | 1 | 11 (0.478) | 11 | 25 | 6 | 7 (0.280) | 12 | 19 | 6 | 5 (0.263) | 8 |

radiolabelled DNA probes (Feinberg and Vogelstein, 1983). Each of the three enzymes generates a diagnostic fragment which was used to characterize mtDNA major length-variant haplotypes (defined as differences of more than 100 base pairs; Wirgin et al., 1990). In addition, *Acc* I digestion revealed an informative, single base substitution. Probes were either highly purified mtDNA isolated from a single striped bass liver (Wirgin et al., 1990) or a gel-purified 1.7 kb PCR product containing the striped bass mtDNA control region (Wirgin et al., 1995). To determine nDNA genotypes, DNAs (10 µg) were digested with *Dra* I, *Eco*R V, and *Hinf* I, and analyzed in Southern blot analysis with the single copy probes developed from a striped bass genomic DNA library: DSB 25, DSB 27, and DSB 22, respectively (Wirgin and Maceda, 1991). Each of these enzyme-probe combinations revealed a single restriction site polymorphism with two alleles. Analysis of controlled laboratory matings demonstrated the Mendelian inheritance and nonlinkage of loci.

Genotypic frequencies derived from nDNA analysis were tested for deviations from Hardy-Weinberg equilibrium with the disequilibrium coefficient approach (Weir, 1990). Mitochondrial DNA haplotype diversity was calculated with the formula of Nei and Tajima (1981). Chi-square significance ($P<0.05$) of the differences between striped bass populations in nDNA allele frequencies and mtDNA haplotype frequencies was tested by using the randomization approach of Roff and Bentzen (1989).

## Results

### Nuclear DNA

Genotypic frequencies (Table 1) at two loci of samples from the Hudson River, San Francisco Bay, and Coos River (wild and hatchery) did not deviate significantly ($P>0.05$) from Hardy-Weinberg equilibrium; however, locus 22 did differ significantly from Hardy-Weinberg equilibrium for the Coos River wild ($P<0.01$) and hatchery ($P<0.05$) samples. Allelic frequencies for the three nDNA loci did not differ significantly ($P>0.05$) between the Hudson River and San Francisco Bay collections. Of the three nDNA loci, only locus 22 differed significantly in allelic frequencies between the San Francisco Bay and Coos River collections ($\chi^2=19.21$; $P<0.0001$).

### Mitochondrial DNA

Mitochondrial DNA haplotypic diversity (based on mtDNA length variants) showed a clear pattern of reduction (0.810 to 0.0) among the striped bass populations along the historical path that led to and includes the wild Coos River population (Table 2). The number of mtDNA haplotypes revealed decreased from 8 among Hudson River specimens to 5 in the San Francisco Bay collection, to 2 in the Umpqua, and 1 in the wild and hatchery-cultured Coos River samples. The third most common haplotype (C-1) found in the Hudson River collection (17%) was observed in the great majority of San Francisco Bay specimens (81%) and in all Coos River specimens. Also, the three least common haplotypes in Hudson River striped bass were those absent in striped bass from San Francisco Bay. Mitochondrial DNA haplotype frequencies were significantly different between the Hudson River and San Francisco Bay samples ($\chi^2=71.47$; $P<0.0001$) and between the San Francisco Bay and Coos River samples ($\chi^2=8.21$; $P<0.05$).

## Discussion

Extensive allelic surveys of Atlantic coast striped bass have shown extreme monomorphism at the pro-

**Table 2**

Mitochondrial DNA composite haplotype frequencies (letters represent length polymorphisms; numerals represent site polymorphisms; percentages in parentheses) and genotypic diversity indices.

| Population | *N* | Haplotype | | | | | | | | Genotypic diversity |
|---|---|---|---|---|---|---|---|---|---|---|
| | | A-1 | A-2 | B-1 | B-2 | C-1 | C-2 | D-1 | D-2 | |
| Hudson River | 110 | 3 (0.03) | 2 (0.02) | 25 (0.23) | 7 (0.06) | 19 (0.17) | 32 (0.29) | 17 (0.15) | 5 (0.04) | 0.810 |
| San Francisco Bay | 63 | | | 4 (0.06) | 4 (0.06) | 51 (0.81) | 2 (0.03) | 2 (0.03) | | 0.340 |
| Coos Bay (wild) | 38 | | | | | 38 (1.0) | | | | 0.0 |
| Coos Bay (hatchery) | 27 | | | | | 27 (1.0) | | | | 0.0 |
| Umpqua River | 12 | | | | | 11 (0.92) | 1 (0.08) | | | 0.167 |

tein level both within and among populations (reviewed in Waldman et al., 1988). For example, Otto (1995) reported mean heterozygosity levels of Atlantic striped bass of approximately 1.0%, and 0.75% for the Hudson River population. Very low genetic diversity for Atlantic coast striped bass has also been shown by several mtDNA studies (Chapman, 1990; Wirgin et al., 1990, 1993; Waldman and Wirgin, 1994). For example, Wirgin et al. (1990) estimated the proportion of nucleotides that differed for the most divergent individuals among mid-Atlantic striped bass stocks at 0.0004, one of the lowest values for any animal species. What mtDNA variation does exist in striped bass primarily is length, rather than site variation (Waldman and Wirgin, 1995). Four mtDNA major length variants have been found in striped bass from the Hudson River (Wirgin et al., 1990, 1993; Waldman and Wirgin, 1994).

Thus, the substrate of genetic variation available among striped bass from the Hudson River and other Atlantic coast estuaries was extremely low in comparison with most fishes (e.g. Waldman et al., 1996). From this unusually narrow gene pool some 430 or so yearlings were collected and transplanted in 1879 and 1882 to San Francisco Bay. It is not known how many of the female yearlings survived to reproduce as founders of all Pacific coast striped bass, but about 215 represents an approximate upper limit (assuming an unrealistic 100% survival rate), and 5 the lower limit, given the 5 haplotypes detected. Estimates of annual expectation of death from natural causes of the San Francisco Bay striped bass population obtained during a period of exploitation (summarized in Westin and Rogers[3]) ranged between 0.31 and 0.12, and averaged about 0.2. Moreover, female striped bass have variable maturation schedules (Berlinsky et al., 1995); in San Francisco Bay, it has been found that females mature at ages 4 and 5 (Stevens et al., 1987). Therefore, a more reasonable estimate for the number of transplanted females that survived to found the San Francisco Bay striped bass population is about 100.

Striped bass then appeared in Coos Bay some 35 years after their introduction to San Francisco Bay. It is not possible to determine the number of founders of the Oregon populations nor their initial genetic makeup. Present Oregon striped bass are restricted to mtDNA length haplotype C. It is not known what the mtDNA haplotype frequencies of the San Francisco Bay stock were circa 1915, but if their present haplotype frequencies are used as an approximation, then the chance of a single female founder having a haplotype other than the C haplotype is only 16%. We believe that given the historical scarcity of striped bass in north Pacific coastal waters (Forrester et al., 1972) and the concordance between the dominant haplotype of the San Francisco Bay stock and the single (major length variant) haplotype of the Coos River and Umpqua River stocks, it is reasonable to assume that the Oregon populations were founded by one or a very low number of female striped bass with the C-haplotype.

Founding of the Oregon striped bass populations by a limited number of females from California, following the initial bottleneck of transplantation from the Atlantic, would have resulted in a greatly reduced level of genetic variation in comparison with the

[3] Westin, D. T., and B. A. Rogers. 1978. Synopsis of biological data on the striped bass, *Morone saxatilis* (Walbaum) 1792. Technical Report 67, Graduate School of Oceanography, Univ. Rhode Island, 154 p.

Hudson River stock. However, genetic variation may have been pared further, i.e. the subsequent history of the Coos River population suggests that some of the demographic and life history factors that contribute to low levels of genetic variation among native populations of striped bass were pronounced in the Coos River population.

The Coos River population has experienced its own bottleneck; recent estimates suggest a reduction in its order of magnitude from $10^4$ to $10^3$ or $10^2$. Fluctuating levels of annual spawning success also reduce the effective population size ($N_e$). Over generations $N_e$ is approximated by the harmonic mean of each generation and strongly reflects periods of low abundance (Crow and Kimura, 1970). Many striped bass populations are sustained by occasional, extremely successful or "dominant" year classes (Raney, 1952). Dominant year classes have been rare but important for the Coos River population, occurring in 1940 and 1958 (McGie and Mullen[4]).

Other factors that may have contributed to a reduced $N_e$ for the Coos River population are intrinsic to all populations of the species. Among these is skewed sex ratios. Males greatly outnumbered females on the Coos River spawning grounds (Morgan and Gerlach[1]). Estimates of male to female ratios on spawning grounds of other systems range from about 10:1 to 100:1 (Chapman, 1990). Another factor is variance in progeny production among females, i.e. nonrandom family size (Gall, 1987). Large female striped bass can produce on the order of $10^6$ eggs per year. Because of variable environmental conditions within a spawning season, some cohorts of eggs may show low or no survival whereas other cohorts may flourish (Dey, 1981; Secor and Houde, 1995). Thus, inordinate success by a few females would cause particular genotypes to be overrepresented (Chapman, 1990).

The significant difference in allele frequencies for nDNA locus 22 between the San Francisco Bay and Coos River collections indicates either a founder effect or subsequent genetic drift. Also, the deviation from Hardy-Weinberg equilibrium of one of the three loci in the Coos River population is suggestive of small $N_e$ or some other violation of the assumptions that lead to Hardy-Weinberg frequencies (Weir, 1990). In general, however, it appears that nDNA diversity was not strongly affected by the multiple bottlenecks that the Oregon populations experienced. In contrast, we have shown a stark decrease in mtDNA diversity. Our findings concerning nDNA and mtDNA diversity in Oregon striped bass are congruent with their having experienced a recent population bottleneck. A single breeding pair of diploid animals contains four nuclear genomes and one transmissible mtDNA; thus, a population that goes through an extreme bottleneck can lose all of its mtDNA; variability while still retaining a significant fraction of its nuclear variability (Wilson et al., 1985). A pattern of highly reduced mtDNA diversity and little altered nDNA diversity is consistent with a recent and unprolonged population bottleneck, as we hypothesize to have occurred during the establishment and history of the Coos River striped bass population.

There is an intriguing inverse relationship between genetic diversity (reflected in mtDNA) of the striped bass populations investigated and the frequency of hermaphroditism. Inbreeding depression has been firmly associated with detrimental effects in captive vertebrate populations (e.g. Kincaid, 1976, Laikre and Ryman, 1991), and recently, strong evidence of reduced fitness and reproductive impairments due to inbreeding depression in wild vertebrates has emerged (e.g. Jimenez et al., 1994; Keller et al., 1994; O'Brien, 1994).

Moser et al. (1983) investigated the phenomenon of hermaphroditism in Coos River striped bass in some detail. Protandry was suspected because young hermaphrodites had ripe, motile sperm and immature eggs, whereas older hermaphrodites (ages 7 to 10) had normal appearing eggs and only small patches of testes. Reproductive impairment of older hermaphrodites was evident. Hermaphrodites with small testes and large ovaries showed annual accretions of eggs and one or more ovarian ducts blocked by adhesions. Each egg mass, representing previous spawning seasons, became progressively more degenerated toward the interior of the gonad. Moser et al. (1983) also found that the oldest hermaphrodites had more constricted stomachs and intestines and more swollen abdomens than normal prespawning females. The four oldest hermaphrodites, 10 years old, had retained their eggs for up to 5 years. Also, it is possible that the absence of hermaphrodites among striped bass greater than 10 years of age ($n$=7) indicates earlier mortality of hermaphroditic individuals, perhaps as a consequence of numerous annual egg mass accretions.

We are aware of only a single observation of hermaphroditism among Atlantic coast striped bass. Westin (1978) reported one hermaphrodite among wild individuals from Chesapeake Bay that were sacrificed after being held in captivity for one year. However, in addition to surveying Coos River striped bass for evidence of hermaphroditism, Moser et al. (1983) also examined striped bass from San Francisco Bay. Of more than 500 individuals, two were hermaphrodites. Thus, hermaphroditism in striped bass appears to be exceedingly rare in native, out-

[4] McGie, A. M., and R. E. Mullen. 1979. Age, growth, and population trends of striped bass, *Morone saxatilis*, in Oregon. Oregon Department of Fish and Wildlife Information Report Series, Fisheries 79-8, 57 p.

bred populations, barely detectable in a non-native, outbred, but somewhat genetically constrained population, and pronounced in a non-native, inbred population. Moreover, the inverse association between abundance and hermaphroditism of the Coos River population suggests (but does not demonstrate) that a depensatory relationship exists because of these factors. That is, demographic influences that continued to reduce genetic diversity of the Coos River population may have promoted this pathological reproductive response, which then hindered reproduction, further reducing abundance and leading to higher levels of inbreeding.

Furthermore, no strong competing hypotheses have emerged to account for hermaphroditism of the Coos River striped bass stock. Chemical contamination is one conceivable cause. However, the Hudson River—the original source of Coos River striped bass—is a heavily polluted estuary, yet hermaphroditism has not been observed in its population. Also, the Coos River is home to American shad (*Alosa sapidissima*), similarly transplanted from the Atlantic (in 1871 to the Sacramento River; Mansueti and Kolb, 1953). In its native east coast rivers, including the Hudson River, American shad overlap with striped bass both spatially and temporally on their spawning runs. Nonetheless, whereas the Coos River striped bass population has approached extinction, its American shad population is flourishing.

It is clear that populations of striped bass in Oregon would benefit from broader genetic diversity (although there is considerable controversy concerning maintenance of non-native fish populations; e.g. Courtenay, 1995). If perpetuation of the Coos River population is desired, consideration should be given to the introduction of striped bass to Oregon waters from one or more additional Atlantic coast stocks. A combination of intention and serendipity resulted in the establishment of striped bass in California and then Oregon; however, the ultimate effect was to promulgate northern, hypothermal, nonmigratory populations from individuals originally obtained from a midlatitude, mesothermal, migratory population. There is some evidence that striped bass from northern latitudes are better adapted to the ambient environmental conditions of those latitudes (Conover, 1990). We suggest that Atlantic coast striped bass from northerly latitudes such as the Canadian Maritimes would be more preadapted to Oregon habitats.

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# Can scales be used to sex winter flounder, *Pleuronectes americanus*?

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We tested the accuracy of a technique to rapidly determine the sex of mature winter flounder, *Pleuronectes americanus*, in the field without sacrificing individuals. Although a number of techniques have been developed for sexing fish by examining reproductive anatomy (Moen, 1959; Driscoll, 1969; Martin et al., 1983; Ross, 1984), they are not well suited for easy and rapid determinations in the field. External characteristics, such as features of the urogenital region (Sigler, 1948; McComish, 1968; Flickinger, 1969; Lebeau and Pageau, 1989) or body shape (Snow, 1963), have been successfully applied in the field for other species but are not applicable to winter flounder which exhibit no obvious sexual dimorphism. Some studies have suggested that male and female winter flounder can be differentiated by the texture of the scales on the blind side; males allegedly have ctenoid scales which feel rough, whereas females allegedly have cycloid scales which feel smooth (Perlmutter, 1947; Lux and Porter, 1963). Unfortunately, the literature is inconclusive and none of the studies have carefully tested the relationship of texture as related to scale type and sex. MacPhee (1978) citing Norman (1934) claimed that scales on the blind side of males are ctenoid rather than cycloid when, in fact, Norman stated that for the species in general the scales are ctenoid on the ocular side and cycloid on the blind side.

## Methods

From March through September, 1989, winter flounder were collected with an otter trawl in New Jersey waters. Fish were collected at 14 inshore sites in Raritan and Sandy Hook Bays (Phelan, 1992) and 22 offshore sites 22.2 km east of Sandy Hook (Studholme et al., 1995). Fish were measured to the nearest millimeter total length. Using the method described by Lux and Porter (1963), we palpated the blind side of the caudal peduncle noting either roughness (males) or smoothness (females). The fish were then dissected to determine (visually) maturity and sex. All immature fish were eliminated from the study. When possible, a sample of ten or more scales was taken from the palpated area. In the laboratory, the scales were examined with a dissecting microscope to determine their type and relation to texture.

## Results and discussion

A total of 730 mature fish, ranging from 12.9 to 39.7 cm, were examined. External palpation resulted in a significantly higher ($\chi^2$=51.528, $P$<0.001) sex ratio (females to males) of 2.7:1 than the actual ratio of 1.2:1 (Fig. 1). The difference in the ratios was due primarily to males being identified as females. Forty six percent (155 of 332) of the

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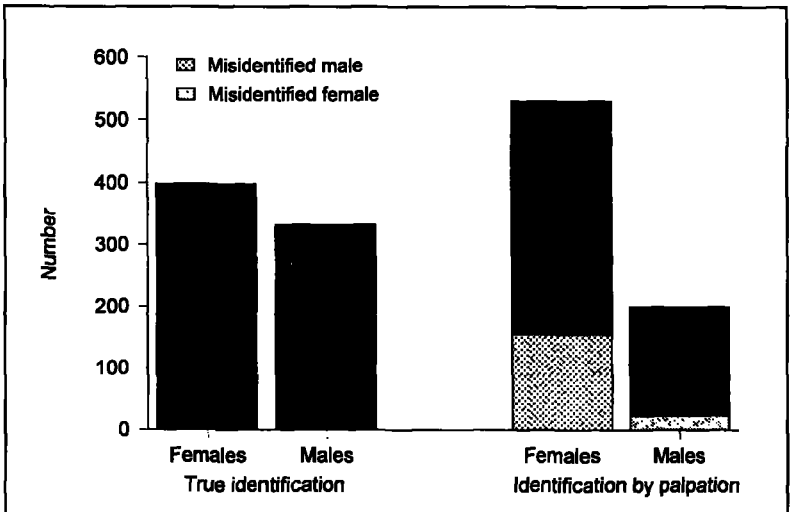


**Figure 1**
Number of female and male winter flounder (*Pleuronectes americanus*) identified by gonadal inspection and palpation of the blind side scales.

**Table 1**

Sex ratio of winter flounder as determined by external palpation and gonad inspection.

| Sex ratio (female:male) | Method | Number of fish | Location | Source |
|---|---|---|---|---|
| 2.5:1 | External | 3711 | New England and New York | Perlmutter, 1947 |
| 2.3:1 | External | 601 | Rhode Island | Saila, 1961 |
| 2.6:1 | External | 1431 | New England | Lux and Porter, 1963; Lux, 1969 |
| 2.3:1 | External | 12,151 | Massachusetts | Howe and Coates, 1975 |
| 1.5:1 | Internal | 940 | Rhode Island | Saila, 1962 |
| 1.2:1 | Internal | 1569 | Rhode Island | Berry et al., 1965 |
| 1:1 | Internal | 227 | Newfoundland | Kennedy and Steele, 1971 |
| 1:1 | Internal | 1465 | Massachusetts | Haedrich and Haedrich, 1974 |

males were misidentified, and six percent (23 of 398) of the females were identified as males. Similar differences between sex ratios derived from palpation of the scales and from gonadal inspection have been reported in the literature (Table 1). In the four studies that used palpation to determine sex, ratios ranged from 2.3 to 2.6:1 compared with ratios of 1:1 to 1.5:1 when gonads were used.

Scales were collected and examined from 672 of the 730 fish. Sex ratios for this subset also differed significantly ($\chi^2$=44.203, $P$<0.001) between the two sexing methods: 2.5:1 for palpation and 1.2:1 for gonadal inspection (Fig. 2). Individual fish exhibited either cycloid (479 fish) or ctenoid (199) scales, a finding that differs from Norman's (1934) observation that scales on the blind side were cycloid. Female fish exhibited primarily cycloid scales (Fig. 2) which were present on 352 (98%) of the 361 females examined. Scale type for male fish, however, was variable; 120 (39%) fish exhibited cycloid scales and 191 (61%) ctenoid (Fig. 2). Discrepancies between texture determinations and scale type (observer error) occurred in 33 (5%) of the fish examined (Fig. 2).

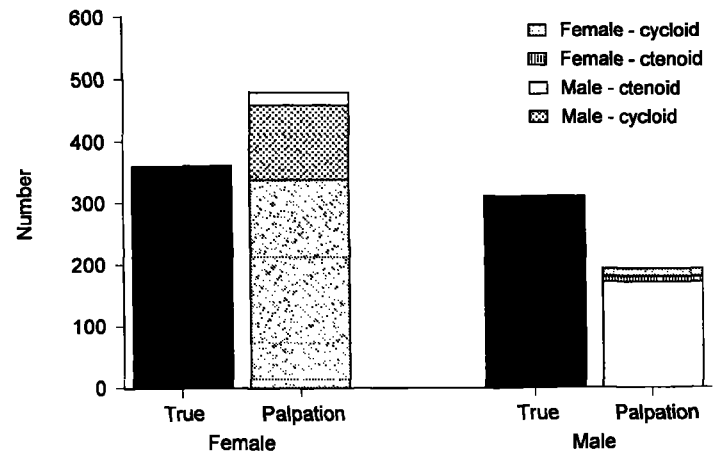


**Figure 2**

Number of female and male winter flounder (*Pleuronectes americanus*) identified by gonadal inspection and palpation in relation to scale type.

It is therefore apparent that the use of texture according to scale type for sexing winter flounder (Perlmutter, 1947; Lux and Porter, 1963; MacPhee, 1978) is not accurate, resulting in a significantly female-biased sex ratio.

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# Evaluation of toxicity of oxytetracycline on growth of captive nurse sharks, *Ginglymostoma cirratum**

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Validation of age estimates derived from calcified structures is an essential component of all fish age and growth studies (Beamish and McFarlane, 1983). In elasmobranchs, age validation is accomplished through injection of tetracycline antibiotics, particularly oxytetracycline hydrochloride [OTC] (Cailliet, 1990). At a standard dosage level of 25 mg/kg body weight (BW), OTC is deposited at sites of active calcification and produces vivid, enduring marks in dorsal-fin spines and vertebral centra (Holden and Vince, 1973; Smith, 1984; Beamish and McFarlane, 1985; Branstetter, 1987; Brown and Gruber, 1988; Natanson and Cailliet, 1990; Kusher et al., 1992; Natanson, 1993; Walker et al.[1]). The location of these fluorescent marks can then be examined to determine if the structure in question accurately reflects age. Such OTC treatment is generally considered benign, yet few scientists have directly examined the potential toxicity of this compound to elasmobranchs. However, if OTC injection alters the growth or health of treated elasmobranchs, its value as a chemical marker for age validation may be severely compromised. Thus, studies on the toxicity of OTC and other potential chemical markers (Gelsleichter et al., 1997) are essential for the improvement of elasmobranch ageing biotechnology.

Chemical toxicity associated with OTC treatment has been well documented in several teleost ageing studies. For example, injection of, or immersion in, OTC at recommended dosage levels (Beamish and McFarlane, 1983) has been reported to produce lethargy, behavioral abnormalities, and mortality in treated specimens (Schmitt, 1984; Wilson et al., 1987; Marking et al., 1988; Monaghan, 1993; Bumguardner and King, 1996). In contrast, Tanaka (1990) reported that various dosage levels of OTC (20–80 mg/kg BW) did not significantly affect growth rates of injected Japanese wobbegongs (*Orectolobus japonicus*) or swell sharks (*Cephaloscyllium umbratile*). Unfortunately, no other studies have investigated the possible implications of OTC treatment in elasmobranchs and, thus, they remain largely unclear.

The goal of the present study was to evaluate the effect of OTC treatment on the growth rate of captive nurse sharks, *Ginglymostoma cirratum*. The potential effect of OTC injection on nurse shark health is also discussed on the basis of serologic and hematologic observations.

## Materials and methods

Nine age-0 and age-1 *G. cirratum* were collected in the Florida Keys and transported to the laboratory, where they were maintained in outdoor circular tanks (capacity ranging from 3,200 to 12,000 L). The experimental tanks can operate as either open or recirculating systems and were subjected to natural photoperiod and temperature

[1] Walker, T. I., R. A. Officer, J. G. Clement, and L. P. Brown. 1995. Southern age validation: Part I—Project overview, vertebral structure and formation of growth increment bands used for age determination. Final Report to the Fisheries Research and Development Corporation, FRDC Project 91/037. Department of Conservation and Natural Resrouces, Queenscliff, Victoria, Australia.

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regimes. After an acclimation period of two weeks, all animals were sexed, measured (stretched total length; STL), weighed, and tagged with rototags for individual identification. Sharks were divided into two groups: an OTC group ($n$=5; mean STL (±SE)=62.6 ± 3.62 cm; mean weight (±SE)=1.7 ±0.36 kg) and a control (CO) group ($n$=4; mean STL=51.2 ±2.09 cm; mean weight = 0.9 ± 0.10 kg). All nine animals were injected in the lateral musculature with an elasmobranch Ringer's solution vehicle (Forster et al., 1972) which, for the OTC group, contained OTC at a dosage level of 25 mg/kg body weight (BW). Following the injections, all nurse sharks were returned to the experimental tanks for captive maintenance over a 7-month period.

During the experimental period, all sharks were measured, weighed, and examined for external lesions on a monthly basis. In addition, the general condition of all sharks was evaluated and recorded in terms of behavioral abnormalities or signs of distress. All animals were fed three times per week ad libitum with Atlantic thread herring, *Polydactylus oligodon,* or sardine, *Sardinella aurita.*

Toxicity of OTC on nurse shark growth was evaluated by comparing the mean growth rate (%BW/d) of control and OTC-injected *G. cirratum*. In addition, blood samples were obtained from all specimens at the end of the experimental period and subjected to white blood cell (WBC) and serologic parameter analyses. Afterwards, all remaining specimens were anesthetized with 1 g/L tricaine methanesulfonate (MS-222) and sacrificed by severing the spinal cord. Necropsies were performed for all specimens to assess general animal health.

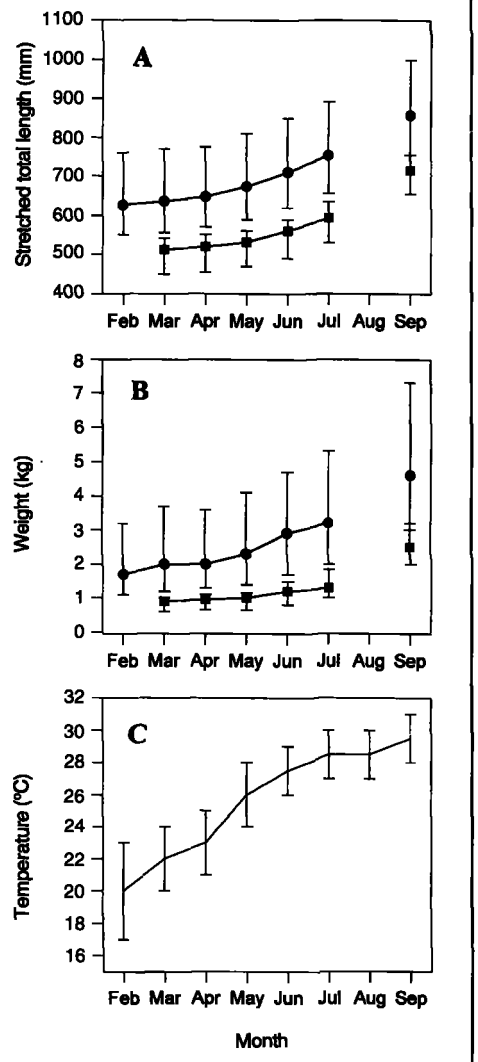


**Figure 1**

Mean monthly growth (± SE) in **(A)** length and **(B)** weight for nurse sharks in the OTC (●, $n$=5) and control (■, $n$=4) groups; **(C)** shows the monthly temperature ranges and midpoints in the experimental tanks.

## Results

All nurse sharks survived the experimental period without any apparent behavioral complications. All grew in length (Fig. 1A) and weight (Fig. 1B) while exposed to identical temperature fluctuations (Fig. 1C). No significant differences in growth rates between control and OTC groups were observed ($t$-test, $P$<0.05, Table 1).

Observations on serum chemistry also indicated little difference between groups, except that both lactate dehydrogenase (LDH) and aspartate aminotransferase (AST) were significantly greater in OTC-injected animals ($t$-test, $P$<0.05, Table 2). Differential WBC counts indicated no significant difference between control and OTC groups ($t$-test, $P$<0.05; Table 3). Both serologic and hematologic

**Table 1**

Growth rates (expressed as %BW/d) of nurse sharks in the control and oxytetracycline-treated (OTC) groups. Body weights (BW) are in kg.

| Group | $n$ | Initial BW (Mean ± SE) | Final BW (Mean ± SE) | Growth rate (Mean ± SE) |
|---|---|---|---|---|
| Control | 4 | 0.88 ± 0.10 | 2.52 ± 0.29 | 0.91 ± 0.11 |
| OTC | 5 | 1.70 ± 0.38 | 4.64 ± 0.73 | 0.79 ± 0.11 |

parameters were comparable with earlier observations by Stoskopf (1993) for captive *G. cirratum*.

## Discussion

Tanaka (1990) determined that OTC injections at dosage levels from 20 to 80 mg/kg BW did not adversely affect growth or cause mortality in Japanese wobbegongs (*O. japonicus*) or swell sharks (*C. umbratile*). In agreement, the present study indicates no adverse effect of OTC treatment on the growth rate of injected *G. cirratum*. Therefore, continued use of OTC injection is still supported as an effective, nontoxic method for determining vertebral growth-band periodicity. In addition, OTC remains the superior chemical marker for elasmobranch age validation in comparison with calcein, which appears highly toxic at similar dosage levels (Gelsleichter et al., 1997).

Although OTC does not appear to affect short-term growth, high serum LDH and AST in OTC-injected *G. cirratum* may suggest that it can be hepatotoxic. High activities of LDH and AST are commonly used in the diagnosis of toxicant stress and hepatocellular injury, when these enzymes are leaked from damaged liver cells (Zimmerman et al., 1965; Racicot et al., 1975; Krajnovic-Ozretic and Ozretic, 1987). Unfortunately, the diagnosis of toxicant stress in elasmobranchs with enzyme activity levels has not been well investigated. In addition, serial blood sampling of injected animals prior to and after injection is necessary for an appropriate evaluation of serologic data. Consequently, interpretation of these data is speculative, yet may still indicate a harmful effect of OTC on elasmobranch physiology and thus require further investigation.

Hepatic dysfunction is a common repercussion of OTC treatment in vertebrates. In several species, OTC administration causes acute hepatocellular injury that is often associated with intracellular fat deposition and cytoplasmic alterations (Weinstein, 1970; Hennigar and Gross, 1977). However, these effects are usually associated with repeated exposure to dosage levels far greater than those used in fish age validation studies (Lepper, 1951; Sborov and Sutherland, 1951). In addition, elasmobranch liver cells regularly contain large deposits of intracellular fat in their normal state. Nevertheless, this standard information may lend some credence to observations on increased LDH and AST in treatment group specimens. Clearly, future studies on OTC toxicity should investigate other characteristics of health that are less conspicuous than animal growth or survival.

In conclusion, the results of the present study indicate that OTC treatment does not produce short-term effects on *G. cirratum* growth that may complicate age validation. However, minor tangential evi-

**Table 2**

Serologic parameters of nurse sharks at the end of the experimental period after injection with oxytetracycline hydrochloride (OTC) or vehicle at a dosage of 25 mg/kg body weight ; BUN = blood urea nitrogen; ALK P = alkaline phosphatase; LDH = lactate dehydrogenase; AST = aspartate aminotransferase; ALT = alanine aminotransferase. Values are means ± SE. The values marked with an asterisk are significantly different from control at $P < 0.05$.

| | Groups | |
|---|---|---|
| Serologic parameter | Control ($n$=4) | OTC ($n$=5) |
| Glucose (mg/dL) | 16.2 ± 0.86 | 18.0 ± 0.63 |
| Sodium (mM/L) | 272.7 ± 1.93 | 275.4 ± 1.63 |
| Potassium (mM/L) | 5.45 ± 0.10 | 5.47 ± 0.08 |
| Chloride (mM/L) | 260.0 ± 2.71 | 261.0 ± 1.48 |
| $CO_2$ (mM /L) | 7.7 ± 0.25 | 7.2 ± 0.20 |
| BUN (mg/dL) | 832.0 ± 12.17 | 811.6 ± 6.22 |
| Creatinine (mg/dL) | 0.10 ± 0 | 0.16 ± 0.02 |
| Uric acid (mg/dL) | 0.12 ± 0.03 | 0.18 ± 0.05 |
| Calcium (mg/dL) | 17.3 ± 0.28 | 17.8 ± 0.24 |
| Phosphorus (mg/dL) | 4.12 ± 0.17 | 4.14 ± 0.12 |
| Total bilirubin (mg/dL) | 0.1 ± 0 | 0.1 ± 0 |
| ALK P (U/L) | 33.5 ± 2.60 | 54.6 ± 9.79 |
| LDH (U/L) | 863.5 ± 122.9 | 1810.8* ± 371.7 |
| AST (U/L) | 24.7 ± 3.77 | 54.6* ± 9.35 |
| ALT (U/L) | 19.7 ± 1.25 | 23.2 ± 1.71 |

**Table 3**

Differential white blood cell counts of nurse sharks at the end of the experimental period after injection with OTC or vehicle at a dosage of 25 mg/kg BW; % WBC is the proportion of all blood cells that are white. Values are means ± SE.

| Group or individual | $n$ | Granulocytes (%) | Lymphocytes (%) | Monocytes (%) | Thrombocytes (%) | % WBC |
|---|---|---|---|---|---|---|
| Control | 4 | 21.4 ± 2.6 | 51.1 ± 2.0 | 1.4 ± 0.3 | 26.1 ± 1.5 | 12.0 ± 0.6 |
| OTC | 5 | 22.4 ± 3.0 | 50.3 ± 3.0 | 1.9 ± 0.6 | 25.4 ± 1.9 | 11.2 ± 0.8 |

dence suggests that OTC may be hepatotoxic, affecting animal health over longer periods of time. Thus, additional studies on OTC toxicity may have important implications for long-term maintenance of marked elasmobranchs.

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# Electrotaxis in American lobsters, *Homarus americanus*, and its potential use in sampling early benthic-phase animals

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The American lobster, *Homarus americanus*, fishery is an important part of the economy in New England and eastern Canada. A reliable predictor of recruitment to this fishery would be useful in stock assessments and economic planning, yet no such predictors are available. The best time for a prerecruit survey is just after the stage-4 postlarva (approx. 5-mm carapace length) settles from the plankton to the benthos, after high larval mortalities have established the size of the year class, but early enough in the growth cycle to allow prediction of recruitment 4–6 years before lobsters are harvested. Unfortunately, this is also the period when lobsters are most difficult to capture. Stage-4 lobsters prefer to settle into cobble-sized rock substrate, often several layers thick, where they remain until they begin to enter commercial traps at a carapace length of about 40 mm (Lawton and Lavalli, 1995). Sampling this "early benthic phase" (EBP) of lobsters is laborious and costly. A team of divers must turn individual rocks and capture escaping animals with suction devices (e.g. Hudon, 1987, Wahle and Steneck, 1992). This method is too time consuming to permit synoptic prerecruit surveys such as are conducted for groundfish. Consequently, we sought a more efficient sampling method for EBP lobster stocks along the coast of Nova Scotia, Canada.

Several previous studies suggested that electrofishing may be a useful approach. Saila and Williams (1972) developed an electric trawl system that increased catches of commercial-size American lobsters. Stewart (1974) described the effects of electric fields on the Norway lobster (*Nephrops norvegicus*), including an induced avoidance behavior that caused animals to leave their burrows. Phillips and Scolard (1980) developed an electrofishing apparatus for juvenile rock lobsters (*Panuliris cygnus*) which looked promising, although it caught a size range similar to that taken by traps. Our approach was fundamentally different from these studies in that we intended to develop a sampling "quadrant" which electrified a small area (<1 $m^2$) of the substrate and took advantage of electrically induced behavior observed in our preliminary laboratory experiments. This paper presents results from these experiments and subsequent trials with several potential electrode arrangements and suggests avenues for further development.

## Methods

Preliminary behavioral experiments were conducted in tanks of various sizes without shelters or substrate to determine if electrotaxis could be induced in lobsters and, if so, what pulse lengths and voltages would be most effective. Lobsters ranging in size from 5–50 mm carapace length were subjected to a wide range of electrical stimulation including voltages from 10 to 100 V and pulse frequencies from 2 to 200 Hz. Pulse lengths were varied independently of frequency during these observations, but it quickly became obvious that a square wave form (pulse duration 50% of cycle length) with a relatively high frequency was most effective in inducing the desired response. Consequently, all experiments with different electrode configurations and cobble shelters were conducted at a DC pulse frequency of 100 Hz, pulse duration of 20 milliseconds, and an input voltage of 50 V. All these experiments were also conducted in a 1.5 $m^3$ tank (1 m × 2 m × 0.75 m), large enough so that the walls did not distort the relatively localized electric currents produced by the apparatus. The tank was filled with sand to a depth of 10 cm, and a group of 15 cobble-size rocks (average weight 2.5 kg) of various shapes obtained from known lobster habitat were placed in the central area of the tank so that they were several layers deep and entirely contained by a 0.35 $m^2$ quadrant. Indirect overhead fluorescent lighting was adjusted to the natural day length. The tank was kept filled

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with 15°C seawater with a continuous flow-through system. Three EBP animals ranging from stage 4 to stage 8 (5–10 mm carapace length) were used in each trial, which is within the range of naturally occurring densities. Each animal was used only once. At least 24 hours before each trial the experimental animals were chosen randomly from a previously unused group kept in 15°C flow through holding trays. The animals were released directly above the cobble (into which they always disappeared within a few seconds) and allowed to acclimate overnight. The released animals almost always remained within the rock pile and were seen on the surrounding sand only on rare occasions. After each trial, all rocks were removed from the tank, uncaptured animals were recovered, and the rocks were replaced haphazardly. This procedure produced a different configuration of burrowing locations and shelters for each trial and simulated the varied cobble habitat that would be encountered while sampling.

The electrical apparatus (Fig. 1) consisted of a rectifier bridge, a capacitor, a 9-V battery, an opticoupler, and a power MOSFET transistor. A rheostat was used to regulate the AC power source. The bridge rectifies the current into and deposits a charge on the capacitor, thereby creating a DC source. A signal generator was used to control the opticoupler, which in turn controlled the gate of the MOSFET and primary DC source by means of the 9-V circuit. All electrodes were made of stainless steel. The only variable was the electrode configuration, each configuration consisting of a particular combination of electrode shapes and locations. These included small 6.5 $cm^2$ plates, 1.5-mm diameter braided wire in which a 2.5-cm length of the plastic insulation had been removed every 3 cm, or a combination of the two. The electrode configurations and the general experimental set up are shown in Figure 2.

To determine if the number of captures between electrode configurations were significantly different, each trial of three animals was treated as a replicate in a one-way analysis of variance, with the number of animals captured in each trial as the variable. Similarly, the capture time of the first, second, and third animal in each trial was treated as a replicate and a one-way analysis of variance was performed separately for each emergence. Differences between means were tested with the LSD post-hoc test.

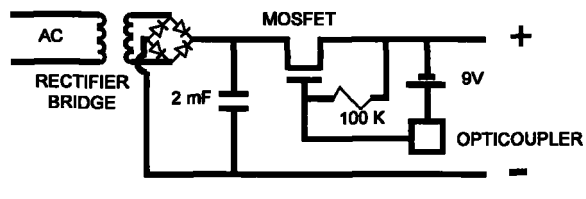


**Figure 1**

Circuit drawing of the electrofishing device (DC source in Fig. 2) used in experiments to determine electrotaxis and capture effciency in early benthic-phase American lobsters, *Homarus americanus*.

## Results and discussion

Preliminary behavioral observations in open tanks without shelters or substrate showed that a wide size range of lobsters (5–50 mm carapace length) reacted to the electric current in a similar manner. This included an initial period of agitation of up to several seconds in which the animal appeared to become aware of the stimulus. This was followed by reorientation of the animal to face the cathode, commencement of involuntary tail flicking, and a resultant movement towards the anode. Animals of different sizes tended to react somewhat differently to the same input voltage. Larger animals (>30 mm carapace length) tended to struggle and often managed to escape the electric current. Once escaped, these animals could usually be re-entrained and induced to reach the anode by increasing the current strength and thus the tail flicking reaction. Overstimulation resulted in the animal lying motionless for several minutes after the current had been switched off. All animals that were affected in this way revived after a few minutes, apparently without ill affects. Small EBP (<10 mm) animals nearly always became motionless, usually lying on their backs, upon reaching the anode when it was situated on the substrate. If the electrode was elevated above the substrate, EBP animals gathered below it and remained motionless, but upright. When the current was switched off, they quickly escaped. EBP animals always reached the anode more quickly than large animals. In many cases the reaction was immediate and the anode was reached in less than a second. Mortalities of experimental animals (pre- and postexperimental) that could not be attributed to accidental mishandling were negligible (total of 3) during the period of observation (60 d).

We concluded that American lobsters exhibit a true electrotaxis, i.e. where an animal in a DC field is compelled to swim to the anode through involuntary muscular contractions. Electrotaxis is well known in fish (Lamarque, 1990), but has rarely been described in crustaceans. Saila and Williams (1972) observed tail muscle contractions in American lobsters subjected to currents (<38 V input), but no taxis was evident. Stewart (1974) concluded that similar tail

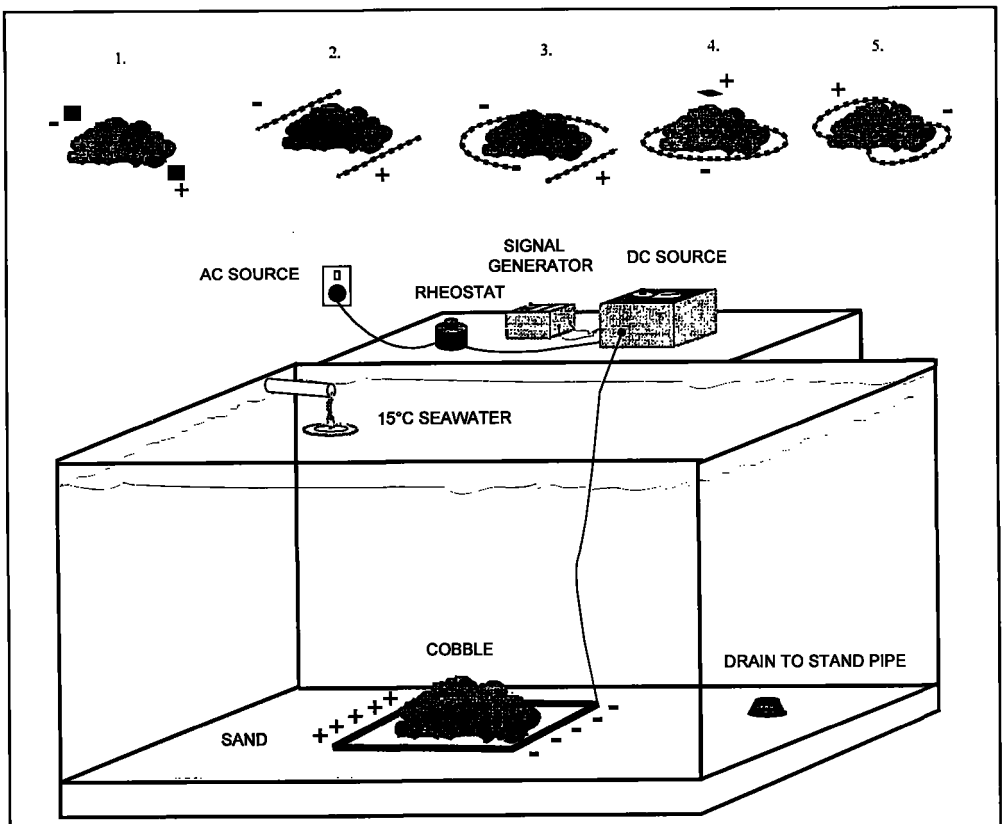


**Figure 2**

Laboratory setup (bottom) used to determine electrotaxis in early benthic-phase American lobsters *Homarus americanus* and capture efficiency of five electrode configurations (top).

flicking in *N. norvegicus* was not involuntary, but rather the animal's natural escape reaction induced by the electric stimulation. We have found only two reports of electrotaxis in crustaceans in which tail flicking and movement toward the anode were observed: one for the penaeid shrimp Penaeus duorarum (Higman, 1956) and the other for the rock lobster, *Panulirus cygnus* (Phillips and Scolaro, 1980).

It was apparent from these observations that the strong electrotactic response of EBP lobsters could be used to develop a quadrant-like field-sampling device. Table 1 gives the results of experiments with five different electrode configurations and EBP animals sheltered under cobble on sand substrate. These tests confirmed the unidirectional nature of the electrotaxis. Of the 81 (59%, $n$=137) animals that emerged from the cobble shelters, all moved directly to the anode. There was a significant difference between electrode configurations in the mean number of animals caught (ANOVA, $P$<0.001). The best capture rate (2.6 animals per trial, or 85% of the total population) was obtained with a semicircular cathode, straight anode and horizontal configuration (configuration 3 in Fig. 2), and the worst capture rate (0.8 animals, 25% of the population) was obtained with the circular cathode, plate anode, and vertical configuration (configuration 4 in Fig. 2). There was a significant difference between electrode configurations in mean capture time for the first animal (ANOVA, $P$=0.008, LSD post-hoc test) but no significant differences in capture times for the other two animals in each trial. Animals tended not to emerge at the same time but in sequence, with the first, second, and third animals emerging after an overall average of 26.3, 51.6, and 64.5 seconds. In all trials combined, one animal was caught in 91%, two in 60%, and all three in 23% of the trials. The lower and slower capture rate of the second and third animals in each test is probably related to the position of the animals in the rock pile. The EBP lobsters placed in close proximity exhibit intense aggressive behavior (Lawton and Lavalli 1995), which would tend to result in an overdispersed distribution within a bounded habitat like the test rock pile. In this situation some animals will be closer to the anode, and

**Table 1**

Results of electrofishing experiments with the five electrode configurations and cobble shelters on sand shown in Figure 2. The pulse frequency, duty cycle, and input voltage was 100 Hz, 50%, and 50 V, respectively, in all cases.

| Electrode configuration | No. of animals[1] | No. of trials[1] ($n$) | Percent moving to | | Mean no. captured | Percent captured | % of trials capturing | | | Mean capture time (sec) by order of appearance | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | anode | cathode | | | 1 animal | 2 animals | 3 animals | 1st animal | 2nd animal | 3rd animal |
| 1 | 39 | 13 | 100 | 0 | 1.23 ± 0.60 | 41 | 92 | 31 | 0 | 66.8 ± 75.2 | 72.5 ± 73.7 | n/a |
| 2 | 39 | 13 | 100 | 0 | 2.08 ± 0.76 | 74 | 100 | 85 | 31 | 4.4 ± 6.1 | 57.5 ± 50.4 | 24.0 ± 19.8 |
| 3 | 27 | 9 | 100 | 0 | 2.56 ± 0.73 | 85 | 100 | 89 | 67 | 13.3 ± 12.0 | 42.6 ± 40.5 | 102.0 ± 60.4 |
| 4 | 24 | 8 | 100 | 0 | 0.75 ± 0.89 | 25 | 50 | 25 | 0 | 37.0 ± 34.5 | 80.0 ± 99.0 | n/a |
| 5 | 9 | 3 | 100 | 0 | 2.33 ± 0.58 | 78 | 100 | 100 | 33 | 1.0 ± 0 | 7.3 ± 11.0 | 1 |
| Overall average | | | | | | 59 | 91 | 60 | 23 | 26.3 | 51.6 | 64.5 |

[1] Note that three animals were used in each trial.

these would tend to be caught more quickly than those farther away. Animals farther from the anode have a lower probability of a clear passage through crevices and a greater probability of being caught in a "dead end" before emerging from the rock pile.

It is apparent that electrofishing is a potentially useful method for sampling EBP lobsters. However, some additional research is necessary before a practical field sampler can be developed and tested successfully. Our study, although using the most common EBP lobster habitat, did not examine other habitats (e.g. eelgrass, mud) or variations of the common habitat, such as different rock sizes and associated crevices, or different thicknesses of cobble. Although the tedium associated with the existing sampling methods could be reduced significantly by using a diver-operated electrosampler, the most cost-effective and efficient sampler would be operated from a small boat without the need for divers. Conceivably, a sampling device that combines the electrotactic response of EBP lobsters with a bottom-to-surface water pump (e.g. Bergstedt and Genovese, 1994) could fulfill these requirements. Finally, it should be noted that the device described was designed only for use in test tanks insulated from the operator. The use of electrofishing devices in saltwater by divers, although quite safe (Stewart and Cameron, 1974), does require special precautions from an engineering as well as a personal safety perspective.

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# Changes in the probability density function of larval fish body length following preservation

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The influence of body size on physiological and developmental processes during the early life history of fishes has been clearly demonstrated (Miller et al., 1988; Houde, 1989; Pepin, 1991). Because of this and to provide a direct comparison of field collections with laboratory observations that often use measurements of fresh specimens, numerous studies have quantified the effects of preservation and handling on the length of larval fish (Table 1). Most of the research has used laboratory-reared animals for which changes in length are assessed using either comparisons among treatments (i.e. ANOVA) or departures from a one-to-one relationship (i.e. regression) (Table 1). Shrinkage in length is the predominant response to preservation (Table 1), and the amount of shrinkage is influenced by handling (Theilacker, 1980, 1986; Theilacker and Porter, 1995; Fox, 1996).

Changes in larval body length due to preservation are relatively small (3–15%) although variations of up to 1 mm are not uncommon (Table 1). The contrast among species led Jennings (1991) to suggest that specific correction factors would be required. An alternative was Hjörleifsson and Klein-Macphee's (1992) simple model of the relative change in larval lengths, based on a review of previous studies, which showed clear evidence of the effects of body length and preservation time on shrinkage. Of course, as with any such review, the effects of unaccounted for or confounding variables are unknown (Pepin and Miller, 1993). However, Hjörleifsson and Klein-Macphee (1992) predicted a maximum mean shrinkage of ~15% for the smallest larvae (~2 mm) followed by an exponential decrease in relative shrinkage with increasing length. This raises an important point. Although differences in mean larval body length may appear significant from a statistical perspective, the importance of correcting for the effects of preservation are most pronounced at the level of the individual because morphological measurements are used in the analysis of each larva's physiological condition (e.g. Theilacker and Porter, 1995) to assess the relative state of a population. Even small changes in length resulting from shrinkage can create important biases at this level of analysis. In contrast, the small relative effects of preservation on body length (Hjörleifsson and Klein-Macphee, 1992) is unlikely to substantially influence estimates of length-frequency distributions.

Fundamental issues yet to be addressed in the assessment of larval shrinkage include 1) the effect of preservation on the distribution of larval length measurements within a given length interval rather than the mean, and 2) the contribution of investigator-induced error on that distribution. The former point is of particular importance because the application of correction factors to individual larvae must maintain the status of that animal in relation to others within the population. Investigator-induced error may be equally important. Few studies have attempted to quantify the variance in repeated estimates for a given operator (Jennings, 1991; Hjörleifsson and Klein-Macphee, 1992; Fox, 1996) and none have contrasted bias and variance among operators. Our failure to address these questions to date probably results from 1) the small sample sizes (i.e. generally <100) presented in most studies of the effects of preservation (Table 1), and 2) the fact that usually only a single investigator is involved in making the measurements of the larvae. Nonetheless, these issues are important because they provide the basis for narrowing the possible sources of error in interpretations of physiological processes that influence ichthyoplankton population dynamics.

In this study we report on an evaluation of the shrinkage effects of preservation on several species of larval fish collected as part of a field study. We consider changes in both the mean and variance of the distribution of individuals within narrow length intervals and assess the null hypothesis that there are no differences among species. We also

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## Table 1

Summary of studies dealing with the effect of formaldehyde preservation on the length of larval fish. Under results the various symbols are S = shrinkage in length (mm); L = length before preservation; P = length following preservation; and CI = 95% confidence interval. Levels of precision recorded in either length range or results are those reported by the authors. With one exception, our summary of data reported from laboratory studies did not include simulated capture.

| Species | Length range (mm) | Formaldehyde solution | Measurement method | Analysis | Sample size | Result | Source of larvae | Reference |
|---|---|---|---|---|---|---|---|---|
| *Clupea harengus pallasi* | 8–26 | 3.7% with calcium borate or sodium borate | Micrometer | ANCOVA | $n = 120$ | $S = 0.564 + 0.016\,L$ | Laboratory | Hay, 1982 |
| *Clupea harengus pallasi* | 12–22<br>8–10 | 4% | Micrometer | ANOVA | $n = 326$<br>$n = 88$ | Significant shrinkage | Sea–caught (dip net) and laboratory | Schnack and Rosenthal, 1978 |
| *Clupea harengus* | 9–20 | 4% with 2.5% sodium acetate trihydrate | Image analysis | ANOVA and regression | $n = 49$ | $L = 1.765 + 0.867\,P$ | Laboratory | Fox ,1996 |
| *Clupea harengus* | 7.75–9.17<br>13.1–17.4 | 0.75–3.7% in 15 or 34 ppt sea water | Micrometer | None | $n = 20$–$50$ | 7–14% shrinkage<br>3–7% shrinkage | Laboratory<br>Sea–caught | Blaxter, 1971 |
| *Coregonus albula* | 8–10 | 4% neutralized with hexametylentetramin | Micrometer | ANOVA | $n = 9$–$15$ | Significant shrinkage | Laboratory | Karjalainen, 1992 |
| *Dicentrarchus labrax* | 10–18 | 4% with 3 g/l sodium acetate trihydrate | Micrometer | ANOVA | $n = 109$ | 7% shrinkage (CI = –2 to 16%) | Laboratory (simulated capture) | Jennings, 1991 |
| *Engraulis mordax* | 3.9–21.6 | 2.2% buffered | Micrometer | Regression | $n = 61$ | 8% shrinkage (SD = 3%) | Laboratory | Theilacker, 1980 |
| *Gadus morhua* | 4–5 | 3.7% in 50% sea water | Micrometer | None | $n = 10$ | 12% shrinkage | Laboratory | Yin and Blaxter, 1986 |
| *Mallotus villosus* | 4.6–19.6 | 2.2% buffered | Micrometer | Regression | $n = 113$ | $L = 0.36 + 1.016\,P$ | Field (bongo) | Kruse and Dalley, 1990 |
| *Merluccius bilinearis* | 3.7–14.4 | 1.5% neutralized | Micrometer | Repeated measures ANOVA | $n = 83$ | 4.3% shrinkage | Sea–caught (bongo) | Fowler and Smith, 1983 |
| *Merluccius productus* | 4–5 | 1.1% | Micrometer | None | $n = 3$ | 8.9–40% shrinkage mean ≈15–20% | Laboratory | Bailey, 1982 |
| *Pagrus major* | 5–7<br>13–19 | 3.7% at pH 4.3 | Micrometer | None | $n = 7$<br>$n = 16$ | 7–12 % shrinkage<br>3–7% shrinkage | Laboratory | Takizawa et al., 1994 |
| *Paralichthys olivaceus* | 7–11<br>12–19 | 3.7% at pH 4.3 | Micrometer | None | $n = 18$<br>$n = 4$ | 9–16% shrinkage<br>2–12% shrinkage | Laboratory | Takizawa et al., 1994 |
| *Paralichthys lethostigma* | 9.49–13.05 | 1.48% buffered | Micrometer | Repeated measures ANOVA | $n = 72$ | 5–10% shrinkage in sea water | Sea–caught (Live trap) | Tucker and Chester, 1984 |
| *Platichthys flesus* | 3–4 | 3.7 % in 50% sea water | Micrometer | None | $n = 11$ | 11% shrinkage | Laboratory | Yin and Blaxter, 1986 |
| *Pleuronectes americanus* | 3–8.5 | 0.75% | Image analysis | Pairwise and regression | $n = 102$ | $P = -0.20 + 0.92\,L$ | Laboratory | Hjörleifsson and Klein–MacPhee, 1992 |
| *Sardinops caerulea* | 3.45–6.19 | 1.1% buffered | Micrometer | Regression | $n = 75$ | $P = -0.26 + 0.9724\,L$ | Sea–caught | Farris, 1963 |
| *Stizostedion vitreum* | 9–21 | 1.9% with sodium borate | Micrometer | Regression | $n = 80$ | $L = 0.087 + 1.014P$ | Laboratory | Johnston and Mathias, 1993 |
| *Theragra chalcogramma* | 4.2–20.0 | 1.85% | Micrometer | ANCOVA | $n = 42$ | $L = 0.344 + 1.021\,P$ | Laboratory | Theilacker and Porter, 1995 |
| *Trachurus symmetricus* | 3.35–4.10 | 1.85% buffered | Micrometer | None | $n = 13$ | 4% shrinkage | Laboratory | Theilacker, 1986 |

evaluate the magnitude of intra- and interoperator differences in performance for repeated measurements of the same specimens.

## Materials and methods

The study was conducted on Conception Bay, Canada (47°45'N, 53°00'W), during the period of 12 July to 4 August 1995. Sampling was performed daily from CSS *Shamook* (23-m boat length) at a single site near the head of the bay.

Larvae from a number of species were obtained from vertical plankton hauls made with a square trawl 4 m long with a 4-$m^2$ mouth fitted with 333-μm mesh nitex and an oversize codend 20 cm in diameter and 30 cm long. The net was lowered to a depth of 20–30 m and retrieved at a rate of 1 m/s. Net design and deployment protocol were chosen to minimize trauma to larvae. On deck, the net was washed and the codend contents poured into a 20-L plastic bucket. Live and freshly dead ichthyoplankton were immediately sorted with flexible forceps and transferred to petri dishes filled with chilled seawater. Moribund larvae, indicative of death or extremely poor condition prior to capture (O'Connell, 1981; Otto and Boggs, 1983; Takizawa et al., 1994), were excluded from our samples to avoid possible bias. Each larva was assigned an indentification number, tentatively identified to the lowest taxonomic level possible, and recorded on videotape with a camera mounted on a Wild M3C dissecting microscope (S-type mount, 0.5× objective). Individual larvae were immediately transferred into 1.5 mL microcentrifuge tubes filled with 2% buffered formaldehyde. Identifications were confirmed in the laboratory and standard lengths were determined to the nearest 0.1 mm using an Optimas© image analysis system. Measurements of the video-recorded fresh standard lengths were performed at the Northwest Atlantic Fisheries Centre by an operator with more than 10 years of experience in the study of larval fish. All laboratory analyses performed on preserved larvae were conducted approximately five months after the sampling cruise at Queen's University by a novice operator with less than 1 year of experience in the study of larval fish. Each preserved larva was extracted from its microcentrifuge tube, videotaped in a manner identical to that employed for recently captured larvae, and measured (standard length) with an Optimas© image analysis system. All measurements were performed by clicking on a series of points through the centre of the head and along the notochord.

To contrast the precision and accuracy of length measurements, the experienced operator repeated a set of measurements on a sample of randomly selected larvae from the initial videotape records. In addition, a random subsample of 72 preserved capelin larvae (*Mallotus villosus*) were selected from the collection for replicate measurements by the experienced and novice operators. In each instance, both operators independently videotaped each larva for both the initial and repeated measurements. In addition, the experienced operator performed duplicate measurements on approximately one half of the samples measured by both operators. All measurements were performed with only knowledge of specimen number and magnification level.

We evaluated individual differences in body length following preservation ($\Delta l = l_{preserved} - l_{fresh}$). For analysis, data were binned into 1-mm length intervals for fresh specimens (e.g. $1 \leq \times < 2$). The hypothesis that there was no significant difference in mean body length ($H_0: \Delta\bar{l} = 0$) was evaluated by using a two-sided *t*-test. Comparison among species was accomplished by using an ANOVA ($H_0: \Delta\bar{l}_1 = \ldots = \bar{l}_n$, for species 1 to *n*). A species was included in the analysis only if there were at least three specimens within a length interval. Homogeneity of the variances in fresh (*f*) and preserved (*p*) larval lengths within each length interval was assessed by using a one-sided *F*-test of the null ($H_0: s_f^2 >= s_p^2$) and alternative ($H_A: s_f^2 < s_p^2$) hypotheses. Changes in individual rank, within a length interval, were assessed by using Kendall's rank correlation coefficient (τ). Operator precision and accuracy were evaluated by using general linear models.

## Results

### Operator accuracy

The experienced operator exhibited consistent performance in repeated measurements of both fresh and preserved capelin larvae (Fig. 1; Table 2). Regression analysis of the independent measurements by the experienced operator showed no significant departure from an intercept of 0 and a slope of 1 for both fresh and preserved specimens (Table 2). Residual variances for the two treatments were not significantly different ($F_{40, 38}$=1.1, $P$>0.05).

Comparison of measurements by experienced and novice operators revealed no significant bias on the part of either operator although the results did approach significance (0.1>$P$>0.05) and the slope was not significantly different from 1 (Table 2). However, the residual variance about the novice-experienced operator regression was significantly greater than the residual variance of repeated measurements

made by the experienced operator ($F_{72, 38}$=4.61, $P$<0.001).

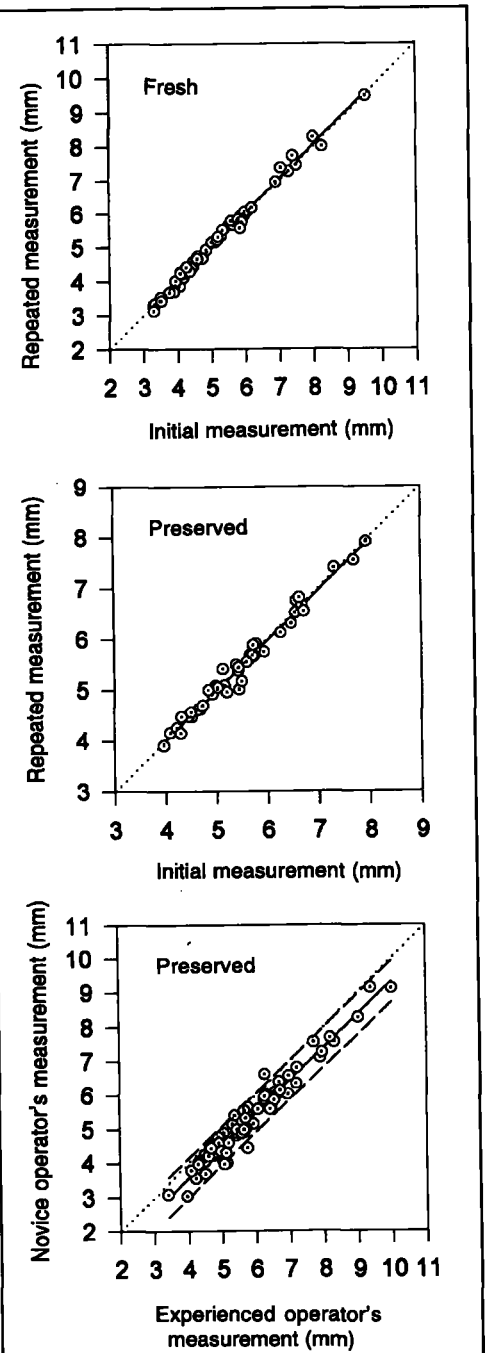


**Figure 1**

Comparison of repeated measurements of the experienced operator on fresh (top panel) and preserved (center panel) specimens as well as the comparison between experienced and novice operators (bottom panel). Solid lines represent least squares regressions (Table 2). Dotted lines show the 1:1 relationship. Dashed lines in the lower panel show the 95% prediction intervals.

### Changes in body length

A total of 1179 larvae representing 9 different species were used in our analyses. Within each length interval, the total number of specimens available ranged from 10 to 281 individuals, representing 1 to 5 species (Table 3).

Within 1-mm length intervals, preservation resulted in significant increases in body length for individuals 3–6 mm fresh standard length and significant decreases in body length for individuals >7 mm fresh standard length (Fig. 2, Table 3). In six instances there were also significant differences among species in preserved body length (Table 3). For fresh length intervals between 5 and 9 mm there was consistency in the order of species; preserved specimens of *Hippoglossoides platessoides* were larger for a given length interval than *Ulvaria subbifurcata* and *Mallotus villosus*. However, above and below the 5–9 mm length intervals there was variation in the order of species. In the larger size classes (≥12 mm), preserved *Stichaeus punctatus* and *Gadus morhua* were larger than *Clupea harengus* and *Hippoglossoides platessoides*.

The initial variance of fresh standard lengths within each length interval ranged from 0.043 to 0.088 mm$^2$, whereas the variance of preserved standard lengths of these same individuals was significantly greater (Table 3) and ranged from 0.18 to 3.5 mm$^2$ (Fig. 3). Furthermore, the variance of the preserved length measurements increased significantly with increasing fresh length ($r^2$=0.70, $P$<0.01, $n$=15) (Fig. 3).

Kendall's correlation coefficient (τ) revealed that individual larvae remained at the same rank about 1 time in 3 (Fig. 4). This effect increased (i.e. 1 time in 4 or 5) with increasing fresh length.

## Discussion

Changes in body length of larval fish due to handling and preservation are neither uniform nor consistent among individual animals: there is substantial variation in reaction to both handling (no matter how gentle) and preservation and variation is greatest in absolute terms for larger larvae.

No previous study (Table 1) has employed sample sizes large enough to permit the evaluation of changes in the distribution or rank of individual larvae within small length intervals. We found clear evidence that changes in body length can be more substantial than previously estimated by means of analyses applied to a broad range of sizes. Despite significant changes in body length for most length intervals, our results show that 1) variation about

**Table 2**

Results of the comparison of initial (I) and repeated (R) measurements on fresh and preserved larvae by the experienced (E) and novice (N) operators. Numbers in square brackets represent the standard error of the intercept ($\alpha$) and slope ($\beta$). The sixth and seventh columns show the test of the hypotheses that the intercept is not significantly different from 0 and that the slope is not significantly different from 1.

| Treatment | Initial | Repeat | Regression ($y = \alpha + \beta x$) | $F$-Value | $t$-value $H_0: \alpha = 0$ | $t$-value $H_0: \beta = 1$ | Residual variance |
|---|---|---|---|---|---|---|---|
| Fresh | E | E | $R$ = 0.074 [0.128] + 0.983 [0.0229] $I$ | $F_{1,40}$=1848, $P < 0.001$ | 0.58, $P > 0.05$ | 0.74, ns | 0.020 |
| Preserved | E | E | $R$ = 0.113 [0.126] + 0.977 [0.0228] $I$ | $F_{1,38}$=1833, $P < 0.001$ | 0.90, $P > 0.05$ | 1.01, ns | 0.018 |
| Preserved | E | N | $R$ = -0.271 [0.149] + 0.959 [0.0263] $I$ | $F_{1,72}$=1414, $P < 0.001$ | 1.81, $0.1 > P > 0.05$ | 1.56, ns | 0.083 |

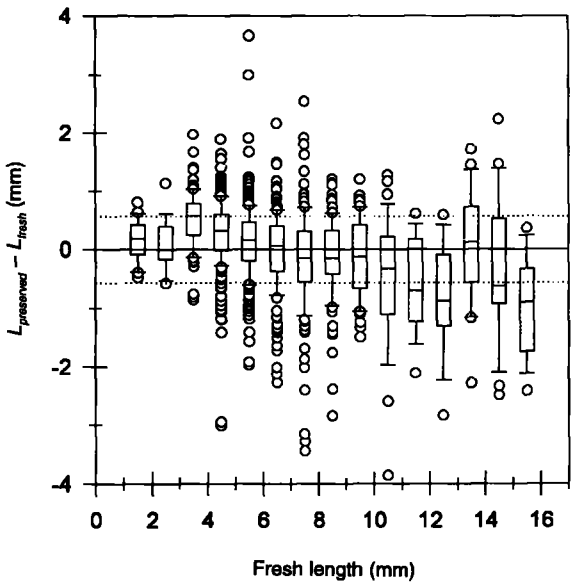


**Figure 2**

Box plot of the 25th, 50th, and 75th percentile of the difference in mean individual length of larval fish within each millimeter fresh length interval. Capped whiskers show the 10th and 90th percentiles and the open circles show the distribution of observations outside those confines. The dotted lines represent the 95% confidence intervals of the residual population variance from the comparison of measurement error between operators.

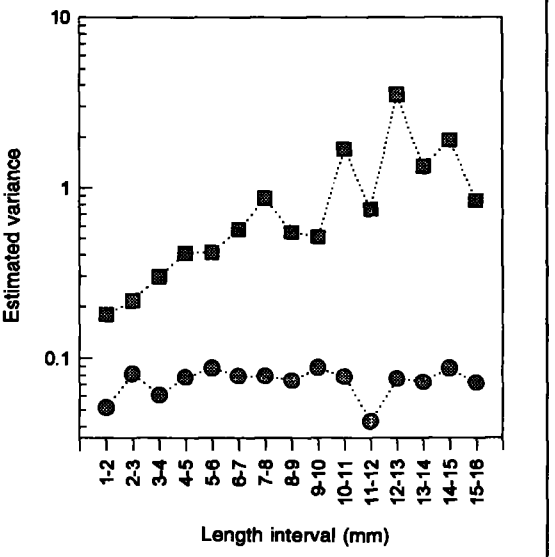


**Figure 3**

Variance in body length of fresh (circles) and preserved (squares) specimens within each millimeter interval.

the mean can be substantial and that 2) the relative position of an individual larva within a length interval may shift substantially.

Our findings are consistent with those of Hay (1982), Theilacker (1986), and Fox (1996) who all found that postpreservation changes in body length were greatest for large larvae. However, the marked increase in variance of preserved larval lengths in relation to the initial measurements was not caused by operator error. The residual variance of repeated measurements among operators was of the same order as the variance in fresh lengths within individual length intervals and was comparable to that obtained by Jennings (1991), Hjörleifsson and Klein-Macphee (1992), and Fox (1996). However, Fox (1996) found some evidence of increased variance with increased length, in contrast with our results. We conclude that remeasurement of larvae per se is unlikely to be a major contributor to our observation that the order of individual larvae, in relation to population estimates, is not maintained following preservation.

Our finding of postpreservation increases in body length, for individuals <6 mm SL, contrasts with most studies of the effects of formaldehyde preservation on larval fish. Fox (1996) and studies of other meth-

**Table 3**

Species specific mean differences in length following preservation within 1-millimeter length intervals. The number of specimens is indicated by $n$. Subscripts in the fourth and seventh columns refer to the species for which information was available within each length interval ($i$=1, . . . , $n$). The standard deviation of the species specific difference in length (SD) is also provided. A positive difference in length indicates expansion whereas a negative value indicates shrinkage. The last three columns present the analytical results for overall changes in length following preservation, differences among species, and homogeneity of variance between fresh and preserved specimens within each length interval.

| Length Interval (mm) | Species | $n$ | $\bar{l}_i$ | SD ($\Delta l_i$) | $t$-value $H_0$:$\Delta\bar{l}=0$ | $F$-value $H_0$:$\Delta\bar{l}_1=\ldots=\bar{l}_n$ | $F$-value $H_0$:$s_f^2>=s_p^2$ |
|---|---|---|---|---|---|---|---|
| 1–2 | *Pleuronectes americanus* | 11 | 0.18 | 0.43 | 1.86, $P>0.05$ | 0.02, $P>0.5$ | 3.21, $P<0.01$ |
| | *Tautogolabrus adspersus* | 5 | 0.15 | 0.19 | | | |
| 2–3 | *Pleuronectes americanus* | 13 | 0.12 | 0.46 | 0.92, $P>0.2$ | N/A | 2.45, $P<0.05$ |
| 3–4 | *Liparis* sp. | 8 | 0.07 | 0.41 | 9.74, $P<0.001$ | 24.6, $P<0.001$ | 4.49, $P<0.001$ |
| | *Mallotus villosus* | 73 | 0.63 | 0.39 | | | |
| | *Pleuronectes americanus* | 6 | –0.39 | 0.35 | | | |
| 4–5 | *Hippoglossoides platessoides* | 3 | –0.33 | 0.75 | 6.96, $P<0.001$ | 2.78, $P<0.05$ | 4.87, $P<0.001$ |
| | *Liparis* sp. | 15 | –0.07 | 0.99 | | | |
| | *Mallotus villosus* | 136 | 0.26 | 0.56 | | | |
| | *Pleuronectes americanus* | 3 | 0.09 | 0.77 | | | |
| | *Ulvaria subbifurcata* | 75 | 0.37 | 0.47 | | | |
| 5–6 | *Hippoglossoides platessoides* | 5 | 0.48 | 0.71 | 3.38, $P<0.001$ | 4.38, $P<0.01$ | 4.33, $P<0.001$ |
| | *Liparis* sp. | 7 | –0.76 | 0.43 | | | |
| | *Mallotus villosus* | 119 | 0.14 | 0.53 | | | |
| | *Pleuronectes americanus* | 3 | –0.10 | 0.49 | | | |
| | *Ulvaria subbifurcata* | 147 | 0.14 | 0.67 | | | |
| 6–7 | *Hippoglossoides platessoides* | 9 | 0.23 | 0.52 | 0.33, $P>0.5$ | 0.76, $P>0.2$ | 6.63, $P<0.001$ |
| | *Mallotus villosus* | 51 | –0.07 | 0.65 | | | |
| | *Ulvaria subbifurcata* | 122 | –0.01 | 0.70 | | | |
| 7–8 | *Hippoglossoides platessoides* | 6 | 0.73 | 0.67 | 2.70, $P<0.01$ | 4.61, $P<0.05$ | 10.1, $P<0.001$ |
| | *Mallotus villosus* | 33 | –0.41 | 1.10 | | | |
| | *Ulvaria subbifurcata* | 96 | –0.19 | 0.76 | | | |
| 8–9 | *Hippoglossoides platessoides* | 4 | 0.34 | 0.66 | 2.13, $P<0.05$ | 3.59, $P<0.05$ | 6.80, $P<0.001$ |
| | *Mallotus villosus* | 6 | –0.79 | 1.54 | | | |
| | *Ulvaria subbifurcata* | 77 | –0.14 | 0.59 | | | |
| 9–10 | *Clupea harengus* | 3 | –0.12 | 1.08 | 1.71, $P>0.05$ | 0.13, $P>0.5$ | 5.35, $P<0.001$ |
| | *Hippoglossoides platessoides* | 7 | –0.06 | 0.65 | | | |
| | *Ulvaria subbifurcata* | 36 | –0.20 | 0.66 | | | |
| 10–11 | *Hippoglossoides platessoides* | 4 | –1.00 | 2.11 | 2.68, $P<0.05$ | 0.42, $P>0.5$ | 19.9, $P<0.001$ |
| | *Ulvaria subbifurcata* | 28 | –0.56 | 1.18 | | | |
| 11–12 | *Hippoglossoides platessoides* | 4 | –0.68 | 0.69 | 2.58, $P<0.05$ | 0.03, $P>0.5$ | 16.3, $P<0.001$ |
| | *Ulvaria subbifurcata* | 8 | –0.58 | 0.93 | | | |
| 12–13 | *Clupea harengus* | 3 | –0.13 | 0.73 | 2.75, $P<0.05$ | 1.26, $P>0.5$ | 42.7, $P<0.001$ |
| | *Hippoglossoides platessoides* | 3 | –1.25 | 0.39 | | | |
| | *Ulvaria subbifurcata* | 4 | –1.09 | 1.29 | | | |
| 13–14 | *Clupea harengus* | 10 | –0.13 | 0.78 | 0.1, $P>0.5$ | 2.64, $P>0.1$ | 16.9, $P<0.001$ |
| | *Hippoglossoides platessoides* | 3 | –0.63 | 1.44 | | | |
| | *Stichaeus punctatus* | 4 | 0.88 | 0.87 | | | |
| 14–15 | *Clupea harengus* | 11 | –0.81 | 0.97 | 0.8, $P>0.2$ | 4.74, $P<0.05$ | 20.2, $P<0.001$ |
| | *Gadus morhua* | 3 | 0.87 | 0.72 | | | |
| | *Stichaeus punctatus* | 3 | 0.72 | 1.50 | | | |
| 15–16 | *Clupea harengus* | 8 | –0.80 | 1.00 | 3.78, $P<0.01$ | 0.82, $P>0.2$ | 10.8, $P<0.001$ |
| | *Hippoglossoides platessoides* | 4 | –1.30 | 0.58 | | | |

ods of preservation (e.g. alcohol, freezing [Theilacker, 1980; Fowler and Smith, 1983; Kruse and Dalley, 1990; Hjörleifsson and Klein-Macphee, 1992]) have shown that individual animals may increase in

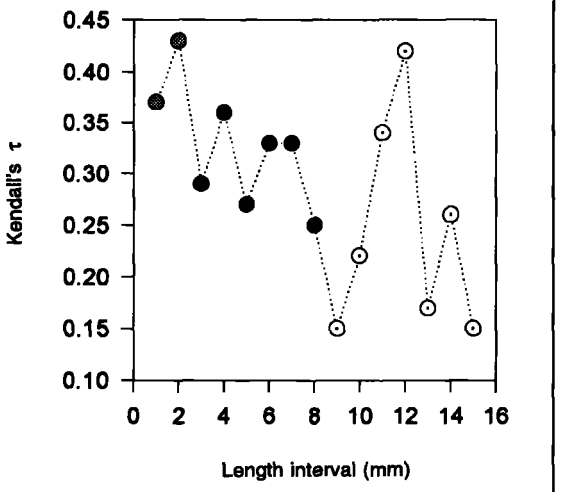


**Figure 4**

Rank correlation (Kendall's τ) of preserved versus fresh lengths, within millimeter intervals of fresh lengths. Open symbols represent values not significantly different from 0, grey symbols present significant values ($P<0.05$), and black symbols represent highly significant values ($P<0.01$).

length following preservation. It is important to note, however, that although our results show that the mean change in length for larvae <6 mm SL was positive, there were also numerous individuals in these same length intervals that either shrank or showed no change in body length after preservation. This finding underscores our contention that responses to preservation vary significantly at the level of the individual as well as among species.

It is possible that the capture, sorting, and preservation approaches used in this study may have led to variations in the general pattern of changes in body length. Following capture, sorting on deck may have caused a change in water temperatures. This procedure may have precipitated the death of individual larvae and resulted in contraction of body tissue in the "fresh length" measurement and consequently may have produced an apparent increase in body length following remeasurement. The source of larvae may also be an important feature to consider. Most preservation studies are based on laboratory-reared animals rather than on field-caught specimens (Table 1). Laboratory-reared animals show greater changes in length than field caught specimens (Table 1), although there is some variation about this general pattern (e.g. Theilacker, 1986).

Change in body length of marine fish larvae following capture and preservation has been attributed mainly to a breakdown of the osmoregulatory capacity of larvae, leading to a net loss of water (Ahlstrom, 1976). Simple laboratory-based studies of shrinkage have concluded that preservation results in relatively small changes in body length (see Hjörleifsson and Klein-Macphee, 1992) but that the impact of net-capture and handling is likely to have the greatest impact on changes in body length (Theilacker, 1980; Jennings, 1991; Fox, 1996). Most laboratory simulations of capture used fixed handling times; however, under field conditions it is unknown when a larva enters the net. Thus correction factors for a fixed handling time may introduce substantial error. Our sampling methods differed dramatically from those normally employed in field situations in both the duration of the residence time of larvae in the net and in the aggressiveness of capture and handling. It is therefore likely that, in comparison with other studies, the effect of capture and handling in our study was small. However, despite the possible importance of capture and handling, the interpretation of the condition of individual larvae or the distribution of population characteristics must be approached with caution.

Our results clearly show that the relative position of an individual within the size distribution of the sample is likely to change considerably following handling and preservation. Thus, attempts to correct for the effects of preservation or handling on fresh larval lengths can, in certain types of analysis (e.g. individual-based approaches to the use of morphometric measurements), introduce significant and unpredictable bias in both the data and their interpretation. There appears to be no simple solution to this problem. Conclusions as to the overall vulnerability of a fractional portion of a population to a given factor must consider the inherent variability in the distribution of measurements caused by operator, handling, and preservation-induced error.

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We thank Tim Shears and Sarah Donald for providing valuable technical assistance. Additional assistance was provided by Steph Carter, Dave Bell, and the officers and crew of CSS *Shamook*. C. J. Fox and two anonymous referees provided valuable criticisms of this study. Funding for this project was provided by the Department of Fisheries and Oceans (PP) and the Natural Sciences and Engineering Research Council (WCL).

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# Sampling juvenile skipjack tuna, *Katsuwonus pelamis*, and other tunas, *Thunnus* spp., using midwater trawls in the tropical western Pacific

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Skipjack tuna, *Katsuwonus pelamis*, a highly migratory species, is one of the most important stocks for commercial fisheries in the western Pacific. The spawning ground of this species extends throughout equatorial and subtropical waters but larvae are more abundant in lower than higher latitudes (Nishikawa et al., 1978). Young and preadult skipjack tuna migrate great distances seasonally between tropical and temperate waters, yet little information is available for juvenile stages of this species.

Exploitation of skipjack tuna in the western Pacific has increased in recent years; an annual catch of 940,000 metric tons was taken in 1993 (FAO, 1995). Stock assessment and management of the species require detailed biological information on each life stage but, largely because of sampling difficulties, data on juveniles of skipjack tuna and other tunas are relatively limited compared with those on adults. Juveniles swim well and thus escape many gear: ring nets, beam trawls, or small pelagic trawls (see Methot, 1986). Other gear and light traps will not provide adequate spatial or temporal coverage (Thorrold, 1993).

Consequently development of appropriate sampling gear has been an important part of our study of the early life history of skipjack tuna and other tunas. Since 1992, we have worked to develop a new method for capturing juvenile skipjack tuna and tuna spp., namely a midwater trawl net with a large mouth opening, capable of high-speed towing. This appeared to be an excellent gear for sampling juveniles. In a trial survey, we captured large numbers of juvenile skipjack tuna and other tuna by using the midwater trawl net in offshore waters of the tropical western Pacific. This study is based on 1992–94 research cruises and confirms the effectiveness of the new midwater trawling gear. We describe the specifications of this net and its effectiveness for collecting juvenile skipjack tuna and other tuna.

## Materials and methods

The midwater trawl net Tansyu has a large mouth opening and was designed to be towed at high speed. It was developed in cooperation with Tohoku National Fisheries Research Institute and Nichimo Co. Ltd., Shimonoseki, Yamaguchi. Targets for the Tansyu included skipjack tuna and other tuna, ranging in size from 10 to 200 mm standard body length (SL). The goal was to capture sufficient numbers to characterize distribution and relative abundance. The Tansyu design was based on the midwater trawl net Yoko-2, which has been used for sampling sardine by Seikai National Fisheries Research Institute, Nagasaki (Takeshita et al., 1988). The total length of the net was 71.6 m and that of the headrope and footrope was 38.6 m (see Fig. 1). The net was composed of 8 wing panels, 12 body panels, and 6 codend panels; all were made of 380 D fine polyethylene ropes. Twine diameter was between 1.91 mm (P-30) and 5.06 mm (P-210). The stretched mesh size was 1000 mm at the wings and the first panels of the body, diminishing successively to 57 mm in the seventh panels of the body. The dimension of the fishing circle was 144 × 1000 mm (where 144 = no. of meshes at mouth of net and 1000 m = mesh size at first panel of net). A codend of 60-mm mesh size was attached to the end of the body. An inner net of 30-mm and 8-mm mesh size was put inside of the codend to collect samples. Attached to the headrope were 74 floats of 300-mm diameter. A steel chain of 28-mm diameter was attached to the footrope. Buoyancy of the floats and weight of the chain were 762.4 kg and 660.4 kg, respectively. The bridles to the bottom, center, and upper wings were 18 mm in diameter and 100 m long. The expected mouth opening was approximately 20 m wide, 18 m high, at a towing speed of 4.5 knots. The net was designed for a maximum towing speed of 5 knots. The Tansyu was designed to be used with 1.7 m × 2.8 m otter doors.

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Fishery Bulletin 96:641–646 (1998).

A scale model of the Tansyu was constructed and tested in a tank at Nichimo Co. Ltd. to test its design and performance.

Research cruises were carried out from late October to early December, 1992–94. The survey covered an area from offshore of Palau past the Calorine Islands in the tropical western Pacific (Fig. 2). A 400-ton class stern trawler was chartered by the Fisheries Agency, Ministry of Agriculture, Forestry, and Fisheries, Tokyo, to conduct the midwater trawl trials.

Midwater trawling was typically conducted four times daily; standard duration of towing was approximately one hour. Towing time was defined as the duration from beginning of the net tow to commencement of warp hauling. Ten strata were occupied from near surface to 200 m, in 20-m increments of water depth; separate tows in each stratum were carried out. Depth of the net was established by noting the warp length, and towing speed was usually set 4 to 5 knots against the currents. A net-depth recorder (Furuno FNR-200) was used to monitor continuously the mouth opening and depth of the net throughout the trawling operation.

As soon as the net was brought on deck, the collection from the codend was weighed as whole wet weight; skipjack tuna and other tunas were sorted from the collection. Samples were fixed in 10% buffered formalin and preserved in 80% ethanol. All skipjack tuna specimens were identified after the cruise following the methods of Matsumoto et al. (1984). The species of tunas were identified as *Thunnus* spp. and samples of skipjack tuna and other tunas were measured individually to the nearest 0.1 mm SL with calipers.

In this report, the early life stages of skipjack tuna were defined as follows: larva: from hatching to less than 10 mm SL; juvenile: from 10 mm SL to less than 100 mm SL; and young: from 100 mm SL to less than 300 mm SL.

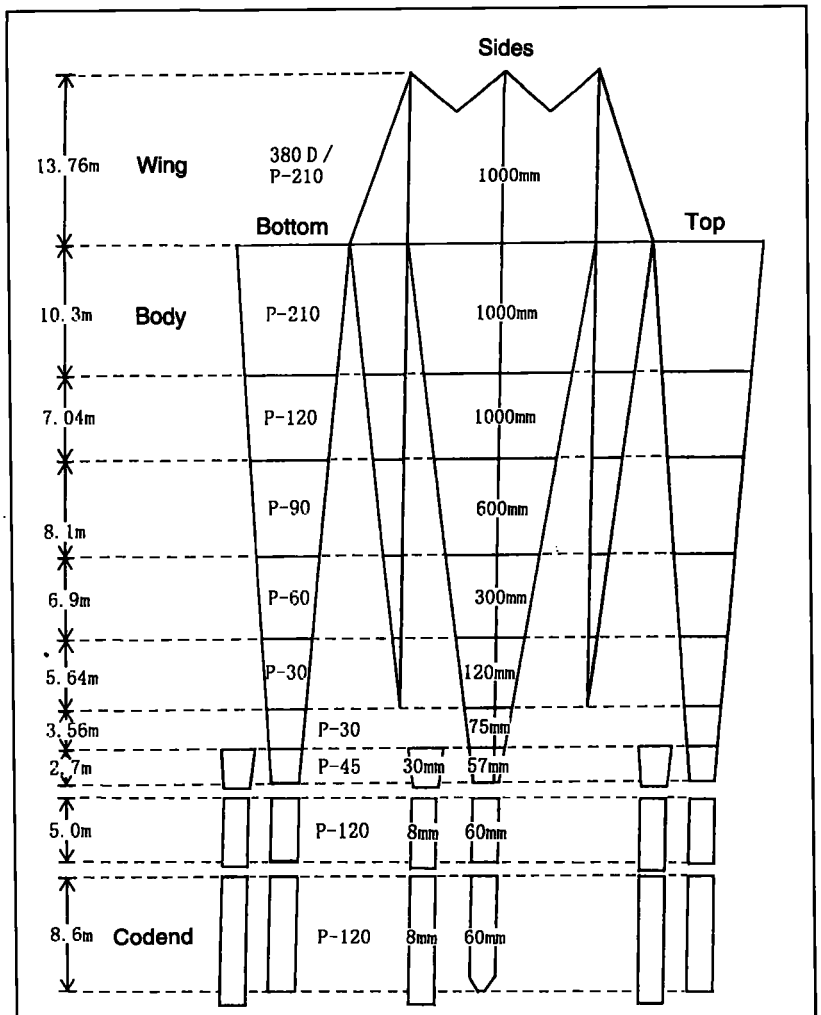


**Figure 1**

A schematic diagram of the midwater trawl net Tansyu that was developed to collect juvenile skipjack tuna and other tunas. The numerals on the left side indicate the length of each panel. The numerals within the diagram indicate twine size and mesh size of the net.

## Results

The new trawl was deployed a total of 327 tows throughout the three years of the study. The target taxa, skipjack tuna and other tunas, were captured in 163 tows; skipjack tuna and other tunas co-occurred in 66 tows. Over four thousand skipjack tuna and other tunas were collected (Table 1). The incidence of juveniles collected remained high in all years. The maximum number of specimens collected in a single tow was over 100 juveniles of both taxa.

The diel distribution of sampling effort was 41.8% during daytime, 58.2% at nighttime (Table 2). For skipjack tuna, the mean daytime occurrence was about 5% higher than that at nighttime, and the mean daylight catch per tow was about four individuals greater than that at nighttime; a similar pattern was observed for other tuna, but the differences were not statistically significant. The whole wet weight for nighttime usually tended to be larger

than that for daytime (Table 2). Other dominant species collected at nighttime were myctophids, cephalopods, and euphausids; those taken in daylight were engraulids and acanthurids.

Size classes of skipjack tuna and other tunas were widely represented; life stages from postlarva to early young were apparent. Where SL could be measured, specimens represented 92.2% of skipjack tuna, 93.5% of other tunas. Skipjack tuna SL ranged from 7.1 mm to 171.6 mm (Fig. 3); other tunas ranged from 8.0 mm to 139.8 mm (Fig. 4). The mean SL was 25.7 mm for skipjack tuna, 27.4 mm for other tunas, with modes at 10–20 mm and 20–30 mm, respectively. Juveniles were abundant and were the dominant life stage of both species in our samples. The composition of larvae, juvenile, and young was 1.6%, 97.6%, and 0.8% for skipjack tuna, 0.7%, 98.6%, and 0.7% for other tunas. Specimens of both taxa collected at night tended to be larger than those collected during daylight. For skipjack tuna, the size of specimens during daytime ranged from 7.1 mm to 81.8 mm (average 23.8 mm); at nighttime lengths ranged from 8.1 mm to 171.6 mm (average 27.7 mm). Tunas captured in daytime ranged from 8.0 mm to 54.7 mm (average 22.6 mm), at night from 11.0 mm to 139.8 mm (average 31.7 mm). There was a significant difference in the average SL of both species between daytime and nighttime (Cochran-Cox $t$-test, $P<0.05$). Young skipjack tuna and other tunas were collected only at night and the number of specimens per tow was less than six. Juveniles were as just as abundant at day as at night.

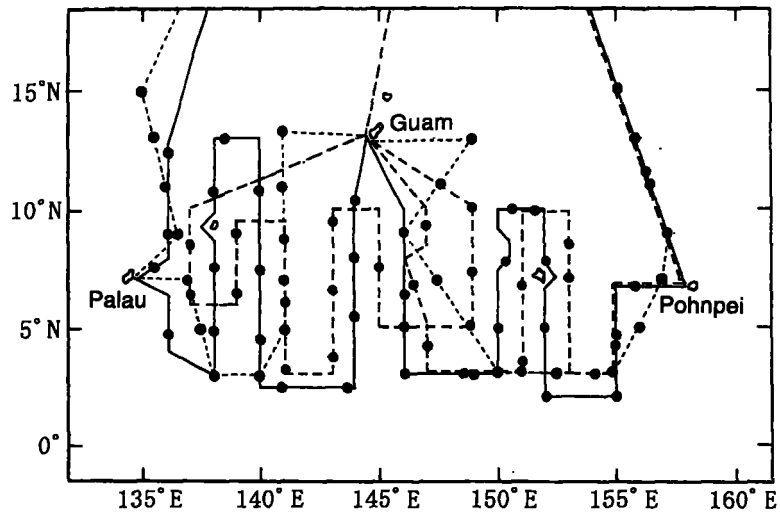


**Figure 2**

The sampling area. Stations (●) on the cruise tracks (---) indicate locations where the midwater trawls were deployed.

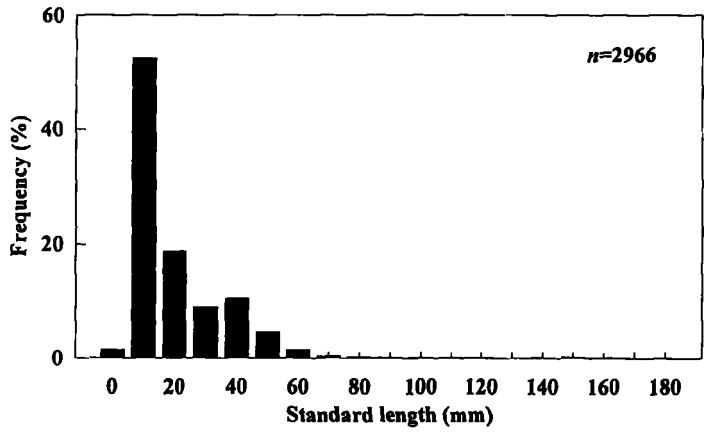


**Figure 3**

Length-frequency distribution of *K. pelamis* collected by the midwater trawl net in 1992–94 trial surveys.

## Discussion

The midwater trawl net Tansyu made it possible to collect large numbers of juvenile skipjack tuna and other tunas during both day and night; this was not possible with the sampling gears previously available. The results of our survey demonstrate that the Tansyu was effective in collecting juveniles of skipjack tuna and other tunas.

In previous studies, various sampling gears were used for sampling larvae of skipjack tuna and other tunas (Table 3), the results of which demonstrate that

**Table 1**

Results of collection of juveniles and young *K. pelamis* and *Thunnus* spp. by the midwater trawl net in 1992–94. Inds. = individuals.

| Species | Occurrence[1] % | Total catch (inds.) | Catch per tow[2] (inds.) |
|---|---|---|---|
| *K. pelamis* | 49.8 | 3218 | 9.8 |
| *Thunnus* spp. | 27.5 | 1074 | 3.3 |

[1] Number of tows in which juveniles were caught/total tows × 100.
[2] Total catch of juveniles/total tows.

the maximum size of skipjack tuna and other tunas that could be collected with smaller plankton nets was about 12 mm; the usual size was 3 to 5 mm. Thus skipjack tuna and other tunas larger than 10 mm could easily escape from these gears. Davis et al. (1990) pointed out that net avoidance by larvae should be considered in calculating estimates of abundance of larval tunas.

Sampling efforts to collect juveniles (larger than 10 mm) have been reported in a few studies; King and Iversen (1962) tried to collect juvenile tunas with four kinds of trawl nets in the central Pacific, but only six juvenile tunas, size 18 to 60 mm, were collected. Higgins (1970) tried to collect juvenile tunas in Hawaiian waters using a midwater trawl net with a mouth opening 12 m × 8 m. He collected 578 skipjack tuna and 417 other tunas. Most samples rarely had juvenile stages of skipjack tuna and other tunas. Takuno and Ueyanagi (1978) tried to capture juveniles with a small pelagic trawl net in the tropical western Pacific, collecting 20 skipjack tuna and six yellowfin tuna, from 6 mm to 31 mm. These various results suggest that juvenile skipjack tuna and other tunas avoided the small trawl nets. The mouth opening and the towing speed of the Tansyu is much greater than those of small trawl nets used in previous studies. We therefore expected that the size of specimens that would be collected would be larger than those collected in previous studies if the survey area and period were chosen appropriately. Indeed, the size range of skipjack tuna and other tunas collected with the Tansyu was much greater than that collected with smaller nets. In addition, large numbers of juvenile skipjack tuna and other tunas could be collected.

Skipjack tuna and other tunas that reach the young stage are able to swim much faster than juveniles. In this study, the number of young skipjack tuna and other tunas collected was low, and these fish were caught only at night. These results indicate that net avoidance by young fish affected the number of specimens captured. The results of previous studies on swimming speeds of scombrids demonstrate that the "burst swimming speed" of adult tunas is usually from 10 to 20 fork lengths (FL) per second (Magnuson, 1978). If the burst swimming speed of young tunas (which might swim slower than adults) is, for discussion, assumed to be 10 FL per second, the speed at 20 cm FL would be estimated at approximately 3.9 knots. Therefore, the nets would need to be towed faster than 4 knots in order to sample young tunas of 20 cm FL. However, few young skipjack tuna and other tunas were collected with the Tansyu with its maximum towing speed of 5 knots. If large numbers of young skipjack tuna and other tunas were able to be collected, we would learn more about the swimming speed of young life stages of these fish and also their ecological characteristics, for example their swimming behavior and vertical distribution.

Other methods exist for collecting juvenile and young tunas, i.e. by means of light traps (Thorrold, 1993) or from stomach contents of tunas and billfish.

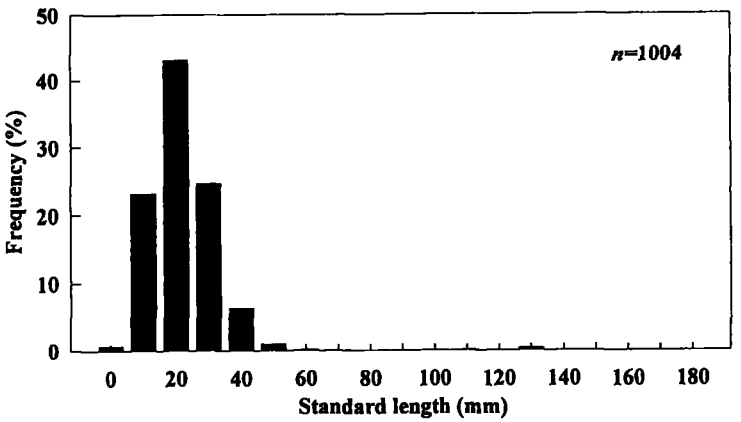


**Figure 4**

Length-frequency distribution of *Thunnus* spp. collected by the midwater trawl net in 1992–94 trial surveys.

**Table 2**

Comparison of catches between daytime and nightime tows for *K. pelamis* and *Thunnus* spp. and total wet weight (g) of collections.

| | | *K. pelamis* | | *Thunnus* spp. | |
|---|---|---|---|---|---|
| | Average catch (g) | Occurrence (%) | Catch per tow (inds.) | Occurrence (%) | Catch per tow (inds.) |
| Day | 5405.5 | 52.9 | 12.5 | 28.7 | 3.7 |
| Night | 7010.1 | 48.1 | 8.1 | 27.0 | 3.0 |

**Table 3**

References for sampling larvae and juvenile skipjack tuna and other tunas.

| Author(s) | Sampling gear | Size of sample |
|---|---|---|
| Strasburg, 1960 | 1-m ring net | 3–12 mm larvae |
| Nishikawa et al., 1978 | 2-m ring net and 1.4-m ring net | <12 mm larvae |
| Davis et al., 1990 | 0.7-m bongo net and 0.7 ring net | 3–11 mm larvae |
| Boehlert and Mundy, 1994 | 1-$m^2$ MOCNESS | 2–8 mm larvae[1] |
| King and Iversen, 1962 | 1-m ring net | 18–60 mm juveniles |
| | 6-ft Isaccs-Kidd trawl | |
| | 6-ft Isaacs-Kidd trawl | |
| | 10-ft Isaacs-Kidd trawl | |
| Higgins, 1970 | anchovy no. 2 Cobb pelagic trawl | 7–47 mm larvae and juveniles |
| Takuno and Ueyanagi, 1978 | midwater trawl | 6–31 mm larvae and juveniles |
| Present study | midwater trawl | 7.1–171.6 mm larvae, juveniles, and young fish |
| Thorrold, 1993 | light trap | 10–30 mm juveniles |

[1] Boehlert, G. 1997. Natl. Mar. Fish. Serv., NOAA, 1352 Lighthouse Ave., Pacific Grove, CA 93950. Personal commun.

Yoshida (1971) studied the early life history of skipjack tuna using 1742 juveniles collected from the stomachs of billfishes in Hawaiian waters and the central South Pacific. Mori (1972) reported on the geographical distribution and the relative abundance of juvenile and young skipjack tuna based on collections from stomachs of tunas and billfishes in the Pacific, Indian, and Atlantic Oceans. This method was convenient and easy for sampling but produced results that should be carefully considered because they were not based on direct sampling from the habitat. Iizuka et al. (1989) using pelagic gill nets conducted research to collect young skipjack in southern Micronesian waters over a period of three years, collecting 49 young skipjack, 120 to 280 mm. The research resulted in small numbers of specimens of young skipjack tuna, and it was not clear whether the number of samples indicated the abundance of young stages.

The results of our study, in light of previous studies sampling skipjack tuna and other tunas, show that a wider size range of juveniles can be collected by using a trawl net with a larger mouth opening and by using a high towing speed, as with the Tansyu. A small ring net is appropriate for research based on sampling larvae because of its simplicity in operation. However, if it is necessary that diel patterns of vertical distribution of juvenile skipjack and other tunas be investigated, then the appropriate time and depth of towing should be selected, because ecological characteristics drastically affect the quantity of collections. Sampling of young skipjack tuna and other tunas, on the other hand, should be conducted at night with a trawl net with a large mouth opening or with a net that would minimize net avoidance by young-stage fish.

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# Entanglement and mortality of bottlenose dolphins, *Tursiops runcatus*, in recreational fishing gear in Florida

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Effects of fishing gear interactions are among the most pressing issues currently being addressed by marine mammal management agencies in the United States. Information is needed on the rates and fates of entangled dolphins for evaluation of mortality caused by different fisheries. Virtually the entire emphasis of management agencies has been on marine mammal interactions with commercial fisheries; little notice has been taken of the impacts of recreational fisheries.

Along the central-west coast of Florida, near Sarasota, ongoing research initiated in 1970 on a resident community of about 100 bottlenose dolphins, *Tursiops truncatus* (Scott et al., 1990; Wells, 1991) has resulted in opportunities to examine closely the effects of interactions between dolphins and human activities, including both commercial and recreational fisheries (e.g. Wells and Scott, 1994; 1997). We report here on one case in which we removed a large quantity of fishing line trailing from a free-swimming bottlenose dolphin, and we include information on the behavior and health of the animal over the first year following entanglement and removal of the gear. We also compare the extent of commercial vs. recreational fishing interactions with dolphins.

On 4 June 1996, a seven-year-old female bottlenose dolphin ("FB03") was observed traveling alone near shore in the Gulf of Mexico off Anna Maria Island (27°33'N, 82°45'W), trailing large quantities of thin line that extended in clumps to 5 m behind the animal. The line was wrapped around the tail flukes and peduncle but did not appear to affect noticeably the dolphin's swimming ability. The dolphin (FB03) was known from birth as a member of a four-generation maternal lineage (Wells et al., 1987; Wells, 1991). She had been seen 146 times in this area prior to this incident, and was within her well-established home range. She had been observed six days earlier without any line.

This dolphin was seen next at 10:28 on 6 June 1996, in Palma Sola Bay (27°29'N, 82°40'W), several miles from her 4 June location and still within her home range. She was alone and surfacing slowly, still trailing the line. She was swimming more slowly than during the previous observation (as measured in relation to boat speed), and the clumps of line extended farther behind her, to a distance of about 8 m. Ventilations occurred at average intervals of 35.7 sec (±12.71 sec SD, $n$=58), comparable to previously measured rates for Sarasota dolphins (Irvine et al., 1981; Waples, 1995). The line was cutting into tissues of her flukes and peduncle. We decided to try to remove the line, assembled a team by 12:47, and approached the dolphin in our 6-m long research vessel powered by a 115-hp outboard engine. Because the trailing line followed the dolphin to the surface at each breath, we were able to reach and retrieve most of it. At 13:10 we secured the line with a boat hook, and cut all but about 2 or 3 m of line from the animal as she continued swimming. The dolphin swam rapidly and "porpoised" for about 3.7 km, left the bay, and continued to the south. We approached her again in shallow water (<2 m deep) and she maintained position, riding slowly beneath the bow of our vessel for the next 38 minutes; this is the longest recorded instance of bow-riding in the history of our research program. Her position beneath the bow afforded us an opportunity to examine closely the wounds and remaining line. Cuts around the peduncle at the insertion of the flukes and through the anterior edges of the flukes were evident. The remaining line circled the peduncle once and two freely trailing ends were draped across and extended about 1.3 m behind the

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flukes. We tried unsuccessfully a number of times to grasp the remaining line with the boat hook as the dolphin rode the bow wave. Throughout these attempts, the dolphin held her position directly below the bow, clearly watching the boat hook as it moved within several cm of her flukes, and she made no effort to move away.

The next observation of the dolphin was on 18 June 1996, on Sister Key Flats (27°27'N, 82°39'W), near where we had left her on 6 June. She was swimming normally and no line was evident, although indications of scarring were seen where the line had been. Through 1 July 1997, she was observed 33 more times and her behavior was considered normal each time. She was alone each time that she was seen while entangled; she was seen alone in only 24% of her unentangled sightings. Prior to entanglement, she was found in groups of 4.9 dolphins on average (SD=4.32, $n$=73). Following removal of the line, she was in groups of 4.4 dolphins on average (SD= 4.56, $n$=30).

On 13 June 1997, this dolphin was examined by veterinarians as part of a dolphin health assessment program. The wounds from the line were well healed, but deep scars remained (Fig. 1). Her health was comparable to that at the time of her previous examination on 17 June 1994. Her weight (132 kg) was 19 kg greater than three years before. Veterinary staff considered her blood chemistry and hematology values to be within acceptable limits, and results of ultrasonic examination of organ condition were unremarkable. Thus, it appears that no long-term effects beyond scarring resulted from this relatively brief entanglement event. The depth of scars, however, suggests that her flukes could potentially have been severed if the line had not been removed. The line was determined to be 80-pound (approx.) test "squidding line," a floating-core braided Dacron line often used locally for tarpon fishing from late spring to early summer. Tarpon fishing occurs in the immediate Gulf coastal waters, especially in the area where this dolphin was first seen with the line around her flukes. A large number of snarls and cuts in the 484 m of line

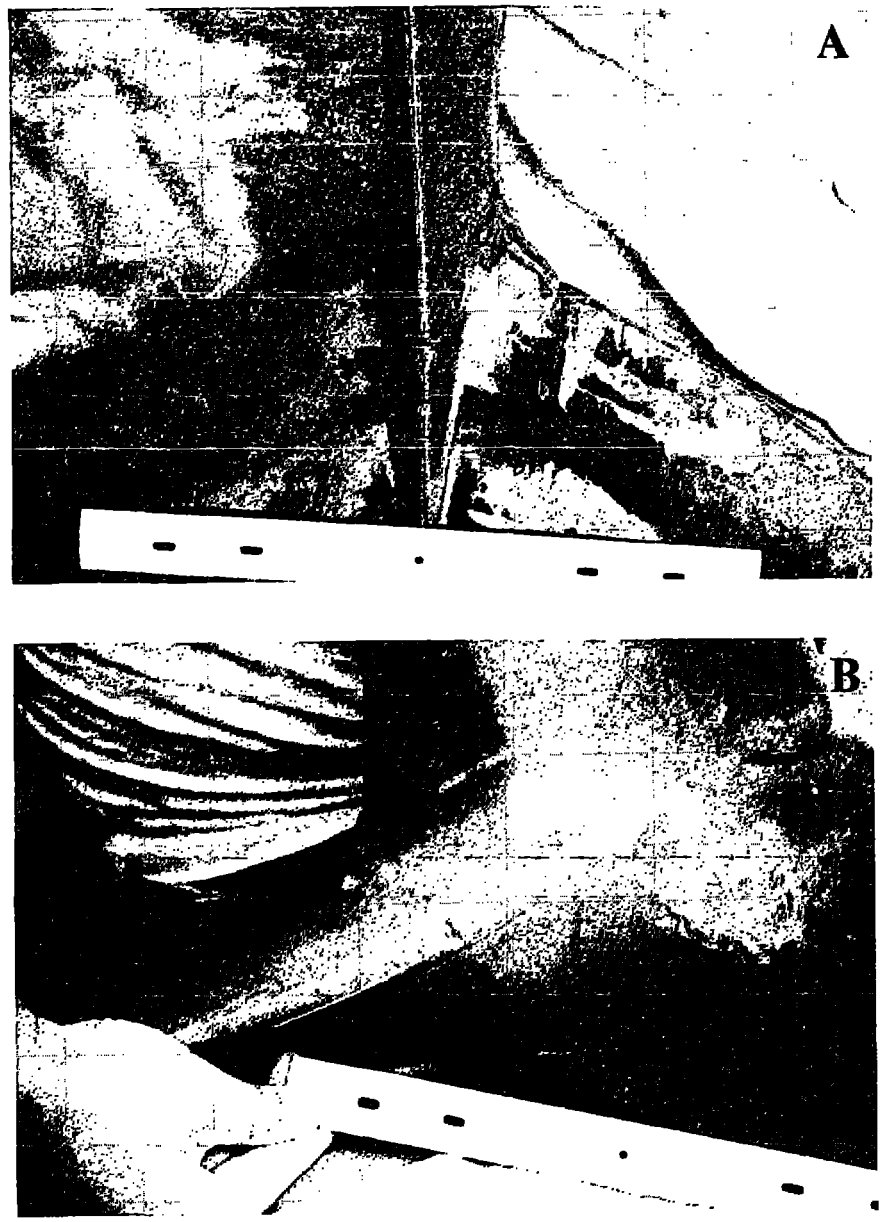


**Figure 1**

(**A**) Dorsal view of the scars on peduncle and flukes of the entangled dolphin (FB03) approximately one year after removal of the fishing line. (**B**) Ventral view of the scars on peduncle and flukes of the same entangled dolphin (FB03) approximately one year after removal of the fishing line.

removed suggested that it had been removed from a reel and discarded, rather than it had been actively involved in fishing at the time of entanglement.

Recreational fishing activities pose a largely ignored threat to bottlenose dolphins near Sarasota. Of 11 carcasses of resident Sarasota Bay dolphins recovered during 1993–1996, monofilament fishing line was implicated as a contributing factor in three deaths (27%). Large quantities of fishing line were found around two dependent calves (MML 9314=1.5 yr old and MML 9417=0.3 yr old). In one of these cases (MML 9314), growth of invertebrates on the line indicated that the line had been discarded prior to entanglement. The third case involved ingestion of line by an adult female (MML 9514) that had consumed a hooked sheepshead (*Archosargus probatocephalus*), as reported by Gorzelany (in press).

Wells and Scott (1994) reported that a disproportionately large number of subadult Sarasota Bay resident dolphins involved in entanglements of all kinds had been recorded through 1989 on the basis of scars observed during veterinary examinations as part of a capture-release program. More than half of the cases involved subadults; the balance were recorded from adults, but the entanglement events had occurred at an undetermined younger age. Dolphin FB03, a subadult at the time of entanglement; and the two dependent calves described above lend further support to this pattern. Similarly, Mann et al. (1995) reported on four cases of infant bottlenose dolphins becoming entangled in Shark Bay, Australia. In three of these cases, it was possible to remove the line from the semiprovisioned calves; in the fourth case, the line came free from the dolphin without human assistance. For many young animals, curiosity, inexperience, and unrefined motor skills place them at greater risk of entanglement through playful and exploratory behavior, the occurrence of which declines as the animal matures. Play may be strongly related to foraging behavior, for example, and may allow younger animals to practice, learn, and develop other behaviors that will be essential to their survival. Such behaviors may have an important role in the development of adult behaviors, but they may also be a costly practice for newborns or subadults who lack the experience of an adult.

In many parts of the world, dolphins are killed in gillnet and other fisheries (Perrin et al., 1994). It is interesting to note that in Sarasota Bay, Florida, an area of heavy recreational fishing activity, the numbers of deaths or serious injuries resulting from recreational fishing could exceed historical levels from small-scale gillnet fisheries. Gill nets were used extensively in this area prior to a state-wide ban, July 1995. Three deaths and one rescue of Sarasota resident dolphins entangled in recreational fishing gear occurred during 1993–96, but only one death (FB20 in 1976) and one rescue from gill nets (FB11 in 1985) were recorded during the 20 years prior to the 1995 gillnet ban. It should be noted, however, that stranding response coverage was uneven prior to the mid-1980s: not all deaths resulted in recovered carcasses, and not all possible entanglement events could be clearly identified as a direct cause of death, nor could they necessarily be distinguished as net or line entanglements.

Mortality and serious injury to dolphins from recreational fisheries have been largely overlooked in management, yet such mortality and injury may be important. Management actions to reduce human-related dolphin mortality are needed to address such issues, particularly in regard to the practice of discarding fishing line. Discarded line poses a risk that is somewhat analogous to that of "ghost-fishing" by commercial nets. Increased education of fishermen, through clear descriptions of the documented consequences of discarded gear is a logical, important, approach to the issue.

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# Publications Awards, 1996

## National Marine Fisheries Service, NOAA

The publications Advisory Committee of the National Marine Fisheries Service is pleased to announce the awards for best publication authored by NMFS scientists and published in the *Fishery Bulletin,* volume 94, and in the *Marine Fisheries Review,* volume 58. Eligible papers are nominated by the Fisheries Science Centers and Regional Offices and are judged by the NMFS Editorial Board. Only articles that significantly contribute to the understanding and knowledge of NMFS-related studies are eligible. We offer congratulations to the following authors for their outstanding efforts.

## *Fishery Bulletin,* volume 94

### Outstanding publication

**Collette, Bruce B., and Christopher R. Aadland.**

Revision of the frigate tunas (Scombridae, *Auxis*), with descriptions of two new subspecies from the eastern Pacific. Fish. Bull. 94(3):423–441.

## *Marine Fisheries Review,* volume 58

### Outstanding publication

**MacKenzie, Clyde L., Jr.**

History of oystering in the United States and Canada, featuring the eight greatest oyster estuaries. Mar. Fish. Rev. 58(4):1–78.

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# Fishery Bulletin

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**Abstract.**—The concentrations of 11 elements in individual whole sagittal otoliths from school mackerel (*Scomberomorus queenslandicus*) and spotted mackerel (*Scomberomorus munroi*) collected in east coast waters of Queensland, Australia (16°S to 28°S) were determined by using inductively coupled plasma atomic emission spectroscopy (ICP-AES). Spatial and ontogenetic variation in otolith elemental composition was examined to make inferences about the stock structure of these species. Stepwise canonical discriminant analyses of the concentrations of barium, potassium, magnesium, manganese, sodium, phosphorus, sulphur, and strontium were used to differentiate groups of fish. These analyses identified an optimum grouping of at least two stocks of school mackerel and a single stock of spotted mackerel in the study region, although our results showed that the most informative comparisons were made among fish of the same year class. The age of fish in collected samples produced strongly significant effects on mean elemental composition of otoliths. These patterns offered independent support for hypotheses about stock structure from previous tagging, catch monitoring, ageing, and reproductive studies. Discrimination between school and spotted mackerel stocks will enable the species to be managed on the basis of stock structure throughout their east coast distribution.

# Stock discrimination of school mackerel, *Scomberomorus queenslandicus*, and spotted mackerel, *Scomberomorus munroi*, in coastal waters of eastern Australia by analysis of minor and trace elements in whole otoliths

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Spanish mackerels of the genus *Scomberomorus* have restricted ranges and are found in coastal waters of eastern Australia within the confines of the 20°C isotherm (Munro, 1943). Throughout their range they form the basis of important commercial, recreational, and artisanal fisheries, which are characterized by mixed gear types, seasonal availability at widespread points of capture, and movement or migration through various coastal jurisdictions (Trent et al., 1987; Johnson et al., 1994). These traits make it necessary, but difficult, to identify the stock structure of *Scomberomorus* species for effective fisheries management.

Tag-recapture information, catch and effort data, reproductive studies, larval surveys, and protein electrophoresis have recently been used to determine the stock structure of king mackerel (*Scomberomorus cavalla*) in the Gulf of Mexico and Atlantic Ocean (Sutter et al., 1991; Johnson et al., 1994). In northern Australia, stock structure of the large narrow-barred Spanish mackerel (*Scomberomorus commerson*) has been inferred from protein electrophoresis (Shaklee et al., 1990), whereas hypothetical stock structures have been developed for the "lesser" mackerels—school mackerel (*Scomberomorus queenslandicus*) and spotted mackerel (*Scom-*

*beromorus munroi*)—from tagging, catch data, and ageing and reproductive patterns (Begg et al., 1997; Begg and Sellin, 1998; Begg, in press).

School and spotted mackerel co-occur in coastal waters of northern Australia and southern Papua New Guinea (Collette and Russo, 1984). Within Australian waters they are a major part of set gillnet and ring-net commercial fisheries and support popular recreational fisheries, especially in the region from Moreton Bay to Townsville (Fig. 1). Between 1992 and 1995 the Queensland commercial catch averaged 160 metric tons, and the recreational landings were estimated to be at least half as large as their commercial counterparts (Cameron and Begg[1]). Tag-recapture data indicate that school mackerel move small distances, in contrast to spotted mackerel that migrate annually along the Australian east coast (Begg et al., 1997). Both species reach 100 cm in fork length (LCF, tip of snout to fork of tail) and 8 kg in weight (Collette and Russo, 1984), and first maturity occurs within 2 years of age, between 35 and 50 cm LCF (Begg, in press). Along the Queensland east coast, school mackerel spawn between October and January, whereas spotted mackerel spawn from August to October in northern Queensland waters (Begg, in press). A number of separate school mackerel stocks are thought to exist along the Queensland east coast, whereas spotted mackerel may form a single stock (Begg et al., 1997; Begg and Sellin, 1998; Begg, in press).

[1] Cameron, D. S., and G. A. Begg. 1998. Fisheries biology and interaction in the northern Australian small mackerel fishery. Fisheries Research and Development Corporation 92/144. Unpublished manuscript.

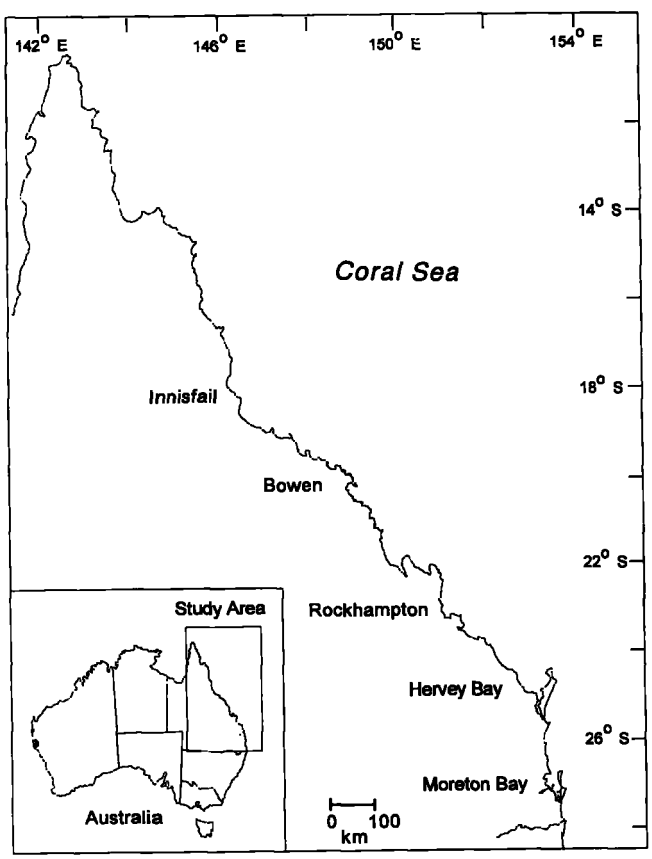


**Figure 1**
Sampling locations for school and spotted mackerel.

The lack of a direct and widely applicable technique to trace larval dispersal has encouraged development of a wide range of methods to deduce stock structure (Thresher et al., 1994) including analysis of the elemental composition of otoliths (Mulligan et al., 1987; Campana et al., 1994; Thresher et al., 1994; Edmonds et al., 1995; Proctor et al., 1995; Kalish et al., 1996). Inference about stock structure from these studies presumes that geographically distinct stocks possess a characteristic elemental composition that reflects the chemical constituents of the environment in which the fish reside.

The elemental composition of otoliths has been measured by analysis of dissolved whole otoliths and by scanning otolith cores or sections with a variety of different electron beam and laser probes (Gunn et al., 1992; Campana et al., 1994). Solution-based or "bulk" chemical analyses of otoliths have the benefits of greater replication in sample sizes through reduced time and cost for preparation, calibration, and measurement (Campana and Gagné, 1995; Campana et al., 1995). However, bulk analysis of whole otoliths incorporate an integrated chemical signal that represents the entire ontogenetic history and home range of individual fish in a nonlinear form that is governed by the growth of the otolith matrix in terms of both rate of deposition and volumetric considerations. Consequently, the mean composition of an otolith in a bulk analysis could be disproportionately dominated by the deposition of material prior to capture, preventing fine-scale resolution of individual affinities with spawning grounds and larval habitats (Campana et al., 1995).

The present study was conducted to determine the utility of elemental analysis of whole otoliths in studying the prevailing hypotheses of a multistock complex for school mackerel and a single stock for spotted mackerel in coastal waters of eastern Australia. Analyses were specifically structured to account for and distinguish the influence of fish age on elemental composition of otoliths. Interpretation of stock structure in this study relates to Ihssen et al.'s (1981) definition of a stock as "a group of randomly mating, reproductively isolated individuals of a single species with temporal or spatial integrity."

## Materials and methods

### Otolith chemistry

School and spotted mackerel were collected monthly from commercial and recreational fisheries along the Queensland east coast, south of 16°S, between June 1992 and February 1995 (Fig. 1). School mackerel were sampled from three geographic areas and spotted mackerel from four (Table 1). Samples were obtained from independent collections at each area, usually representing fish caught from several different schools. Specimens were kept on ice, then frozen until length to caudal fork (LCF, mm) was measured, sex was determined, and both sagittae were removed, washed, dried, and weighed. Fish were aged from whole and sectioned sagittae according to Begg and Sellin (1998).

Precautions were taken to prevent confounding of results based on sexual maturity, size, and age. All samples were sexually mature, between the lengths of 492 mm and 790 mm LCF (Table 1). Fish of the same age (2-year-old school mackerel; 3-year-old spotted mackerel) were selected to minimize age-related variation amongst samples. Additional samples of 1-year-old school mackerel from Rockhampton and 1-year-old spotted mackerel from Moreton Bay and Hervey Bay were examined in relation to the older samples from the same areas to investigate the effects of age on the concentrations of elements in sagittae.

Whole otoliths used in the analysis were cleaned of oil and organic residuals in an ultrasonic bath, rinsed in distilled water, and oven-dried at 60°C for 15 hours. Otoliths were dissolved in 0.5 mL of a Lefort aqua regia solution (75% nitric and 25% hydrochloric acid) and placed in an AIM500 block digester at 90°C for 30 minutes. After cooling, the solutions were made up to 10 mL with distilled water and analyzed with a Varian Liberty 220 inductively coupled plasma atomic emission spectrometer (ICP-AES). Eleven elements (Ba, Ca, Fe, K, Li, Mg, Mn, Na, P, S, and Sr) were analyzed from each otolith, and the concentrations were standardized for individual otolith weights.

Minimum detection limits for the elements were determined by averaging a series of acid blank solutions for both species that were regularly interspersed throughout the samples. The minimum detectable solution concentration for each element (mg/L) was converted to the minimum detectable otolith concentration (mg/Kg) by using the solution volume and the smallest whole otolith weight actually analyzed. This procedure ensured that the most conservative (largest) minimum detection limits were used in the analyses. Three standard solutions were included regularly among the samples to calibrate measurements. The standards covered the entire weight range of otolith material used in the analyses. Only those elements measured in concentrations above the minimum detection limits of the ICP-AES were used in the statistical analyses.

### Data analysis

The chemical composition of school and spotted mackerel whole otoliths sampled from the different areas was analyzed to identify the optimum groupings of fish in order to make inferences about stock structure. All data were examined for normality and homogeneity of variances, and concentrations of Mg and Na in school mackerel otoliths, and K, Mg, Na, and P in otoliths of spotted mackerel, were $\log_e$-transformed to enable statistical analysis. Analysis of covariance (ANCOVA) was used to determine the effect of area of collection (the main effect) on the concentration of each element, while controlling for effects due to fish length (the covariate). Elemental concentrations for which area-by-length interactions were significant were not included in further analy-

**Table 1**

Data from school and spotted mackerel samples used in otolith trace element analyses.

| School mackerel | | | | | Spotted mackerel | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Date | Area | *n* | Length range (mm) | Age (yr) | Date | Area | *n* | Length range (mm) | Age (yr) |
| Nov 1993 | Moreton Bay | 19 | 512–614 | 2 | Feb 1994 | Moreton Bay | 30 | 555–685 | 1 |
| Jun 1993 | Rockhampton | 25 | 492–574 | 1 | Feb 1994 | Hervey Bay | 28 | 544–715 | 1 |
| Jun 1993 | Rockhampton | 19 | 552–640 | 2 | Dec 1993 | Hervey Bay | 29 | 552–790 | 3 |
| Aug 1993 | Bowen | 22 | 545–632 | 2 | Aug 1993 | Bowen | 32 | 605–670 | 3 |
| | | | | | Jul 1993 | Innisfail | 28 | 585–665 | 3 |

ses. Elements for which concentrations were significantly correlated with length were corrected for statistical analysis as

$$AC = C - rL,$$

where $AC$ = the corrected concentration, adjusted for fish length;
$C$ = the concentration of a given element (mg/Kg) for a fish of fork length $L$ (mm); and
$r$ = the regression coefficient or the "common slope" for the covariate length (Edmonds et al., 1989).

ANCOVA and other subsequent analyses were also performed with otolith weight as the covariate, but they showed lower power in discriminating among groupings of fish. This lower discriminatory power was probably a result of the greater measurement errors in obtaining otolith weights in relation to measurement of fish length. Therefore, concentrations of elements corrected for length only were used in the final discriminant analyses.

Multivariate analysis of variance (MANOVA) was used to compare the mean corrected elemental concentrations of samples from the different areas. One-way fixed effects and unbalanced analyses of variance (ANOVA) were then used to compare concentrations of individual elements in samples from different areas to explain differences detected by the MANOVAs. Significance levels were corrected for multiple testing with the Bonferroni adjustment factor. Tukey's studentized range (HSD) tests were used for *a posteriori* comparisons of the different areas for each significant element.

Principal component analysis (PCA) of the corrected concentrations of elements was used to investigate grouping patterns by area and fish age. ANOVA was performed on the first (PC I) and second (PC II) principal components to test differences among proposed groups. Forward stepwise canonical discriminant analyses were used to detect differences in the length-corrected chemical composition of otoliths for school and spotted mackerel from the different areas. The significant ($P<0.05$) canonical variates (CV) provided by each analysis represented the optimal combination of areas and elements that provided the best overall discrimination between the samples. The pooled-within-groups correlations of significant length-corrected elemental concentrations with each canonical variate approximated the contribution of the respective element to the discrimination between areas. Wilks's lambda denoted the statistical significance of the discriminatory power of the overall model, ranging from 1.0 to 0.0 (perfect discrimination). ANOVA and HSD were used on the significant discriminant functions to test pairwise comparisons among groups detected by the discriminant analysis. Jack-knifed cross-validation procedures were used to give an unbiased estimate of classification success (SYSTAT, 1997).

## Results

### School mackerel

We measured the concentration of 11 trace and minor elements in whole otoliths of school mackerel (Fig. 2). Iron and lithium were highly variable, often at concentrations below the detection limits of the spectrometer, and were excluded from data analyses. Calcium was also excluded because its high concentration (31.4–44.7%) would mask contribution of trace elements in the data analyses. The remaining elements (Ba, K, Mg, Mn, Na, P, S, and Sr) were present in measurable quantities, suitable for statistical analyses. ANCOVA indicated that none of these eight elements were correlated with fish length for school mackerel. However, there was a significant interaction in the concentration of Ba with area of collection and fish length (ANCOVA, $F=2.75$, df=3, 76, $P<0.05$); therefore the Ba data were not used in the discriminatory analyses. This interaction was caused by an inverse relationship between Ba concentration and fish length for school mackerel from Bowen, whereas samples from the other areas all showed positive correlations between Ba concentration and fish length.

School mackerel from each age class in each area were found to have significantly different mean elemental composition of otoliths (MANOVA, Pillai's trace=1.013, $F=5.54$, df=21, 228, $P<0.0001$). Mean concentrations of individual elements, except for S and Sr, varied significantly among school mackerel from the different areas and between different age classes (Fig. 2). Sodium, P, and Mg concentrations differed the most among the study areas, and there were significant differences in concentrations of Na and P between fish from Bowen and those from Rockhampton and Moreton Bay. There were also significantly higher concentrations of K in otoliths of Bowen fish, compared with those from Rockhampton (HSD, $P<0.05$). No significant differences in elemental composition of otoliths were detected between 2-year-old school mackerel from Rockhampton and Moreton Bay. In contrast, significant differences were found for Mg, Mn, Na, and P concentrations between 1- and 2-year-old fish from Rockhampton, suggest-

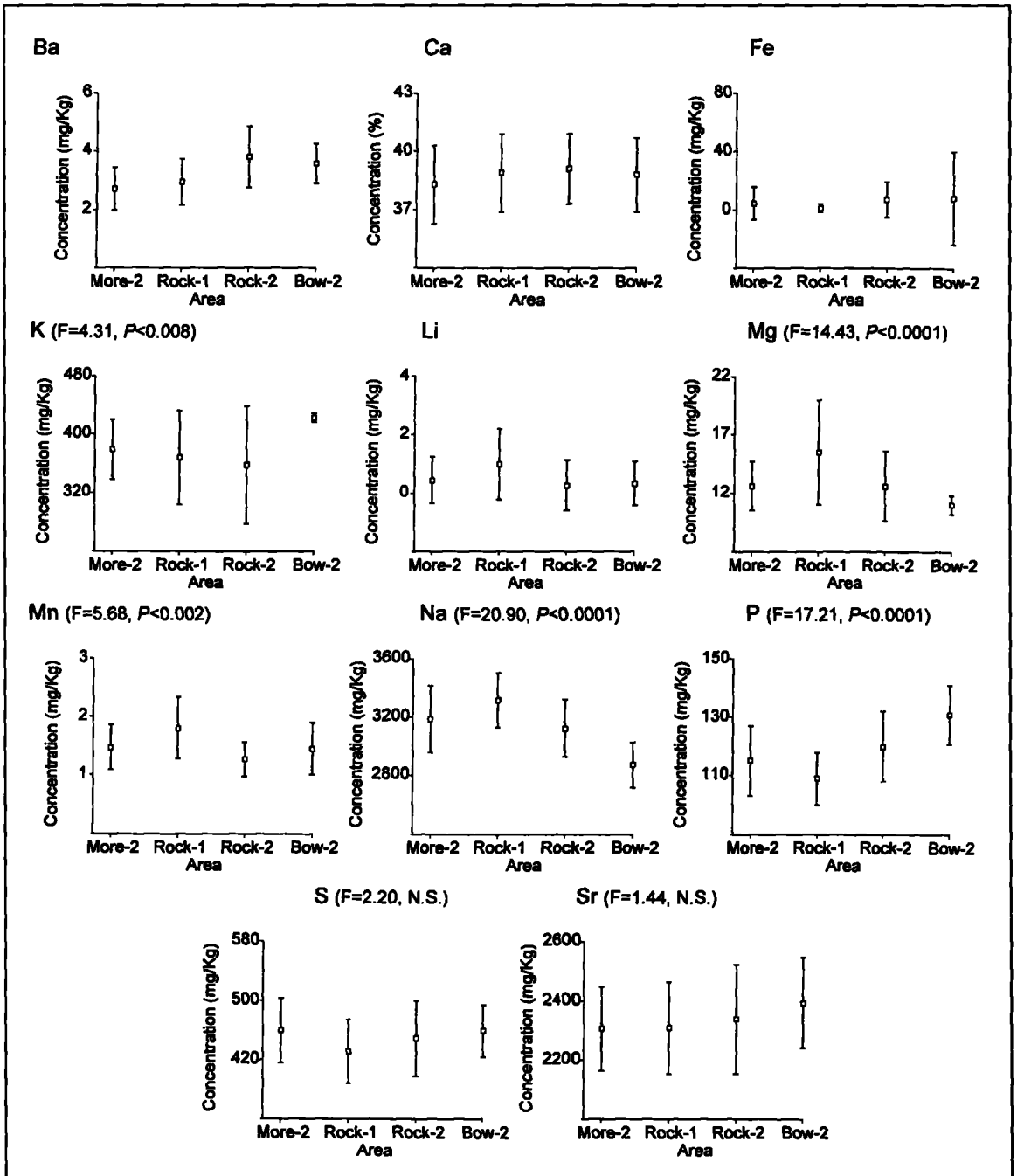


**Figure 2**

Mean elemental concentrations (± standard deviation) of school mackerel otoliths sampled from the different areas and *F*-values determined from ANOVA showing significant elements among samples (df=3, 80; N.S.=nonsignificant result). Minimum elemental detection limits of the inductively coupled plasma atomic emission spectroscopy (ICP-AES) (all units are in mg/Kg, except Ca which is measured as a %): Ba = 0.78; Ca = 544; Fe = 23.9; K = 353; Li = 15.0; Mg =10.9; Mn = 1.10; Na = 1250; P = 54.1; S =191; Sr = 3.24.

ing a strong effect of age at collection in measurement of the elemental composition of otoliths in this area (HSD, $P<0.05$). Sodium showed the most significant differences in these univariate analyses (Fig. 2) and was selected as the common variable for scatterplots in Figure 3. Scatterplots of the relationships between Na and the other significant elemental concentrations revealed similar spatial patterns

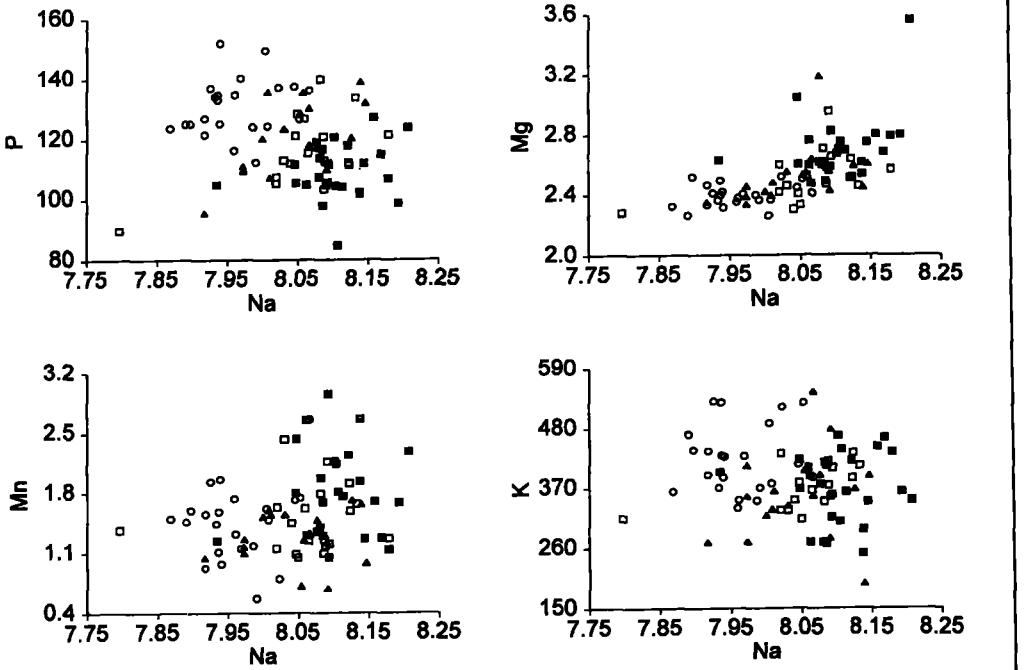


**Figure 3**

Scatterplots of significant elemental ratios showing grouping patterns of area and age school mackerel samples. Open circle = Bowen 2-year-old fish; open square = Moreton Bay 2-year-old fish; solid square = Rockhampton 1-year-old fish; and solid triangle = Rockhampton 2-year-old fish. Mg and Na are $\log_e$-transformed concentrations.

in the otolith chemical composition among samples from the different areas (Fig. 3). The ratio of Na to P concentrations provided the best discrimination among areas, with Bowen samples distinguishable from Rockhampton and Moreton Bay, and samples from Rockhampton and Moreton Bay once again overlapping in their elemental composition (Fig. 3).

Principal component analysis provided further support for the strength of these proposed grouping patterns (Fig. 4). Bowen samples were distinguished from those from the other areas mainly on the first principal component (PC I) where most of the variation was explained by differences in P concentration, whereas Na and Mg contributed most to the variation in the second principal component (PC II). These two components described almost 57% of the total variation in the data. Rockhampton and Moreton Bay samples showed a similar distribution of PC scores, in contrast to samples from Rockhampton that showed some degree of separation between 1- and 2-year-old fish. ANOVA supported these patterns with significant differences detected for both the PC I ($F$=24.89, df=3, 80, $P$<0.0001) and PC II scores ($F$=6.30, df=3, 80, $P$<0.0007) among the samples. Bowen samples had significantly higher PC I scores

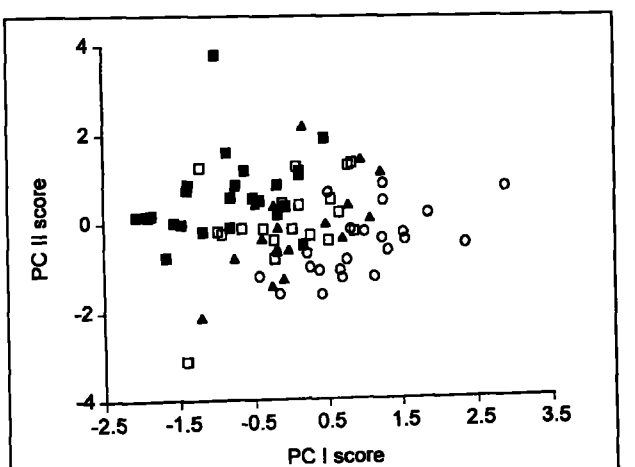


**Figure 4**

Principal component (PC) analysis of school mackerel otolith elemental concentrations indicating grouping patterns. Open circle = Bowen 2-year-old fish; open square = Moreton Bay 2-year-old fish; solid square = Rockhampton 1-year-old fish; and solid triangle = Rockhampton 2-year-old fish.

than those from Rockhampton and Moreton Bay, and no differences were found between 2-year-old fish

from Rockhampton and Moreton Bay. The samples of 1-year-old fish from Rockhampton had PC I scores that were significantly different from all the 2-year-old samples, and PC II scores that also were significantly different from the other samples, but not from Moreton Bay (HSD, $P<0.05$).

Analyses indicated that school mackerel samples are best separated into three groups: 1) Bowen 2-year-old fish; 2) Moreton Bay and Rockhampton 2-year-old fish; and 3) Rockhampton 1-year-old fish (Wilks's lambda=0.195) (Fig. 5). Similar discriminant patterns were observed when the "significant" elements (K, Mg, Mn, Na, P; Wilks's lambda=0.214) were used in isolation. Significant differences in the discriminant scores were found between these groups for both the first canonical variate (CV I) (ANOVA, $F=74.10$, df=3, 80, $P<0.0001$) and the second (CV II) (ANOVA, $F=6.61$, df=3, 80, $P<0.0001$). Like the results of the PCA analyses, Bowen samples had significantly different CV I scores than those from Rockhampton and Moreton Bay; no differences were found between Rockhampton and Moreton Bay 2-year-old fish; and Rockhampton 1-year-old samples had CV I scores significantly different from all the other groups. The Rockhampton 1-year-old samples also had CV II scores that were significantly different from the other groups, with the exception of fish from Bowen (HSD, $P<0.05$).

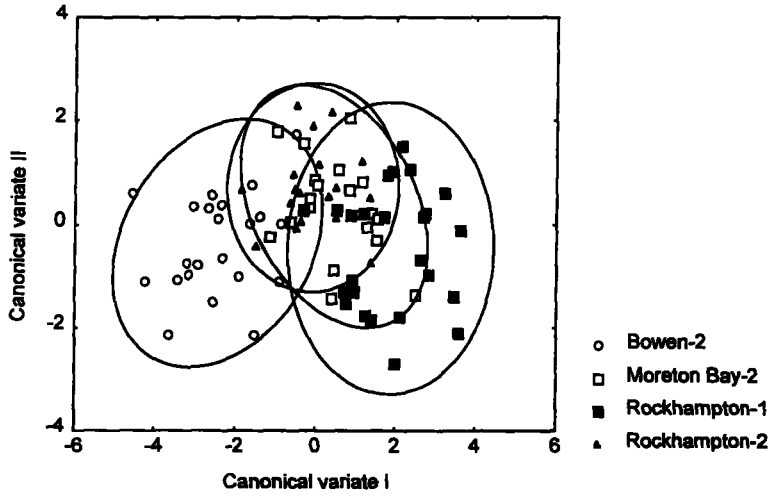


**Figure 5**

Discrimination between school mackerel samples based on the concentrations of 7 trace elements (± 95% confidence ellipses around the sample mean for each area).

Variation in Na, P, and Mg concentrations were primarily responsible for the separations apparent among the samples (89%) according to the first canonical variate (Table 2). Bowen fish tended to have lower Na and Mg and higher P concentrations than Moreton Bay and Rockhampton samples (Fig. 2). Approximately 62% of the school mackerel samples were classified into their correct groupings, indicating an overlap in otolith composition of Rockhampton and Moreton Bay samples (Table 3). Overall classification success increased to 77% when these areas were pooled, and individual classification rates improved for Bowen 2-yr-old fish (86%), Moreton Bay and Rockhampton 2-year-old fish (70%), and Rockhampton 1-year-old fish (80%), providing further support for the notion of three distinct groups in elemental composition of otoliths.

**Table 2**

Discrimination between samples of school mackerel determined by the pooled within-group correlations of elemental concentrations with the significant ($P<0.05$) canonical variates I and II, and the cumulative proportion of the explained variance accounted for by each function for seven elements (Wilks's lambda=0.195).

| | Canonical variate | |
|---|---|---|
| Element | I | II |
| Na | 0.53 | 0.07 |
| P | –0.48 | 0.02 |
| Mn | 0.17 | –0.72 |
| K | –0.20 | –0.40 |
| Mg | 0.42 | –0.38 |
| S | –0.13 | 0.24 |
| Sr | –0.13 | –0.11 |
| Cumulative proportion | 0.89 | 0.97 |

## Spotted mackerel

The same suite of 11 elements that were used for school mackerel were measured and analyzed for spotted mackerel (Fig. 6). Iron, Li, and Ca were excluded from statistical analyses for the same reasons as they were for school mackerel. Concentrations of Na (ANCOVA, $F=14.02$, df=1, 141, $P<0.0003$; $r=-0.0004597$) and Sr (ANCOVA, $F=6.03$, df=1, 141, $P<0.02$; $r=-0.9227$) in spotted mackerel otoliths were highly correlated with fish length; therefore the data were corrected for length with the respective regression coefficient for the length covariate. Manganese was not used in statistical analyses because a significant interaction in concentrations existed be-

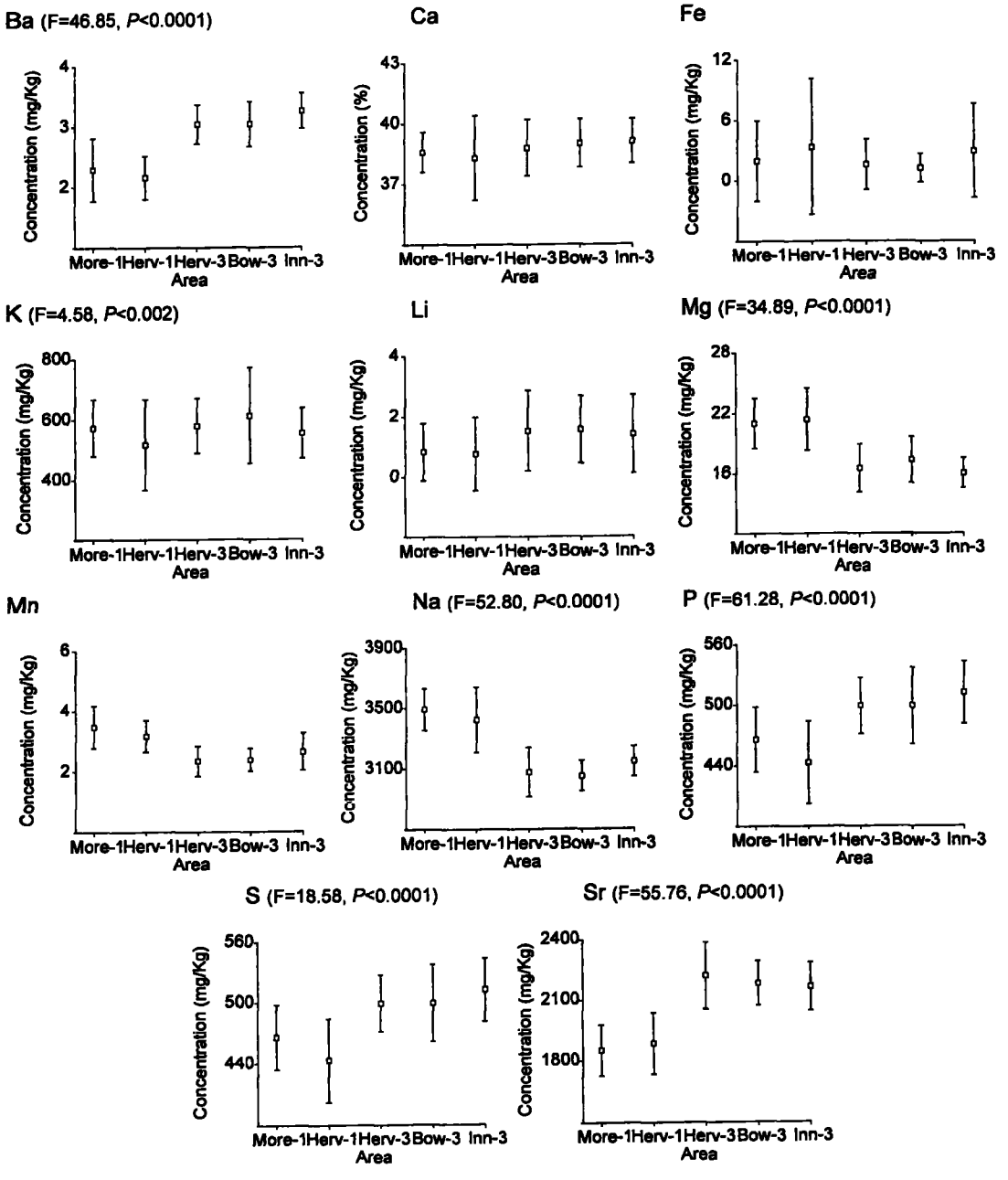


**Figure 6**

Mean elemental concentrations (± standard deviation) of spotted mackerel otoliths sampled from the different areas and *F*-values determined from ANOVA showing significant elements among samples (df=4, 140). Minimum elemental detection limits of the ICP-AES (all units are in mg/Kg, except Ca which is measured as a %): Ba = 0.78; Ca = 544; Fe = 23.9; K = 353; Li = 15.0; Mg = 10.9; Mn = 1.10; Na = 1250; P = 54.1; S = 191; Sr = 3.24.

tween area of collection and fish length (ANCOVA, $F$=3.87, df=4, 137, $P$<0.005). Manganese concentration increased linearly with fish length for Hervey Bay 1-year-old fish, in contrast with the other samples that all showed negative correlations.

Spotted mackerel samples from each area and for each age were found to have significant differences in mean elemental composition of the otoliths (MANOVA, Pillai's trace=1.316, $F$=9.59, df=28, 548, $P$<0.0001). Little variation was evident in mean ele-

**Table 3**

Jack-knifed cross-validation classification matrix of the frequency of assigned cases in each area (and age) used to differentiate school mackerel samples.

| | | Classification of individual school mackerel by area | | | |
|---|---|---|---|---|---|
| Area | Correct (%) | Bowen (2) | Rock (2) | Rock (1) | Moreton (2) |
| Bowen (2) | 82 | 18 | 3 | 0 | 1 |
| Rock (2) | 50 | 2 | 9 | 1 | 6 |
| Rock (1) | 64 | 0 | 3 | 16 | 6 |
| Moreton (2) | 47 | 1 | 4 | 5 | 9 |
| Total | 62 | 21 | 19 | 22 | 22 |

ment concentrations among spotted mackerel of the same age among all areas, whereas most elements varied significantly between samples of different ages (Fig. 6). The samples of 3-year-old fish from Innisfail and Hervey Bay had concentrations of P that were significantly lower than those in otoliths from Bowen fish. Samples from Innisfail also had concentrations of K that were significantly lower than those from Bowen fish (HSD, $P<0.05$). No other significant difference in elemental concentrations were detected between spotted mackerel of the same age. In contrast, significant differences were found for Ba, Mg, Na, P, S, and Sr between 1- and 3-year-old fish (HSD, $P<0.05$), independent of the area from where the samples were taken, once again emphasizing the strong effect of fish age in determining the results of elemental analyses of otolith composition. Scatterplots of the elements showing significant differences, with P as the most significant and common variable, also showed differences between fish of different ages (Fig. 7). In contrast, samples of fish of the same age showed no evidence of differences in otolith composition among areas.

Principal component analysis also showed a strong separation among spotted mackerel of different ages, but no separation of groups by area of collection (Fig. 8). One-year-old and 3-year-old samples were separated on the first principal component that explained almost 50% of the total variation in the data, largely on differences in concentration of P, Sr, Ba, Na, and S. The second principal component explained another 18% of the total variation on the basis of differences in K concentration among the samples. ANOVA showed significant differences among the PC I scores ($F=318.32$, df=4, 140, $P<0.0001$), further confirming pooling of spatial samples of the same age. Bowen, Innisfail, and Hervey Bay samples of 3-year-old fish were all significantly different from Moreton Bay and Hervey Bay 1-year-old fish, whereas no differences were found among samples of the same age (HSD, $P<0.05$).

Spotted mackerel samples were best discriminated into two main groups on the basis of statistically significant differences in elemental composition of the otoliths: 1) 1-year-old fish; and 2) 3-year-old fish (Wilks's lambda 0.045) (Fig. 9). ANOVA on the CV I scores detected significant differences between the different aged samples, providing further support for these patterns ($F=472.09$, df=4, 140, $P<0.0001$). The samples of 3-year-old fish from Bowen, Innisfail, and Hervey Bay all showed significant differences from the 1-year-old fish from Moreton Bay and Hervey Bay, whereas no differences were found among samples of the same age (HSD, $P<0.05$).

Phosphorus, Sr, Na, Ba, and Mg were the main elements that caused the grouping patterns in the first discriminant function that accounted for 97% of the total variation (Table 4). One-year-old spotted mackerel tended to have higher Mg and Na concentrations and lower Ba, P, and Sr concentrations than 3-year-old fish (Fig. 6). The separation patterns observed in the individual discriminations resulted in only 57% of the spotted mackerel samples being correctly classified into their respective groups owing to the strong grouping effect of the samples into their specific age classes, rather than by area (Table 5). Pooling of the results for fish of the same age resulted in a classification success of 100% for each age class, independent of the area from where the samples were collected.

**Table 4**

Discrimination between samples of spotted mackerel determined by the pooled within-groups correlations of length-corrected elemental concentrations with the significant ($P<0.05$) canonical variates I, II, and III, and the cumulative proportion of the variance accounted for by each function, for the seven significant elements (Wilks' s lambda=0.045).

| | Canonical variate | | |
|---|---|---|---|
| Element | I | II | III |
| Ba | −0.31 | −0.45 | 0.06 |
| K | −0.06 | 0.27 | 0.64 |
| Mg | 0.26 | 0.40 | 0.23 |
| Na (length corrected) | 0.33 | −0.30 | 0.26 |
| P | −0.35 | 0.39 | 0.50 |
| S | −0.19 | −0.38 | 0.30 |
| Sr (length corrected) | −0.34 | 0.13 | −0.34 |
| Cumulative proportion | 0.97 | 0.99 | 1.00 |

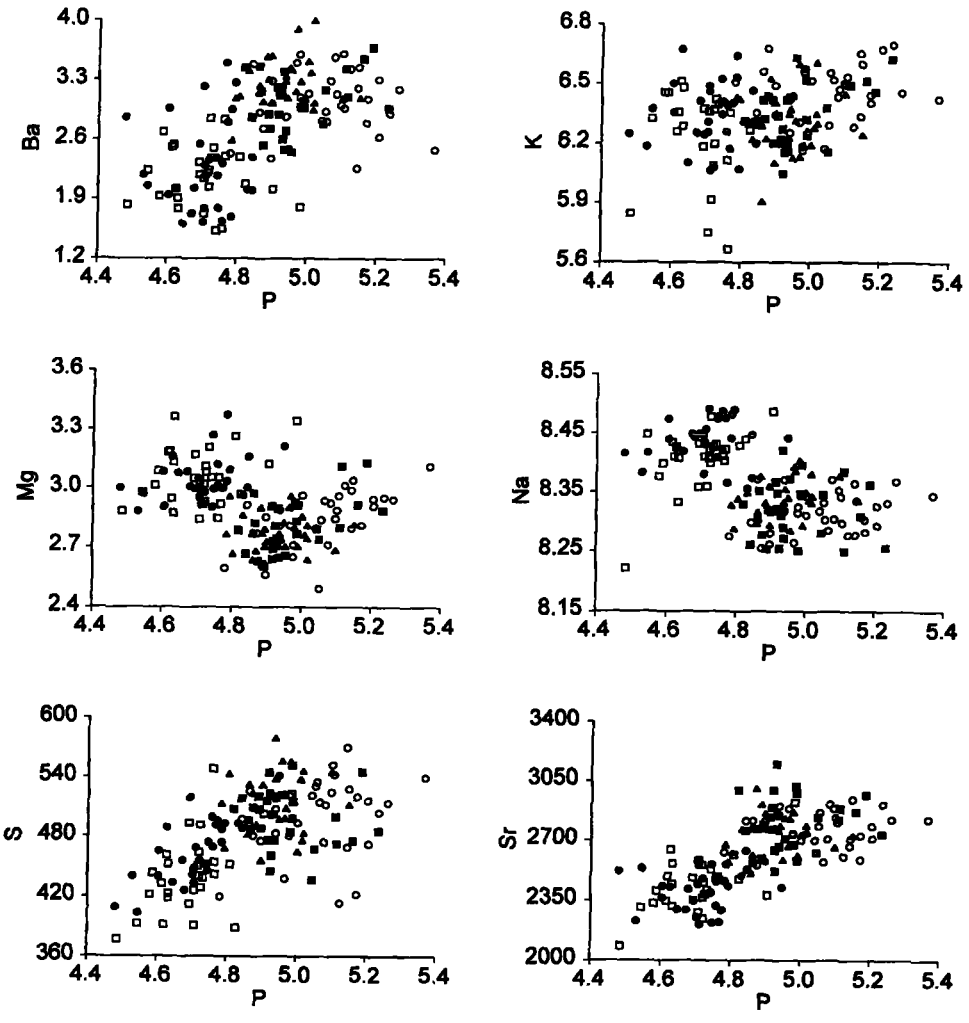


**Figure 7**

Scatterplots of significant elemental ratios showing grouping patterns of area and age spotted mackerel samples. Open circle = Bowen 3-year-old fish; open square = Hervey Bay 1-year-old fish; solid square = Hervey Bay 3-year-old fish; solid triangle = Innisfail 3-year-old fish; and solid circle = Moreton Bay 1-year-old fish. K, Mg, Na, and P are $\log_e$ transformed concentrations.

**Table 5**

Jack-knifed cross-validation classification matrix of the frequency of assigned cases in each area (and age) used to differentiate spotted mackerel samples.

| | | Classification of individual spotted mackerel by area | | | | |
|---|---|---|---|---|---|---|
| Area | Correct (%) | Bowen (3) | Hervey (1) | Hervey (3) | Innisfail (3) | Moreton (1) |
| Bowen (3) | 58 | 18 | 0 | 9 | 4 | 0 |
| Hervey (1) | 63 | 0 | 17 | 0 | 0 | 10 |
| Hervey (3) | 34 | 9 | 0 | 10 | 10 | 0 |
| Innisfail (3) | 68 | 2 | 0 | 7 | 19 | 0 |
| Moreton (1) | 63 | 0 | 11 | 0 | 0 | 19 |
| Total | 57 | 29 | 28 | 26 | 33 | 29 |

## Discussion

### Limitations of elemental analysis of whole otoliths

We found evidence of two separate groups of school mackerel and one group of spotted mackerel in the study region based on the variation in the mean elemental composition of individual fish otoliths of the same age. Such variation has been commonly presumed to reflect prolonged separation of the populations and ultimately stock divergence (Edmonds et al., 1991). However, it is not possible to infer from such studies alone what environmental, dietary, or genetic factors cause spatial patterns. Consequently, a number of wholly different but equally plausible hypotheses could be considered in determining the cause of the patterns observed in the elemental compositions of the otoliths of the two mackerel species, depending on what factors are considered important in determining otolith chemistry.

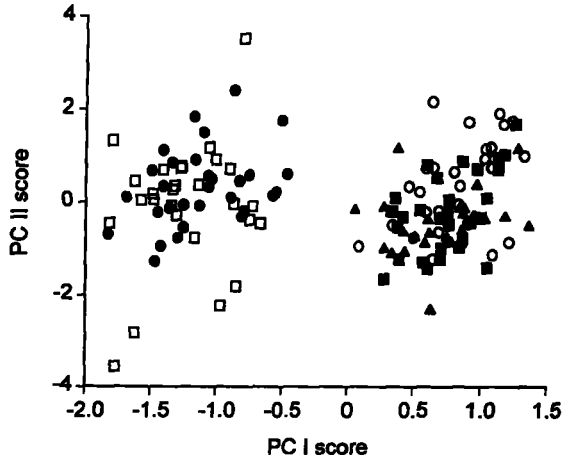


**Figure 8**

Principal component (PC) analysis of spotted mackerel otolith elemental concentrations indicating grouping patterns. Open circle = Bowen 3-year-old fish; open square = Hervey Bay 1-year-old fish; solid square = Hervey Bay 3-year-old fish; solid triangle = Innisfail 3-year- old fish; and solid circle = Moreton Bay 1-year-old fish.

An obvious explanation is that mean otolith composition differs spatially for school mackerel because their environment (or diet) varies among locations along the east coast, whereas there are no such differences for spotted mackerel because their environment (or diet) is more uniform throughout their range. For example, Proctor et al. (1995) concluded that an inability to discriminate among southern bluefin tuna (*Thunnus maccoyii*) samples with trace-element analysis was due partly to the uniformity of the pelagic environment. Water chemistry and food sources along the east coast of Queensland might be expected to vary among coastal bays, between inshore and offshore waters and between deep and shallow parts of the water column, especially given the strong influence of freshwater input in the wet-dry tropics (Thorrold and McKinnon, 1995). Indeed, the clupeid and engraulid species that form major parts of the diet of both school and spotted mackerel are generally found only in the southern half of the study area (Begg and Hopper, 1997).

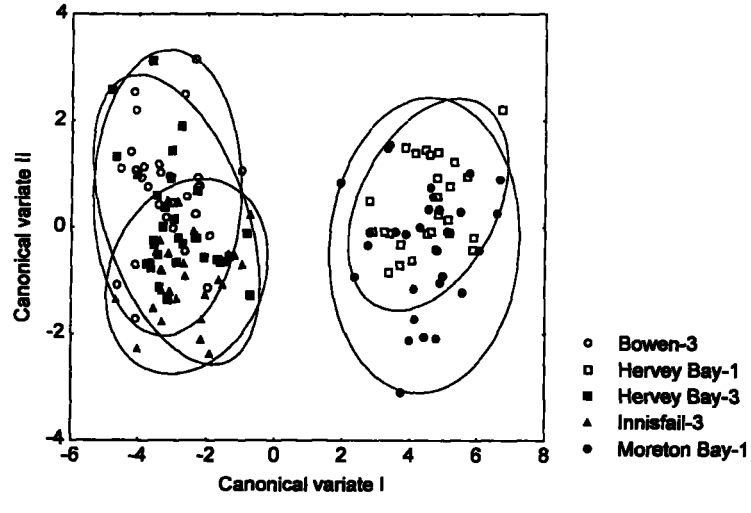


**Figure 9**

Discrimination between spotted mackerel samples based on the concentrations of the seven (length corrected) trace elements (±95% confidence ellipses around the sample mean for each area).

At present there is no fishery-independent information on the cross-shelf distribution and habitat of school and spotted mackerel and only a coarse understanding of the feeding patterns of both species. School mackerel are thought to inhabit mainly inshore waters, whereas spotted mackerel are thought to be more common offshore (Munro, 1943; Collette and Russo, 1984), although they do move to inshore waters to feed when undertaking seasonal migrations along the coastline (Begg and Hopper, 1997; Begg et al., 1997). School and spotted mackerel are often caught together in the same mixed schools during winter in the shallow northern bays

of the Queensland east coast and in summer in the southern bays, but the location and habitats of juveniles is not well known, particularly for spotted mackerel.

Complementary biological information from other stock identification methods is therefore essential to help interpret results from whole otolith analyses, but some hypotheses regarding stock structure cannot be tested in the absence of knowledge about the factors governing otolith composition. The resolution of the technique is limited further by volumetric considerations and the nature of otolith growth. Even if there were very large consistent differences in composition among individuals at the otolith core during larval and postlarval life, these would be virtually undetectable with bulk analysis, whereas relatively small differences accumulated during later life before capture would have a disproportionately large effect on mean composition. To overcome these problems—which may be accentuated for pelagic species with complex ontogenetic movements (Proctor et al., 1995)—bulk analysis of whole otoliths from juveniles, or excision and analysis of the core regions of otoliths from adult fish (Dove et al., 1996), may provide other, solution-based alternatives to sectioning and electron- or laser-probe techniques.

There may also be temporal variation in stock discrimination patterns, particularly for pelagic species living in coastal areas influenced by boundary currents; Edmonds et al. (1995) demonstrated that variation in composition of pilchard (*Sardinops sagax*) otoliths among years was significantly greater than the variation among sites. Stock discrimination patterns of pilchards were not persistent from one sampling era to the next within a decade. Further bias may be introduced by uneven representation of all life history stages within collections (Edmonds et al., 1995).

## Age-related variation

Spatial variation in the concentration of trace elements of school and spotted mackerel was strongly influenced by the age of fish in the samples at time of collection. Differential otolith elemental patterns were found between 1- and 2-year-old school mackerel, and 1- and 3-year-old spotted mackerel throughout the study region. Numerous studies, including this one, support Kalish's (1989) hypothesis that incorporation of trace elements into otoliths is related to growth (Grady et al., 1989; Thresher et al., 1994; Edmonds et al., 1995; Fowler et al., 1995). Consequently, spatial variation in elemental composition of otoliths can be difficult to interpret because of biases related to the size and age of fish in the samples from separate areas.

School and spotted mackerel of different ages from the same area have significantly different patterns in the elemental composition of their otoliths. One-year-old school and spotted mackerel tended to have lower concentrations of P, S, and Sr, while having higher levels of Mg, Mn, and Na in their otoliths compared with older fish. Grady et al. (1989) found similar results for king mackerel where heavy metal concentrations were generally higher in otoliths of younger fish. Differences in the concentrations of trace elements accumulated in the otoliths of fish of different ages from the same stock are not unexpected, particularly if irreversible deposition of elements in otoliths is assumed. Distinct chemical patterns in otoliths of fish of different ages may reflect exposure to similar environments, but for different accumulation periods, or alternatively, may reflect life history differences, such as younger fish inhabiting distinct nursery grounds that are separate from adult habitats.

Not all factors affecting deposition of elements in otoliths are strictly environmental or ontogenetic, nor do they necessarily act in a simplistic manner that reflects ambient environmental chemistry (Kalish, 1989; Campana et al., 1994). Chemical deposition can be regulated by many interacting factors, including water temperature, salinity, age, physiology, growth rates, and activity levels of individual fish (Kalish, 1989, 1990, 1991; Radtke and Shafer, 1992; Rieman et al., 1994; Fowler et al., 1995).

## Stock structure and management

Although further research is required to determine the mechanisms responsible for elemental deposition in otoliths of *Scomberomorus* species, particularly the interaction between environmental and genomic controls, the validity of using stock and site-specific elemental "fingerprints" does not rest upon the mechanism underlying otolith formation (Campana and Gagné, 1995). Optimal groupings of mean elemental composition of school mackerel otoliths strongly supported the hypothesis of at least two stocks in the study region—a hypothesis that has been developed with complementary stock identification techniques. Localized movements of tagged school mackerel have shown that there is little exchange between adult fish from different areas throughout Queensland east coast waters; most recaptures occur within the same area of release (Begg et al., 1997). Studies of the timing and location of spawning have also shown that school mackerel spawn concurrently at a number of localities along the east coast (Begg, in press). The species also exhibits differences in growth patterns and genetic variation throughout its distribution on

the east coast (Begg and Sellin, 1998; Begg et al., in press).

The limited movements of school mackerel indicated by tag-recapture data may also explain the overlap observed in the otolith composition of 2-year-old fish collected in Moreton Bay and Rockhampton. Small numbers of tagged school mackerel released in both these locations were recaptured in Hervey Bay between August and January, where they appear to be mixing on a common feeding ground (Begg et al., 1997; Begg and Hopper, 1997).

In contrast, spotted mackerel of the same year class sampled in Queensland east coast waters had similar patterns of elemental composition in their otoliths regardless of the region in which they were collected. This finding strongly supports the hypothesis of a single intermixing stock in the region of sampling derived from previous tagging, genetic, and reproductive studies, and seasonal changes in the location of commercial harvesting. These sources of information suggest an annual large-scale movement of spotted mackerel along the Queensland east coast to southern feeding grounds in summer and a return migration in winter to northern spawning grounds (Begg and Hopper, 1997; Begg et al., 1997; Begg, in press). In addition, similar growth rates and homogeneous genetic conditions of spotted mackerel throughout the study region support the hypothesis of a single east coast stock (Begg and Sellin, 1998; Begg et al., in press).

The longshore East Australian Current possibly provides cues for the migratory cycle of spotted mackerel and may facilitate larval dispersal from the spawning grounds and ultimately stock homogeneity throughout Queensland east coast waters. Proctor et al. (1995) proposed a similar stock structure for southern bluefin tuna on the basis of chemical composition of otoliths from juveniles collected along the major migration route of the species.

Identification of a species' stock structure is an important requirement for effective fisheries management (Rounsefell, 1975). The inability to define stock boundaries could unknowingly prejudice otherwise well-designed management protection efforts (Kutkuhn, 1981). Management of spotted mackerel in Queensland would be best addressed at the state level, because fishing effort in areas remote from one another may have an interaction on a single stock. In contrast, more localized (regional-level) management actions could proceed for school mackerel within Queensland—especially if the stock boundaries can be refined by further tests of the temporal persistence of the patterns described in this study.

The use of otolith trace element analysis holds great potential for stock discrimination in fisheries for other *Scomberomorus* species that share common characteristics of migration through multiple jurisdictions and fishery types. However, the use of bulk analysis of whole otoliths allows us to infer only that there has been prolonged separation of fish at some stage in their life history. Without "life history scans" across otoliths, with techniques such as electron-probe microanalysis (Gunn et al., 1992), we cannot explore the possibility that mean elemental composition is dominated by high concentrations specific to any particular life history stage. There is also need for careful selection of samples among year classes and time periods. Replication of sampling at intervals separated by several years and representation of all ontogenetic stages need to be incorporated in analyses to test for the consistency of spatial patterns in order to provide a more accurate environmental "fingerprint" for discrimination of mackerel stocks.

## Acknowledgments

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# Pelagic sharks associated with the swordfish, *Xiphias gladius*, fishery in the eastern North Atlantic Ocean and the Strait of Gibraltar

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**Abstract.**—We report on 175 landings from 106 longline and 69 gillnet boats operating in the eastern North Atlantic Ocean and Mediterranean Sea, July 1991 to July 1992. Information on the catch and biology of five shark species (*Isurus oxyrinchus*, *Prionace glauca*, *Alopias superciliosus*, *Alopias vulpinus*, and *Sphyrna zygaena*) is analyzed and contrasted with swordfish (*Xiphias gladius*) landings. A total of 51,205 fish were sampled, of which 40,198 were sharks, 9,990 swordfish, and the rest other bony fish. Spatial, temporal, and gear analyses were performed to show the importance of shark bycatch in longline and gillnet fisheries operating from the south of Spain. We present information on population structures of the shark species, along with hypotheses about shortfin mako movements as suggested by landing data.

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The Spanish longline fleet operates in the eastern North Atlantic (FAO fishing area 27), north-central Atlantic (FAO 34), and the Mediterranean Sea (FAO 37). Sharks are the most important bycatch of swordfish (*Xiphias gladius* Linnaeus, 1758) fishing in all of these areas (Moreno and Morón, 1992b; Mejuto and Garcés[1]; Mejuto[2]). The fleets use surface longlines to catch swordfish and some sharks have become target species as well.

Three types of longliners operate along the south Spanish coast: "coastal longliners" that fish two to five days in the area of the Strait of Gibraltar and that in some cases use gill nets in spring and summer; "offshore longliners" that spend 15 to 25 days fishing as far south as Senegal; and "long distance freezer longliners" that operate mainly in the tropical Atlantic Ocean (Gulf of Guinea and off Brazil). Little is known about shark fishing off southern Spain (García, 1970; Bravo and Santaella, 1973; Amorín et al., 1979; Garcés and Rey, 1983; Moreno and Morón, 1992b); more is known about shark catches from the northern Spanish longline fleet (Mejuto and Garcés[1]; Mejuto[2]).

The biology of eastern Atlantic pelagic sharks has not been well investigated although detailed taxonomic studies (Moreno, 1982), morphology and growth studies (Blasco and Muñoz-Chápuli, 1981; Muñoz-Chápuli and Blasco, 1984; Moreno and Morón, 1992b), reproduction (Muñoz-Chápuli, 1984; Moreno et al., 1989; Moreno and Morón, 1992a), and faunistic studies (Belloc, 1934; Lozano Cabo, 1950; Bravo, 1974; Bravo[3]) are available.

The most common shark species taken by longliners are blue shark, *Prionace glauca* (Linnaeus, 1758) and shortfin mako shark, *Isurus oxyrinchus* Rafinesque, 1810, which represent 80% of the total shark bycatch (Garcés and Rey, 1983; Moreno and Morón, 1992b). Other sharks caught include the porbeagle, *Lamna nasus* (Bonnaterre, 1788), the hammerheads, *Sphyrna* spp., the bigeye thresher, *Alopias superciliosus* (Lowe, 1839), the common thresher, *Alopias vulpinus*

[1] Mejuto, J., and A. Garcés. 1984. Shortfin mako, *Isurus oxyrinchus*, and porbeagle, *Lamna nasus*, associated with longline swordfish fishery in NW and N Spain. ICES, Council Meeting 1984/G: 72.

[2] Mejuto, J. 1985 Associated catches of sharks, *Prionace glauca*, *Isurus oxyrinchus* and *Lamna nasus*, with NW and N Spanish swordfish fishery, in 1984. ICES, Council Meeting 1985/H: 42.

[3] Bravo, J. 1973. Elasmobranchii off Canary Islands. ICES, Council Meeting 1973/J: 17.

(Bonnaterre, 1788), and the requiem sharks, *Carcharhinus* spp. (Garcés and Rey, 1984). Bony fish are caught occasionally, including the northern bluefin tuna, *Thunnus thynnus* (Linnaeus, 1758), bigeye tuna, *Thunnus obesus* (Lowe, 1839), albacore tuna, *Thunnus alalunga* (Bonnaterre, 1788), oilfish, *Ruvettus pretiosus* Cocco, 1829, escolar, *Lepidocybium flavobrunneum* (Smith, 1849), and longbill spearfish, *Tetrapturus pfluegeri* Robins and de Sylva, 1963, (Mejuto and Garcés[1]; Mejuto[2]).

## Materials and methods

Between July 1991 and July 1992, 106 longline and 69 gillnet landings (85.4% and 87.3% respectively of total longline and gillnet landings) were sampled at the Algeciras fish market (Cádiz, southern Spain), the largest market in southwestern Spain receiving 80% of the longline catch from this area (Anonymous, 1986). Data on the number of fish landed by species, days of each trip, active fishing days, number of sets and hooks for longliners, and net length and fishing time for gillnetters were collected during interviews with skippers.

The longline catch rate was calculated as hook rate (HR=number of fish/1,000 hooks), and gillnet catch rate was calculated as the average net length by trip multiplied by the number of sets. No total catch and effort data were available; catch rates are approximate indicators and do not reflect actual abundance. Fishing time was not included in effort calculations because it was constant for every boat and gear. The gears were set at dusk and retrieved before sunrise. Longlines ranged from 18 to 29 km in length and on average had 1500 hooks (range: 475 to 2500), set at a depth of 11 to 55 m. Gill nets were 2.5 km long, 14 m high, and had a mesh size of 40 cm.

All fish landed were identified to species level and counted. Most sharks were sexed and measured to the nearest centimeter for total length (TL) or fork length (FL), or both. Total length was measured from the rear tip of the upper caudal lobe to the snout tip, along the horizontal line of the body axis. Length data were grouped in 5-cm intervals of FL (shortfin mako and blue sharks) and TL (thresher and hammerhead sharks) for length-frequency analysis. Biometrical relationships between sexes were performed by simple linear regression analysis when the sample size was sufficiently large (shortfin mako, blue, and bigeye thresher sharks). Standard length (SL) has been used as the reference length for the relation with fork length (FL), total length (TL), and upper caudal lobe (UCL) (dorsal-caudal margin). The relation between FL and TL was also calculated. The area sampled (Fig. 1) was divided into 5° latitude sectors from 20°N to 40°N. Sectors 4 and 5 have the same latitude (35°N–40°N) but different longitudes, 3°W–8°W for sector 5, 8°W–13°W for sector 4. This division separates the gillnet fishing ground (sector 5) from the longline Atlantic area (sector 4).

A chi-square ($\chi^2$) test was performed to test the fit of the sample to a normal distribution and to observe the variations in species by sector and month. Strong bias was expected because of the effect of discarded fish at sea. Single factor ANOVA was performed to compare the means of the samples by area.

## Results

A total of 40,198 sharks and 11,007 bony fish were sampled from 175 landings from July 1991 to July 1992 (Table 1). The proportion of sharks landed was higher with longlines than with gill nets, but this might be related to the seasonal abundance of sharks and swordfish in the Strait of Gibraltar during the period when gill nets were used (Fig. 2).

The most common species landed by longlines in the areas studied were blue shark, shortfin mako shark, and swordfish (Table 2). Other chondrichthyans were less common, some rarely occurring in more than 10% of the landings.

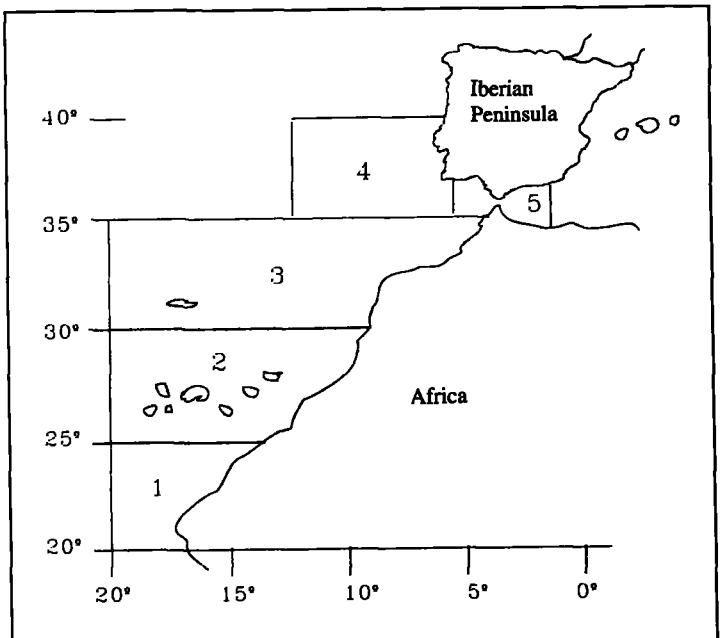


**Figure 1**

Map of the study area showing the five sectors into which the area was divided for the present paper.

Proportions of swordfish and the five most common shark species landed by longlines were significantly different ($\chi^2$=5.41; df=20; $P$<0.001) in each sector (Table 3). The highest proportion of fish in all the sectors, except one (sector 1), was that of blue sharks, whereas the lowest proportion in all five sectors was that of the common thresher shark. Swordfish occurred with decreasing proportion from south to north in the Atlantic sectors, reaching a minimum in the Mediterranean sector. Shortfin mako sharks steadily decreased from sector 1 to sector 4. The proportion of sharks, overall, was greater than the proportion of swordfish in all sectors, and sharks were included in at least 80% of the landings in all sectors, where they were slightly greater in numbers than swordfish, except in sector 1.

**Table 1**

Total number of fish sampled from 175 landings at the Algeciras (Cádiz) fish market and percentage by species from July 1991 to July 1992.

| Species | Number | Percentage |
|---|---|---|
| *Isurus oxyrinchus* | 5947 | 11.6 |
| *Prionace glauca* | 32,661 | 63.7 |
| *Alopias vulpinus* | 52 | 0.1 |
| *Alopias superciliosus* | 557 | 1.1 |
| *Sphyrna zygaena* | 757 | 1.4 |
| Other sharks | 224 | 0.4 |
| Total sharks | 40,198 | 78.5 |
| *Xiphias gladius* | 9990 | 19.5 |
| Other bony fish | 1017 | 2.0 |
| Total | 51,205 | 100.0 |

The proportional distribution of fish from gillnet landings was significantly different from that of fish from longline landings in the same sector ($\chi^2$=2.97; df=5; $P$<0.001) (Table 3). Gill nets were operated only in sector 5. Swordfish represented a much higher proportion in total gillnet landings than in longline landings; sharks represented only one third of total gillnet landings. The drop in the relative importance of sharks was due mainly to a much lower number of blue sharks in gillnet landings than in longline landings (8% compared with 82%). Bigeye thresher sharks slightly increased in landings (from 0.01% to 6%).

The proportions of fish landed by longline differed significantly by month ($\chi^2$=3.55; df=48; $P$<0.001) (*A. vulpinus* not considered) (Table 4), although blue shark was always the most predominant. Swordfish and shortfin mako sharks had the next highest proportions, whereas the other species never reached more than 5% of monthly catches. Sharks always accounted for more than 50% of the monthly catch, and more than 80% in 10 out the 13 months sampled.

Proportions of fish in gillnet landings also differed significantly by month ($\chi^2$=1.10; df=35; $P$<0.001) (March not considered) (Table 4). Swordfish had the highest proportion, except during the month of April. Blue sharks were taken in small proportions for most months (0–37%). The proportion of thresher sharks varied from month to month. Bigeye thresher sharks were taken at a maximum (10%) in August 1991 and July 1992; common thresher sharks also reached 10% in January 1992. The proportion of sharks exceeded

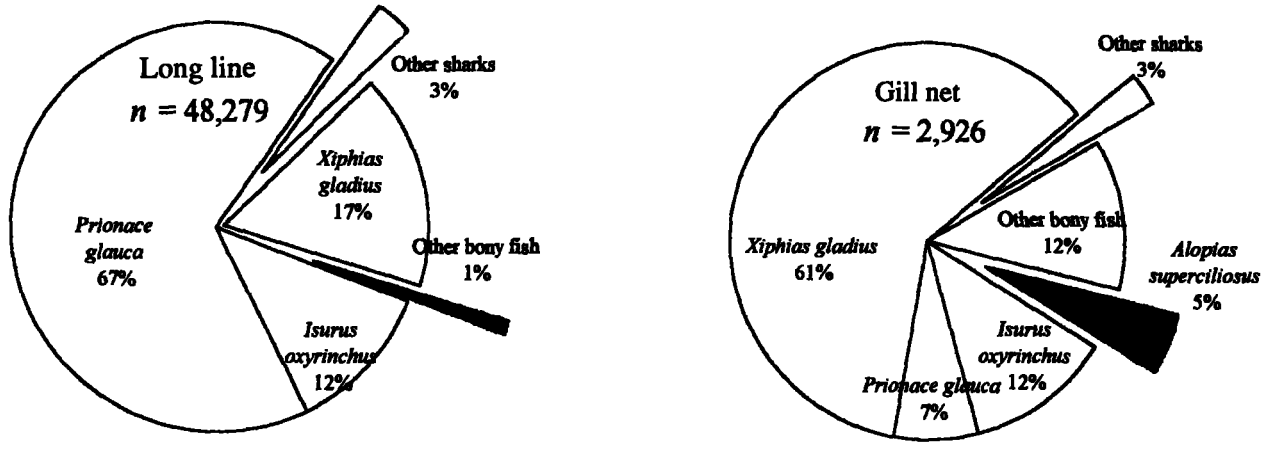


**Figure 2**

Species composition (% of fish) landed by the gillnet and longline fisheries operating in the eastern Atlantic Ocean and western Mediterranean Sea.

## Table 2

Species occurrence by number of landings and proportion (%) by gear.

| Species | Appearance (no. of landings) | | | Percentage | | |
|---|---|---|---|---|---|---|
| | Longline | Gillnet | Total | Longline | Gillnet | Total |
| *Isurus oxyrinchus* Rafinesque, 1810 | 102 | 45 | 147 | 96.2 | 65.2 | 84.0 |
| *Isurus paucus* Guitart Manday, 1966 | 11 | 1 | 12 | 10.4 | 1.4 | 6.8 |
| *Lamna nasus* (Bonnaterre, 1788) | 2 | 5 | 7 | 1.9 | 7.2 | 4.0 |
| *Alopias superciliosus* (Lowe, 1839) | 61 | 23 | 84 | 57.5 | 33.3 | 48.0 |
| *Alopias vulpinus* (Bonnaterre, 1788) | 11 | 11 | 22 | 10.4 | 15.9 | 12.6 |
| *Carcharhinus* spp. | 7 | 0 | 7 | 6.6 | 0 | 4.0 |
| *Carcharhinus falciformis* (Bibron, 1841) | 2 | 0 | 2 | 1.9 | 0 | 1.1 |
| *Galeocerdo cuvier* (Péron and Lesueur, 1822) | 1 | 0 | 1 | 0.9 | 0 | 0.6 |
| *Prionace glauca* (Linnaeus, 1758) | 102 | 19 | 121 | 96.2 | 27.5 | 69.1 |
| *Sphyrna zygaena* (Linnaeus, 1758) | 43 | 26 | 69 | 40.6 | 37.7 | 39.4 |
| *Mobula mobular* (Bonnaterre, 1788) | 2 | 0 | 2 | 1.9 | 0 | 1.1 |
| *Polyprion americanus* (Schneider, 1801) | 2 | 0 | 2 | 1.9 | 0 | 1.1 |
| *Coryphaena hippurus* Linnaeus, 1758 | 3 | 7 | 10 | 2.8 | 10.1 | 5.7 |
| *Brama brama* (Bonnaterre, 1788) | 0 | 1 | 1 | 0 | 1.4 | 0.6 |
| *Sparus pagrus* Linnaeus, 1758 | 1 | 0 | 1 | 0.9 | 0 | 0.6 |
| *Lepidocybium flavobrunneum* (Smith, 1849) | 37 | 1 | 38 | 34.9 | 1.4 | 21.7 |
| *Ruvettus pretiosus* Cocco, 1829 | 5 | 0 | 5 | 4.7 | 0 | 2.8 |
| *Acanthocybium solandri* (Cuvier, 1832) | 1 | 1 | 2 | 0.9 | 1.4 | 1.1 |
| *Auxis* spp. | 0 | 4 | 4 | 0 | 5.8 | 2.3 |
| *Auxis rochei* (Risso, 1810) | 0 | 1 | 1 | 0 | 1.4 | 0.6 |
| *Katsuwonus pelamis* (Linnaeus, 1758) | 1 | 2 | 3 | 0.9 | 2.9 | 1.7 |
| *Thunnus alalunga* (Bonnaterre, 1788) | 6 | 3 | 9 | 5.7 | 4.3 | 5.1 |
| *Thunnus albacares* (Bonnaterre, 1788) | 4 | 0 | 4 | 3.8 | 0 | 2.3 |
| *Thunnus obesus* (Lowe, 1839) | 16 | 1 | 17 | 15.1 | 1.4 | 9.7 |
| *Thunnus thynnus* (Linnaeus, 1758) | 4 | 3 | 7 | 3.8 | 4.3 | 4.0 |
| *Makaira nigricans* Lacépède, 1801 | 0 | 4 | 4 | 0 | 5.8 | 2.3 |
| *Tetrapturus* spp. | 14 | 21 | 35 | 13.2 | 30.4 | 20.0 |
| *Tetrapturus albidus* Poey, 1860 | 1 | 2 | 3 | 0.9 | 2.9 | 1.7 |
| *Xiphias gladius* Linnaeus, 1758 | 101 | 63 | 164 | 95.3 | 91.3 | 93.7 |
| Total landings | 106 | 69 | 175 | 60.6 | 39.4 | 100.0 |

## Table 3

Total number of the five most important shark species and swordfish recorded in landings and percentage by species, gear, and sector. Sectors (1–5) are indicated under gear type.

| | Number | | | | | | Percentage | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Longline | | | | | Gillnet | Longline | | | | | Gillnet |
| | 1 | 2 | 3 | 4 | 5 | 5 | 1 | 2 | 3 | 4 | 5 | 5 |
| *I. oxyrinchus* | 915 | 1648 | 2211 | 578 | 241 | 354 | 17 | 14 | 12 | 7 | 10 | 14 |
| *P. glauca* | 1865 | 7757 | 14207 | 6538 | 2082 | 212 | 34 | 64 | 76 | 76 | 82 | 8 |
| *A. vulpinus* | 4 | 1 | 7 | 2 | 2 | 36 | 0 | 0 | 0 | 0 | 0 | 1 |
| *A. superciliosus* | 28 | 266 | 101 | 7 | 9 | 146 | 1 | 2 | 1 | 0 | 0 | 6 |
| *S. zygaena* | 188 | 39 | 392 | 82 | 2 | 54 | 3 | 0 | 2 | 1 | 0 | 2 |
| Total sharks | 3000 | 9711 | 16918 | 7207 | 2336 | 802 | 55 | 80 | 90 | 84 | 92 | 31 |
| *X. gladius* | 2410 | 2426 | 1822 | 1386 | 199 | 1747 | 45 | 20 | 10 | 16 | 8 | 69 |
| Total | 5410 | 12137 | 18740 | 8593 | 2535 | 2549 | 11 | 24 | 38 | 17 | 5 | 5 |

swordfish in only one of nine months sampled for gillnet landings.

### Shortfin mako shark

Longline catch rates are shown in Table 5; Atlantic catch rates were always higher than those in the Mediterranean. Variation in the longline catch rate (Table 6) was at a minimum in December and May, peaking in April and September. In gillnet fishing (Table 7), shortfin mako shark catch rates were relatively lower than swordfish catch rates.

Table 8 gives biometrical information by sex, and longline and gillnet frequency distributions of different lengths by sex are presented in Figures 3 and 4. The distribution was not significantly different between sexes in longline ($\chi^2$=54.4; df=39; $P$>0.05) and gillnet ($\chi^2$=20.5; df=23; $P$>0.5) landings. The distribution by size of males varied significantly by sector ($F$=28.796; df=5, 1428; $P$<0.001). The distribution by size of females also varied significantly by sector ($F$=14.985; df=5, 1429; $P$<0.001).

The maximum size of females landed by longlines tended to increase from sector 1 to sector 3 (Fig. 5A). The maximum size of males tended to increase in Atlantic sectors from south to north (Fig. 5B). Smallest maximum sizes for both sexes occurred in the Mediterranean Sea, and in sector 1 for males. Gill nets catch bigger females and smaller males than do longlines in the same sector. The monthly variations

**Table 4**

Monthly longline and gillnet catch distribution for the five most important shark species and for swordfish by number of fish ($n$) and percentage (%). Species codes: IO = *Isurus oxyrinchus*; PG = *Prionace glauca*; AV = *Alopias vulpinus*; AS = *Alopias superciliosus*; SZ = *Sphyrna zygaena*; TOT-SHX = Total sharks; XG = *Xiphias gladius*;

| Gear and month | IO | | PG | | AV | | AS | | SZ | | TOT-SHX | | XG | | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *n* | % | *n* | % | *n* | % | *n* | % | *n* | % | *n* | % | *n* | % | *n* |
| Longline | | | | | | | | | | | | | | | |
| Jul 91 | 224 | 16.85 | 992 | 74.64 | 2 | 0.15 | 31 | 2.33 | 21 | 1.58 | 1270 | 95.56 | 59 | 4.44 | 1329 |
| Aug 91 | 891 | 19.96 | 2865 | 64.19 | 1 | 0.02 | 3 | 0.07 | 147 | 3.29 | 3907 | 87.54 | 556 | 12.46 | 4463 |
| Sep 91 | 422 | 15.93 | 2158 | 81.46 | 0 | 0 | 7 | 0.26 | 28 | 1.06 | 2615 | 98.72 | 34 | 1.28 | 2649 |
| Oct 91 | 584 | 9.57 | 3338 | 54.68 | 0 | 0 | 32 | 0.52 | 131 | 2.15 | 4085 | 66.91 | 2020 | 33.09 | 6105 |
| Nov 91 | 970 | 14.10 | 4333 | 62.99 | 4 | 0.06 | 25 | 0.36 | 252 | 3.66 | 5584 | 81.17 | 1295 | 18.83 | 6879 |
| Dec 91 | 30 | 12.35 | 105 | 43.21 | 0 | 0 | 5 | 2.06 | 0 | 0 | 140 | 57.61 | 103 | 42.39 | 243 |
| Jan 92 | 863 | 10.02 | 6117 | 71.03 | 4 | 0.05 | 110 | 1.28 | 30 | 0.35 | 7124 | 82.72 | 1488 | 17.28 | 8612 |
| Feb 92 | 868 | 9.07 | 6988 | 73.03 | 2 | 0.02 | 135 | 1.41 | 79 | 0.83 | 8072 | 84.36 | 1497 | 15.64 | 9569 |
| Mar 92 | 423 | 9.04 | 3208 | 68.53 | 1 | 0.02 | 54 | 1.15 | 1 | 0.02 | 3687 | 78:77 | 994 | 21.23 | 4681 |
| Apr 92 | 109 | 10.64 | 913 | 89.16 | 0 | 0 | 1 | 0.10 | 0 | 0 | 1023 | 99.90 | 1 | 0.10 | 1024 |
| May 92 | 25 | 8.01 | 283 | 90.71 | 1 | 0.32 | 0 | 0 | 0 | 0 | 309 | 99.04 | 3 | 0.96 | 312 |
| Jun 92 | 114 | 10.45 | 783 | 71.77 | 1 | 0.09 | 8 | 0.73 | 2 | 0.18 | 908 | 83.23 | 183 | 16.77 | 1091 |
| Jul 92 | 70 | 15.28 | 366 | 79.91 | 0 | 0 | 0 | 0 | 12 | 2.62 | 448 | 97.82 | 10 | 2.18 | 458 |
| Total | 5593 | 11.80 | 32449 | 68.44 | 16 | 0.03 | 411 | 0.87 | 703 | 1.48 | 39172 | 82.62 | 8243 | 17.38 | 47415 |

| Gear and month | IO | | PG | | AV | | AS | | SZ | | TOT-SHX | | XG | | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | *n* | % | *n* | % | *n* | % | *n* | % | *n* | % | *n* | % | *n* | % | *n* |
| Gillnet | | | | | | | | | | | | | | | |
| Jul 91 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| Aug 91 | 19 | 7.39 | 0 | 0 | 1 | 0.39 | 37 | 14.40 | 5 | 1.95 | 62 | 24.12 | 195 | 75.88 | 257 |
| Sep 91 | 106 | 22.70 | 30 | 6.42 | 2 | 0.43 | 27 | 5.78 | 22 | 4.71 | 187 | 40.04 | 280 | 59.96 | 467 |
| Oct 91 | 53 | 9.62 | 2 | 0.36 | 0 | 0 | 3 | 0.54 | 12 | 2.18 | 70 | 12.70 | 481 | 87.30 | 551 |
| Nov 91 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| Dec 91 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| Jan 92 | 6 | 6.25 | 0 | 0 | 15 | 15.6 | 0 | 0 | 1 | 1.04 | 22 | 22.92 | 74 | 77.08 | 96 |
| Feb 92 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| Mar 92 | 0 | 0 | 1 | 33.33 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 33.33 | 2 | 66.67 | 3 |
| Apr 92 | 54 | 24.00 | 83 | 36.89 | 15 | 6.67 | 7 | 3.11 | 2 | 0.89 | 161 | 71.56 | 64 | 28.44 | 225 |
| May 92 | 76 | 11.66 | 90 | 13.80 | 1 | 0.15 | 0 | 0 | 0 | 0 | 167 | 25.61 | 485 | 74.39 | 652 |
| Jun 92 | 14 | 15.22 | 1 | 1.09 | 0 | 0 | 6 | 6.52 | 4 | 4.35 | 25 | 27.17 | 67 | 72.83 | 92 |
| Jul 92 | 26 | 12.62 | 5 | 2.43 | 2 | 0.97 | 66 | 32.04 | 8 | 3.88 | 107 | 51.94 | 99 | 48.06 | 206 |
| Total | 354 | 13.89 | 212 | 8.32 | 36 | 1.41 | 146 | 5.73 | 54 | 2.12 | 802 | 31.46 | 1747 | 68.54 | 2549 |

**Table 5**

Longline effort (number of hooks × 1000) and catch rates (number of fish/1000 hooks) by species and sector.

| Sector | Effort | *I. oxyrinchus* | *P. glauca* | *A. vulpinus* | *A. superciliosus* | *S. zygaena* | Total sharks | *X. gladius* |
|---|---|---|---|---|---|---|---|---|
| 1 | 302.4 | 3.03 | 6.17 | 0.013 | 0.09 | 0.62 | 9.92 | 7.97 |
| 2 | 534.0 | 3.09 | 14.53 | 0.002 | 0.50 | 0.07 | 18.19 | 4.54 |
| 3 | 462.9 | 4.78 | 30.69 | 0.015 | 0.22 | 0.85 | 36.55 | 3.94 |
| 4 | 61.8 | 3.90 | 33.69 | 0.032 | 0.15 | 0.03 | 37.80 | 3.22 |
| 5 | 297.5 | 1.94 | 21.98 | 0.007 | 0.02 | 0.28 | 24.23 | 4.66 |
| Total | 1658.6 | 3.37 | 19.56 | 0.010 | 0.25 | 0.42 | 23.62 | 4.97 |

**Table 6**

Longline effort (number of hooks × 1000) and catch rates (number of fish/1000 hooks) by species and month.

| Month | Effort | *I. oxyrinchus* | *P. glauca* | *A. vulpinus* | *A. superciliosus* | *S. zygaena* | Total sharks | *X. gladius* |
|---|---|---|---|---|---|---|---|---|
| Jul 91 | 67.40 | 3.32 | 14.72 | 0.03 | 0.46 | 0.31 | 18.84 | 0.88 |
| Aug 91 | 180.40 | 4.94 | 15.88 | 0.01 | 0.02 | 0.81 | 21.66 | 3.08 |
| Sep 91 | 41.30 | 10.22 | 52.25 | 0.00 | 0.17 | 0.68 | 63.32 | 0.82 |
| Oct 91 | 195.00 | 2.99 | 17.12 | 0.00 | 0.16 | 0.67 | 20.95 | 10.36 |
| Nov 91 | 185.20 | 5.24 | 23.40 | 0.02 | 0.13 | 1.36 | 30.15 | 6.99 |
| Dec 91 | 16.80 | 1.79 | 6.25 | 0.00 | 0.30 | 0.00 | 8.33 | 6.13 |
| Jan 92 | 296.60 | 2.91 | 20.62 | 0.01 | 0.37 | 0.10 | 24.02 | 5.02 |
| Feb 92 | 393.20 | 2.21 | 17.77 | 0.01 | 0.34 | 0.20 | 20.53 | 3.81 |
| Mar 92 | 206.90 | 2.04 | 15.51 | 0.00 | 0.26 | 0.00 | 17.82 | 4.80 |
| Apr 92 | 5.00 | 21.80 | 182.60 | 0.00 | 0.20 | 0.00 | 204.60 | 0.20 |
| May 92 | 12.80 | 1.95 | 22.11 | 0.08 | 0.00 | 0.00 | 24.14 | 0.23 |
| Jun 92 | 47.00 | 2.43 | 16.66 | 0.02 | 0.17 | 0.04 | 19.32 | 3.89 |
| Jul 92 | 11.00 | 6.36 | 33.27 | 0.00 | 0.00 | 1.09 | 40.73 | 0.91 |
| Total | 1,658.60 | 3.37 | 19.56 | 0.01 | 0.25 | 0.42 | 23.62 | 4.97 |

**Table 7**

Gillnet effort (average net length (number of sets) and catch rates (number of fish/unit of effort) by species and month.

| Sector | Effort | *I. oxyrinchus* | *P. glauca* | *A. vulpinus* | *A. superciliosus* | *S. zygaena* | Total sharks | *X. gladius* |
|---|---|---|---|---|---|---|---|---|
| Jul 91 | — | — | — | — | — | — | — | — |
| Aug 91 | 118.50 | 0.16 | 0.00 | 0.01 | 0.31 | 0.04 | 0.52 | 1.65 |
| Sep 91 | 152.90 | 0.69 | 0.20 | 0.01 | 0.18 | 0.14 | 1.22 | 1.83 |
| Oct 91 | 90.90 | 0.58 | 0.02 | 0.00 | 0.03 | 0.13 | 0.77 | 5.29 |
| Nov 91 | — | — | — | — | — | — | — | — |
| Dec 91 | — | — | — | — | — | — | — | — |
| Jan 92 | 36.50 | 0.16 | 0.00 | 0.41 | 0.00 | 0.03 | 0.60 | 2.03 |
| Feb 92 | — | — | — | — | — | — | — | — |
| Mar 92 | 2.00 | 0.00 | 0.50 | 0.00 | 0.00 | 0.00 | 0.50 | 1.00 |
| Apr 92 | 48.00 | 1.13 | 1.73 | 0.31 | 0.15 | 0.04 | 3.35 | 1.33 |
| May 92 | 122.50 | 0.62 | 0.73 | 0.01 | 0.00 | 0.00 | 1.36 | 3.96 |
| Jun 92 | 30.00 | 0.47 | 0.03 | 0.00 | 0.20 | 0.13 | 0.83 | 2.23 |
| Jul 92 | 56.00 | 0.46 | 0.09 | 0.04 | 1.18 | 0.14 | 1.91 | 1.77 |
| Total | 657.30 | 0.54 | 0.32 | 0.05 | 0.22 | 0.08 | 1.22 | 2.66 |

of maximum, median, and minimum sizes are presented in Figure 6, A and B.

## Blue shark

Blue sharks are often discarded at sea because they are not commercially valuable in the Spanish market; real catch rates are biased by this factor, especially in the more distant sectors where the tendency is to try to improve long trips with more valuable species, i.e. with swordfish and shortfin mako shark. Therefore, sectors 1 and 2 had lower catch rates, based on landings, than sectors 3, 4, and 5 (Table 5). Longline catch rates by month (Table 6) ranged from 6 to 52 fish/1000 hooks, except for an extremely high rate in April (182 fish/1000 hooks). Gillnet catch rates for this species were very low in relation to other species, in some months almost negligible (Table 7).

In the longline fishery, sex ratio by sector was close to 1 male:0.25 females, except in sector 3 where it was almost equal (1 male:0.92 females); gillnet sex ratio (1 male:2.45 females) was inverse to that observed for longlines in the same sector. Monthly data were not sufficient to be analyzed and therefore were grouped by quarter, i.e. July–September 1991, October–December 1991, January–March 1992, and April–June 1992. Because of the effect of discarded fish at sea and inappropriate sex sampling, we were unable to make significant assertations about sex ratio variability.

The distribution of overall length frequency is presented in Figure 7A. In longline landings, modal

**Table 8**

Biometric relations of standard length (*SL*) with fork length (*FL*), total length (*TL*), and upper caudal lobe length (UCL); and of fork length with total length by sex for *Isurus oxyrinchus*, *Prionace glauca*, and *Alopias superciliosus*, and both sexes combined for *Alopias vulpinus* and *Sphyrna zygaena*.

| Females | Males | Total |
|---|---|---|
| *Isurus oxyrinchus* | | |
| $FL = 1.086\ SL + 1.630$ | $FL = 1.086\ SL + 1.409$ | $FL = 1.086\ SL + 1.515$ |
| $r^2 = 0.993\ n = 852$ | $r^2 = 0.993\ n = 911$ | $r^2 = 0.993\ n = 1{,}763$ |
| $TL = 0.817\ SL + 0.400$ | $TL = 1.209\ SL + 0.435$ | $TL = 1.207\ SL + 0.971$ |
| $r^2 = 0.986\ n = 852$ | $r^2 = 0.983\ n = 681$ | $r^2 = 0.985\ n = 1{,}533$ |
| $UCL = 3.693\ SL + 13.094$ | $UCL = 3.795\ SL + 10.452$ | $UCL = 3.758\ SL + 11.640$ |
| $r^2 = 0.874\ n = 507$ | $r^2 = 0.898\ n = 477$ | $r^2 = 0.903\ n = 1{,}054$ |
| $TL = 1.106\ FL + 0.052$ | $TL = 1.111\ FL - 0.870$ | $TL = 1.108\ FL$-0.480 |
| $r^2 = 0.985\ n = 853$ | $r^2 = 0.984\ n = 911$ | $r^2 = 0.984\ n = 1{,}746$ |
| *Prionace glauca* | | |
| $FL = 1.076\ SL + 1.862$ | $FL = 1.080\ SL + 1.552$ | $FL = 1.079\ SL + 1.668$ |
| $r^2 = 0.993\ n = 1{,}043$ | $r^2 = 0.997\ n = 1{,}276$ | $r^2 = 0.996\ n = 2{,}319$ |
| $TL = 1.249\ SL + 7.476$ | $TL = 1.272\ SL + 4.466$ | $TL = 1.262\ SL + 5.746$ |
| $r^2 = 0.986\ n = 1{,}043$ | $r^2 = 0.993\ n = 1{,}272$ | $r^2 = 0.990\ n = 2{,}315$ |
| $UCL = 0.219\ SL + 4.861$ | $UCL = 0.316\ SL + 2.191$ | $UCL = 0.306\ SL + 3.288$ |
| $r^2 = 0.903\ n = 1{,}038$ | $r^2 = 0.948\ n = 1{,}264$ | $r^2 = 0.929\ n = 2{,}302$ |
| $TL = 1.158\ FL + 5.678$ | $TL = 1.117\ FL + 2.958$ | $TL = 1.167\ FL$+ 4.133 |
| $r^2 = 0.988\ n = 1{,}043$ | $r^2 = 0.992\ n = 1{,}272$ | $r^2 = 0.990\ n = 2{,}315$ |
| *Alopias superciliosus* | | |
| $FL = 1.075\ SL + 3.346$ | $FL = 1.081\ SL + 3.324$ | $FL = 1.073\ SL + 4.150$ |
| $r^2 = 0.987\ n = 90$ | $r^2 = 0.980\ n = 76$ | $r^2 = 0.986\ n = 166$ |
| $TL = 1.939\ SL - 11.990$ | $TL = 1.897\ SL - 7.359$ | $TL = 1.937\ SL$ -12.630 |
| $r^2 = 0.976\ n = 77$ | $r^2 = 0.946\ n = 70$ | $r^2 = 0.970\ n = 147$ |
| $UCL = 0.967\ SL$ -9.588 | $UCL = 0.922\ SL$ -5.353 | $UCL = 0.966\ SL - 10.908$ |
| $r^2 = 0.952\ n = 75$ | $r^2 = 0.869\ n = 71$ | $r^2 = 0.932\ n = 146$ |
| $TL = 1.775\ FL - 13.007$ | $TL = 1.722\ FL - 7.295$ | $TL = 1.773\ FL$- 14.456 |
| $r^2 = 0.956\ n = 77$ | $r^2 = 0.923\ n = 70$ | $r^2 = 0.949\ n = 147$ |

| *Alopias vulpinus* | | | *Sphyrna zygaena* | | |
|---|---|---|---|---|---|
| Relation | $r^2$ | $n$ | Relation | $r^2$ | $n$ |
| $FL = 1.118\ SL - 2.29$ | 0.989 | 22 | $FL = 0.845\ SL + 1.077$ | 0.998 | 56 |
| $TL = 1.930\ SL + 9.331$ | 0.956 | 22 | $TL = 1.322\ SL + 8.397$ | 0.994 | 56 |
| $UCL = 0.926\ SL + 25.670$ | 0.949 | 22 | $UCL = 0.329\ SL + 8.799$ | 0.975 | 55 |
| $TL = 1.687\ FL + 20.483$ | 0.932 | 22 | $TL = 1.225\ FL + 7.528$ | 0.994 | 56 |

length for males (95 cm FL) was slightly greater than for females (80 cm FL), whereas in gillnet landings it was equivalent (100 cm FL). Mean lengths in the longline landings, including nonsexed specimens, ranged from 85 cm FL in sector 5 to 205 cm FL in sector 1. The mean length for gill nets was the same for

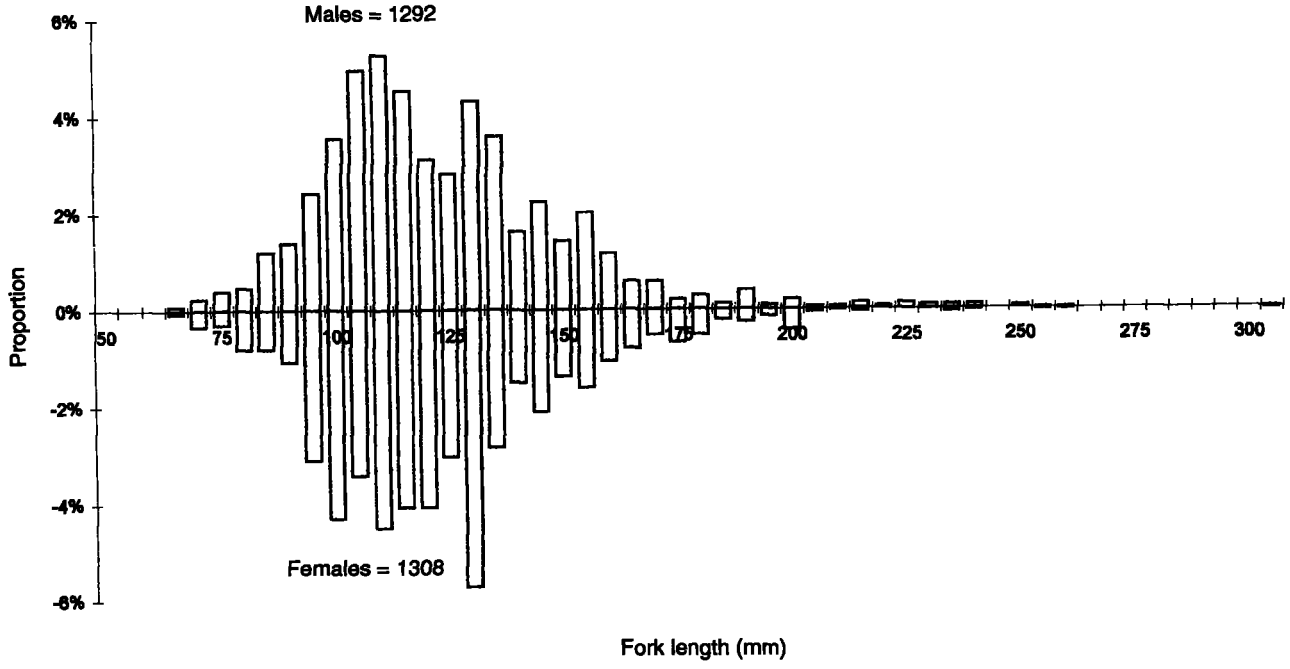


**Figure 3**

Total length-frequency distribution by sex of the shortfin mako shark longline landings from all sectors from July 1991 to July 1992.

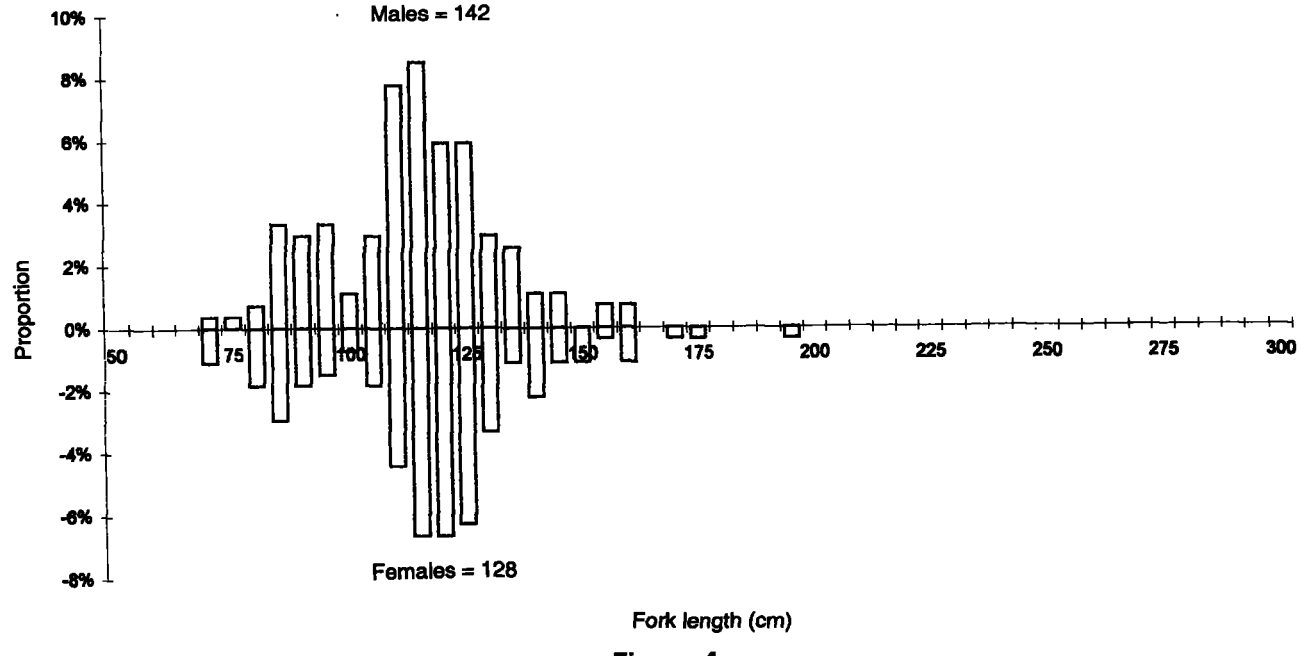


**Figure 4**

Total length-frequency distribution by sex of the shortfin mako shark gillnet landings from sector 5 from July 1991 to July 1992.

males and females (100 cm FL). The incompleteness of these data did not allow any temporal analyses.

Size distribution by sector varied significantly ($F$=387.130; df=5, 8214; $P$<0.001). Total mean size was greatest in sector 1, lowest in sector 5. Sector 3 had minimum-size females and males. The largest size females were found in sector 1; the largest males, in sector 4 (Fig. 7, B and C).

Table 8 shows biometrical comparisons by sex.

## Bigeye thresher shark

Longline catch rates for bigeye thresher sharks were very low. However, this species was caught in all sectors, sector 2 having the highest rate (Table 5). There was a slight increase in the longline catch rate, from

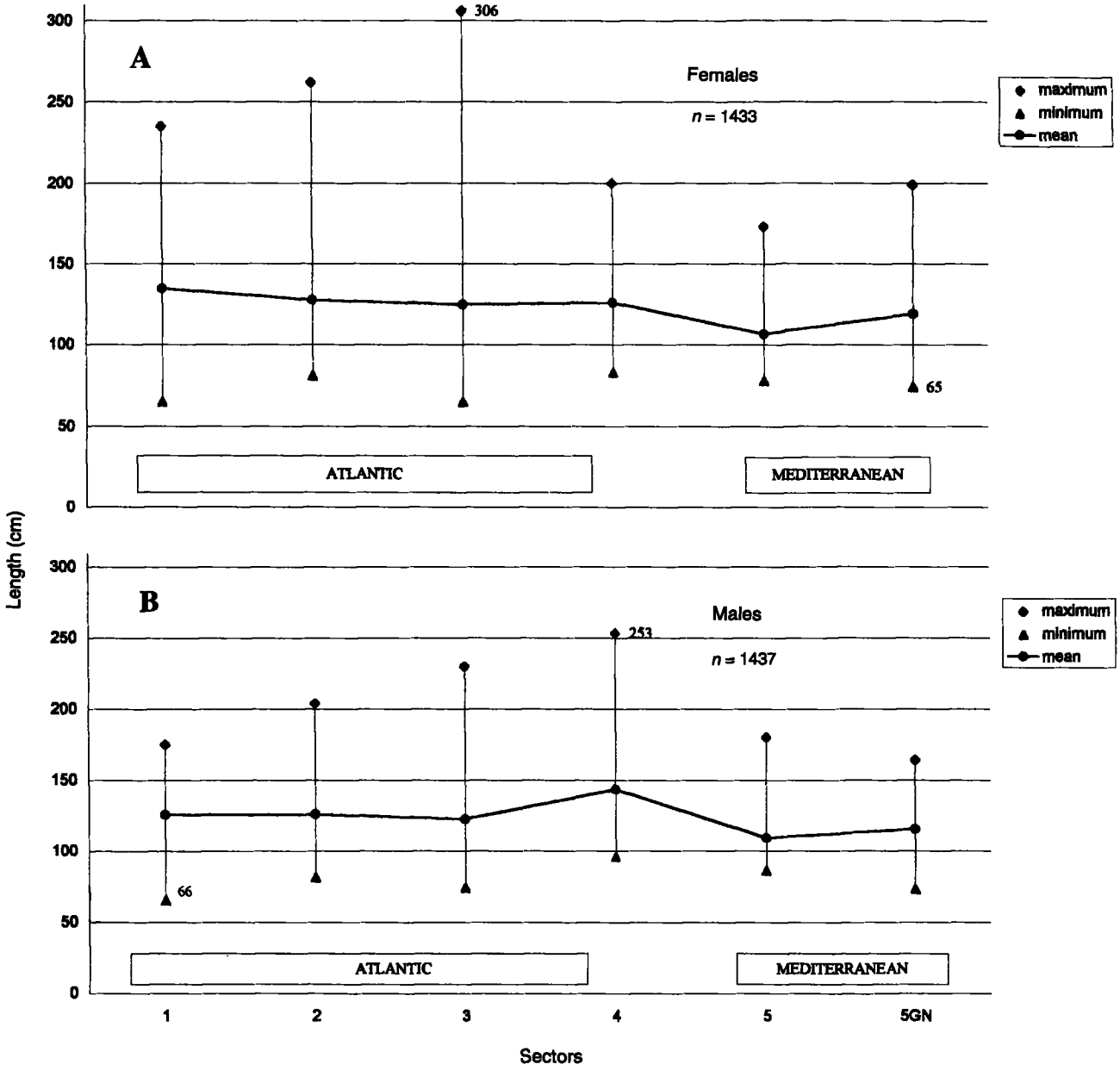


**Figure 5**

(**A**) Size range variation of shortfin mako shark females landed by longlines and gill nets (5GN) by sector from July 1991 to July 1992; (**B**) size range variation of the shortfin mako shark males landed by longlines and gill nets (5GN) by sector from July 1991 to July 1992.

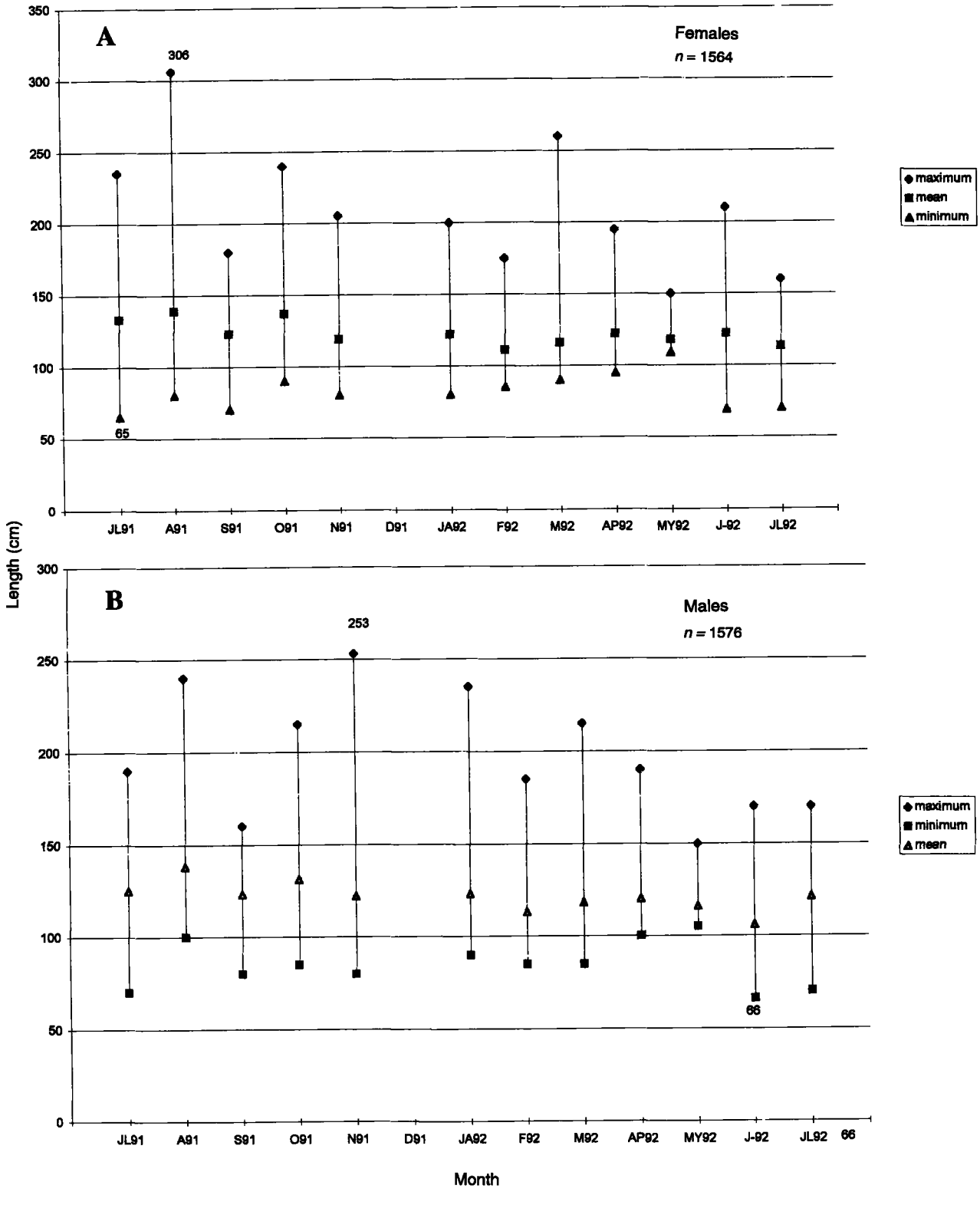


**Figure 6**

(**A**) Size range variation of the shortfin mako shark females landed by month (December 91 excluded); (**B**) size range variation of the shortfin mako shark males landed by month (December 91 excluded).

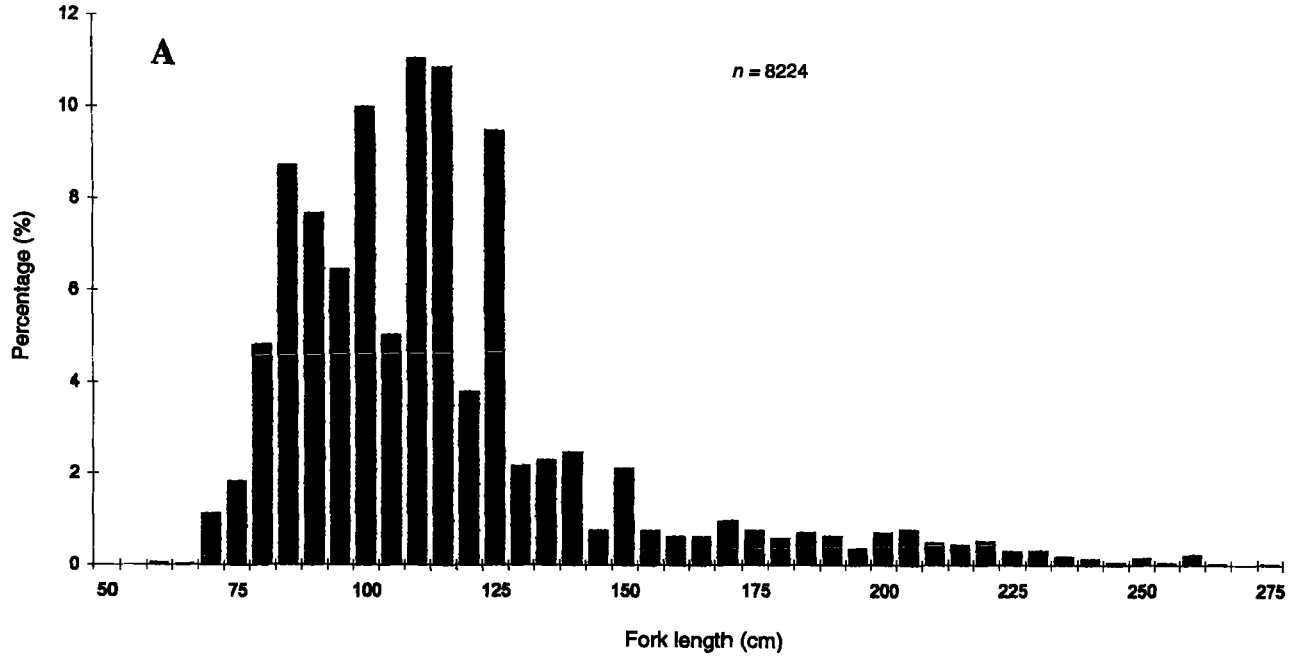


**Figure 7**

(**A**) Total length-frequency distribution of blue shark from longline and gillnet landings from all sectors from July 1991 to July 1992. (**B**) Size range variation of blue shark females landed by longlines and gill net (5GN) by sector from July 1991 to July 1992. (**C**) Size range variation of blue shark males landed by longlines and gill net (5GN) by sector from July 1991 to July 1992.

fall to winter, dropping during spring. A maximun catch rate was reached in July 1991 (Table 6). In gillnet fishing, catch rates were highest during summer months, with a maximum in July 1992 (Table 7).

The sex ratio found in longline fishing was fairly balanced, 1 male to 1.1 females in sector 2 to 1 to 0.93 females in sector 3. Females were more abundant than males in gillnet fishing (1 male:1.43 females). The distribution of sex ratio by sector was not significantly different ($\chi^2$=9.14; df=5; $P$>0.1). The distribution of sex ratio varied significantly by month ($\chi^2$=38.7; df=11; $P$<0.001). In longline fishing there were more males than females (1 male:0.66–0.69 females), except in February and March when the ratio was 1 male:1.45 females, and in September, when the proportion of females rose dramatically to 1 male:6.1 females. Gillnet fishing reflected a similar proportion during the same month (1 male:13.21 females).

The frequency distribution by size of fish from longline landings was quite similar for males and females (Fig. 8). Modal length for all sectors and months was near to 285 cm TL, the mean size approximately 280 cm TL. Minimum size was 180 cm TL for females, 195 cm TL for males. Maximum size was 40 cm greater for females (430 cm TL) than for males (390 cm TL).

The frequency distribution by size of fish from gillnet landings differed by sex (Fig. 9), with two modes for males (290 and 330 cm TL) and for females (395 and 410 cm TL).

The size range of fish by sector for longline landings was greater for females (183–432 cm TL) than for males (195–391 cm TL). Minimum sizes were found in sector 2 for both sexes, whereas the maximum for males was recorded in sector 3 and for females in sector 5. In gillnet landings, females ranged from 236 to 446 cm TL, with a mean size of 352 cm TL, 45 cm larger than the mean size of males (307 cm TL). As in longline landings, males had a smaller size range (246–373 cm TL). The length mode for females was 80 cm larger than for males (410 cm TL compared with 330 cm TL).

The size variation over time was not outstanding for males in either fishery, but there was a marked presence of large females during July–September in gillnet landings (288–446 cm TL) corroborated by longline landings in the same period (230–432 cm TL). The period of January to March was when the greatest number of fish were recorded (128) with the smallest size range (183–360 cm TL). Only one pregnant female (385 cm TL), with one pup, was recorded in gillnet landings in September 1991.

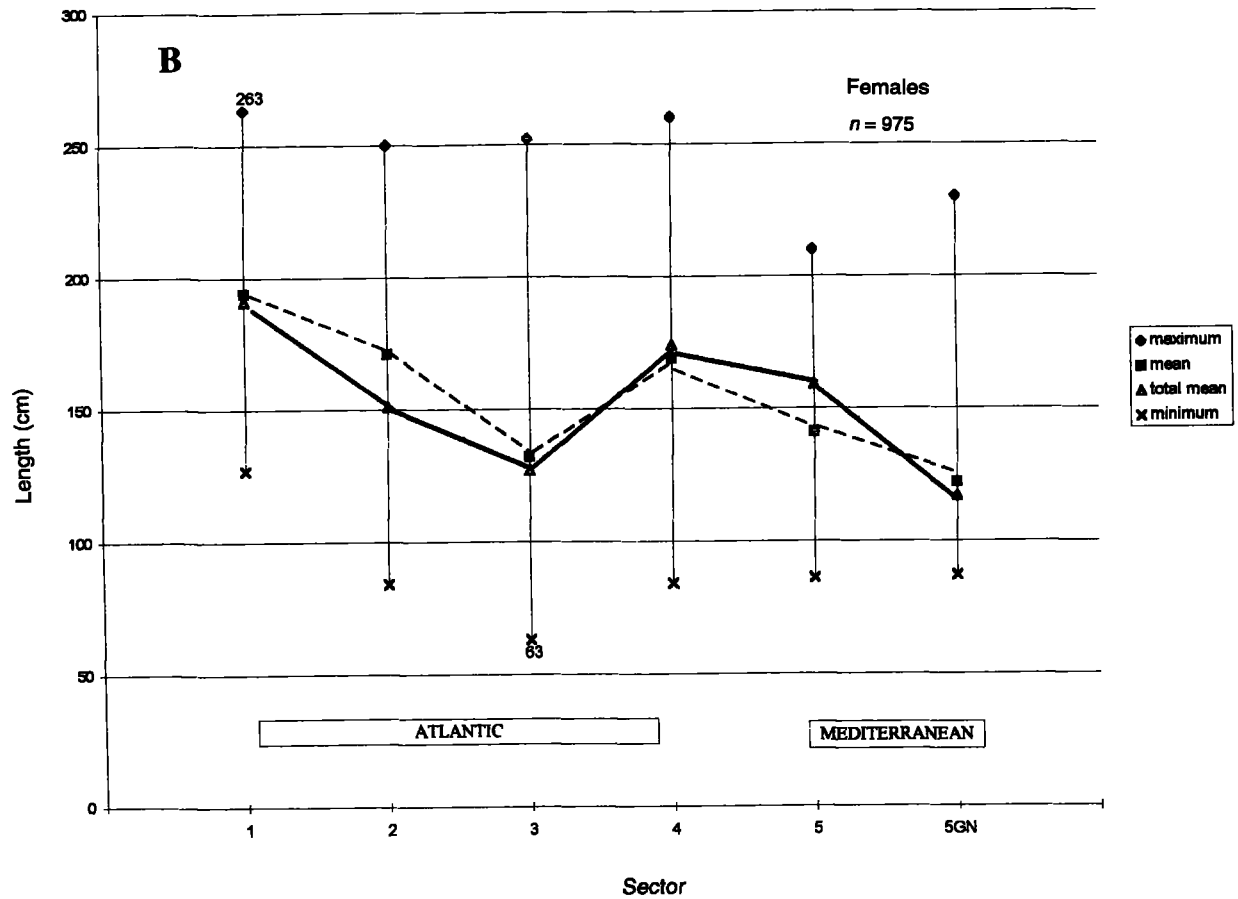


**Figure 7 (continued)**

## Common thresher shark

Only 52 common thresher sharks were recorded during the sampling period; hence the catch rate never went beyond 0.1 fish/1000 hooks (Tables 5 and 6). The overall sex ratio was close to 1 male:2 females, with some differences between longline (1 male:2.16 females) and gillnet (1 male:1.75 females) landings.

The size range of fish was similar for longline and gillnet landings, as was the mean size for both sexes (325 cm TL for males, 350 cm TL for females). Maximum size was similar in longline (360 cm TL for males, 425 cm TL for females) and gillnet landings (355 cm TL for males, 435 cm TL for females). Minimum size was comparable for females in both fisheries (295 and 285 cm TL in longline and gillnet, respectively), but not for males; in longline landings, a 245-cm-TL male was recorded, whereas in gillnet landings the minimum-size male recorded was about the same size as the minimum-size female (280 cm TL). Although biometrical information on this species is found in Table 8, our small sample size did not permit analyses by sex. Only one pregnant female was recorded, measuring 385 cm TL; it was caught in sector 4 by longline in May and carried 4 embryos (3 males and 1 female), 75 to 80 cm FL.

## Scalloped hammerhead shark

The catch rate for this species was low in all sectors and months, slightly greater for sectors 1 and 3 (0.6 and 0.8 fish/1000 hooks respectively), and never higher than 1 fish/1000 hooks (Tables 5–7). The highest overall catch rates by month in longline landings was in November 1991 and July 1992 (1.3 and 1.1 fish/1000 hooks). In gillnet landings the greatest catch rates were in September–October and June–July (0.1 fish/unit effort). Males were more abundant in the longline (1 male:0.61 females) than in the gillnet fishery, where females were dominant (1 male:1.37 females).

Females had a larger maximum size than males in both fisheries, 320 cm and 305 cm TL for females,

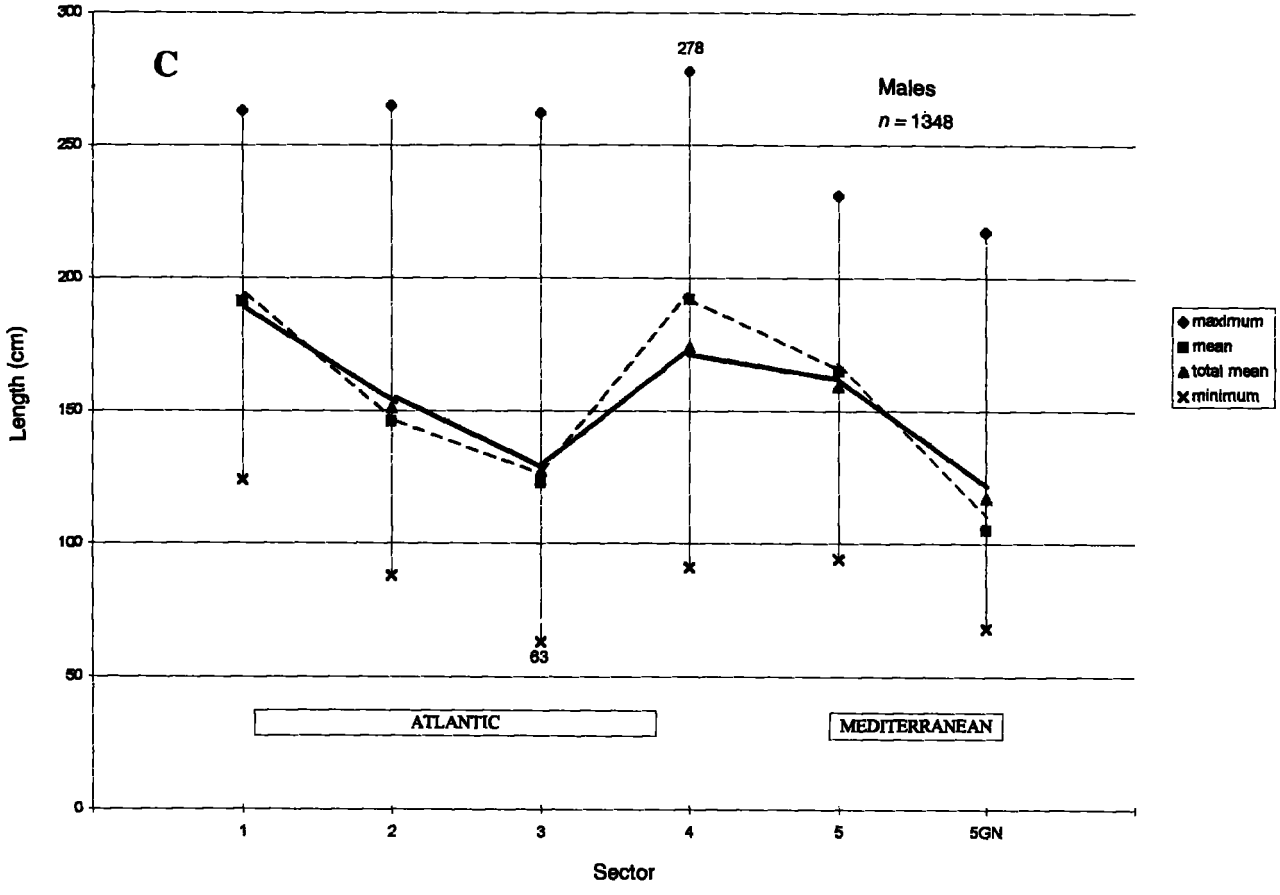


**Figure 7 (continued)**

280 and 275 cm TL for males, respectively, in longline and gillnet landings. Minimum size was greater in the gillnet fishery (185 cm TL for males, 165 cm TL for females) than in the longline fishery (105 cm TL for males, 115 cm TL for females). The mean size from longline landings was slightly greater for females (170 cm TL) than for males (150 cm TL). The mean size from the gillnet fishery was greater than from the longline fishery, with no difference between sexes (220 cm TL). Although biometrical information can be found in Table 8, the small sample size did not permit analyses by sex.

## Discussion

The total proportion of sharks in relation to swordfish observed in the present study was similar to that found by Gouveia (1992) for an adjacent area, but the species composition was different (*P. glauca*, *I. oxyrinchus*, *Dasyatis violacea*, *Alopias* spp., *Mustelus mustelus*, *Sphyrna* spp., *T. obesus*, and *Alepisaurus ferox*). Sharks comprised a greater proportion of landings in the study area than in other Atlantic longline fishing grounds, i.e. off the Florida coast (Berkeley and Campos, 1988), the Caribbean coast (Tobias, 1991), and the northwestern coast of Cuba (Guitart, 1975). "Other bony fish" (the other category of fish) taken by longlines had a similar proportion to that found in data from other Mediterranean longline fisheries (Rey and Alot, 1984). The abundance of the most common shark species, blue and shortfin mako sharks, also agrees with results presented for the same area by Garcés and Rey (1984).

### Shortfin mako shark

This species was very common in the study area. This finding agrees with reports by Muñoz-Chápuli (1985), although catch rates obtained were slightly lower than estimates of Moreno and Morón (1992b) from the same area. Proportions of shortfin mako sharks,

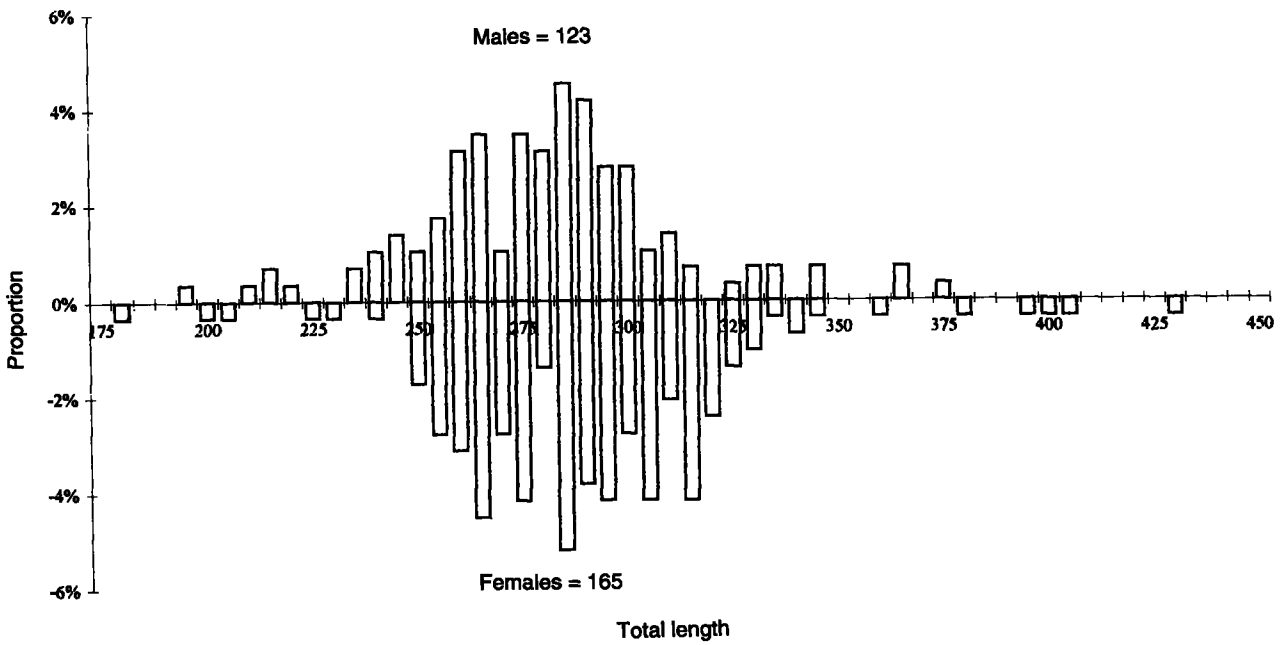


**Figure 8**

Total length-frequency distribution of the bigeye thresher shark by sex from longline landings from all sectors from July 1991 to July 1992.

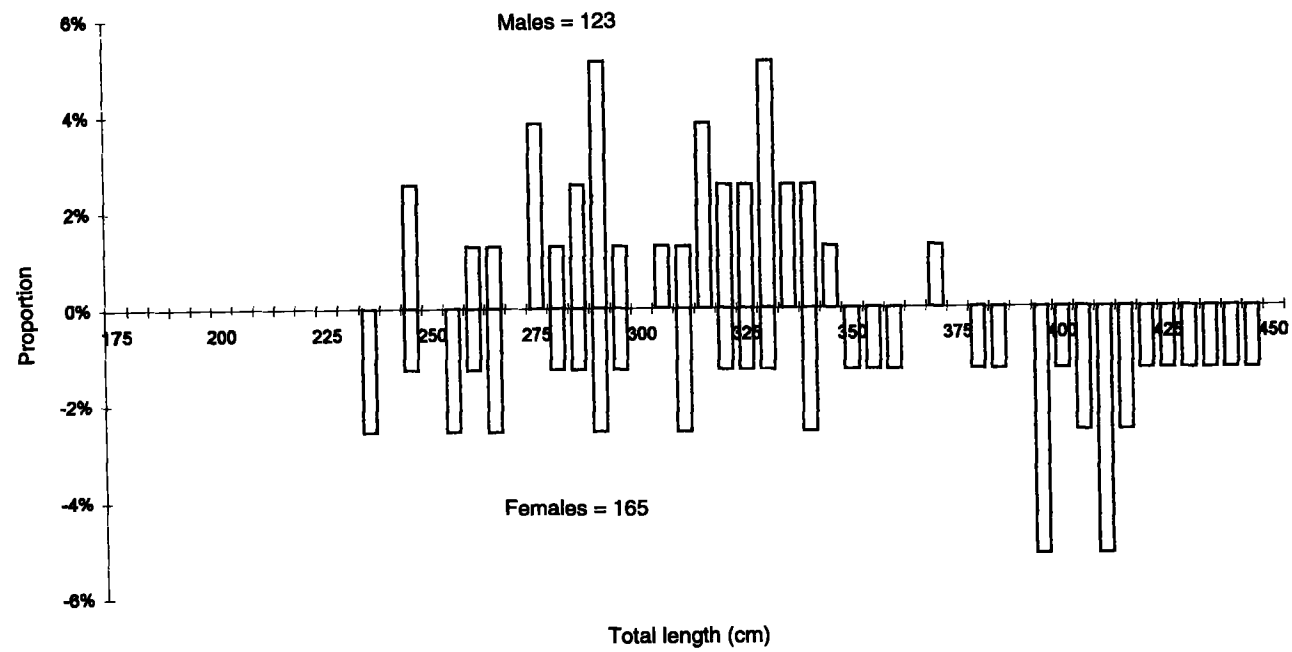


**Figure 9**

Total length frequency distribution of the bigeye thresher shark by sex from the gillnet landings from all the sectors from July 1991 to July 1992.

compared with swordfish, were similar to proportions calculated by Garcés and Rey (1983) for the northeastern Atlantic and Mediterranean Sea but were greater than the estimates of Rey and Alot (1984) for the western Mediterranean Sea and those of Mejuto[2] for the northeastern Atlantic just immediately north of the study area. Monthly variation in the longline catch rate in this study was different from that found off the northwestern Spanish coast by Mejuto and Garcés[1] and Mejuto[2], although it coincides with the increased trend observed during the last few months of the year. Monthly catch rate variation did not agree with results obtained on the other side of the Atlantic Ocean off the northwestern Cuban coast (Guitart, 1975). Shortfin mako shark and swordfish catch rates followed a similar decreasing trend from fall to March; in April the catch rate for shortfin mako sharks increased and that for swordfish dropped (Fig. 10), thus complementing each other.

Sex ratio (1 male:0.9 females) is different from that observed by Mejuto and Garcés[1] and Mejuto[2] in the northeastern Atlantic above 40°N, where males were more abundant (approx. 1 male:0.4 females). The increasing presence of males northwards (up to 1 male:0.6 females in sector 4) correlates with results observed by Mejuto and Garcés[1] and Mejuto[2] and may suggest sexual segregation to the north. For the same area of the present study, Muñoz-Chápuli (1984) observed a lower proportion of females (1 male:0.35 females) than we did, and although the sample size was small in that study ($n$=113), there was a similar trend in the increasing number of males northwards. The overall sex ratio observed in this study agrees with results presented by Moreno and Morón (1992b) from August 1983 to August 1985 for the same fleet operating in the same area. Mejuto[2] reported a trend of increase in percentage of males with increasing size (for size range 105–260 cm FL). This trend was not found in our study (Fig. 11).

The length-frequency distribution of the two fisheries was different from that found by Mejuto and Garcés[1] and Mejuto[2] for the area immediately north. It was also different from the one presented for the east coast of the United States (Pratt and Casey, 1983). In our study, modal values were always lower than those presented by the above-mentioned authors. Following the age structure proposed by Pratt and Casey (1983), we estimated that most of the fish in this study belonged to age class 1 and 2 for both sexes. The largest size of females corresponded to age class 5 (sector 3), and the largest size of males to

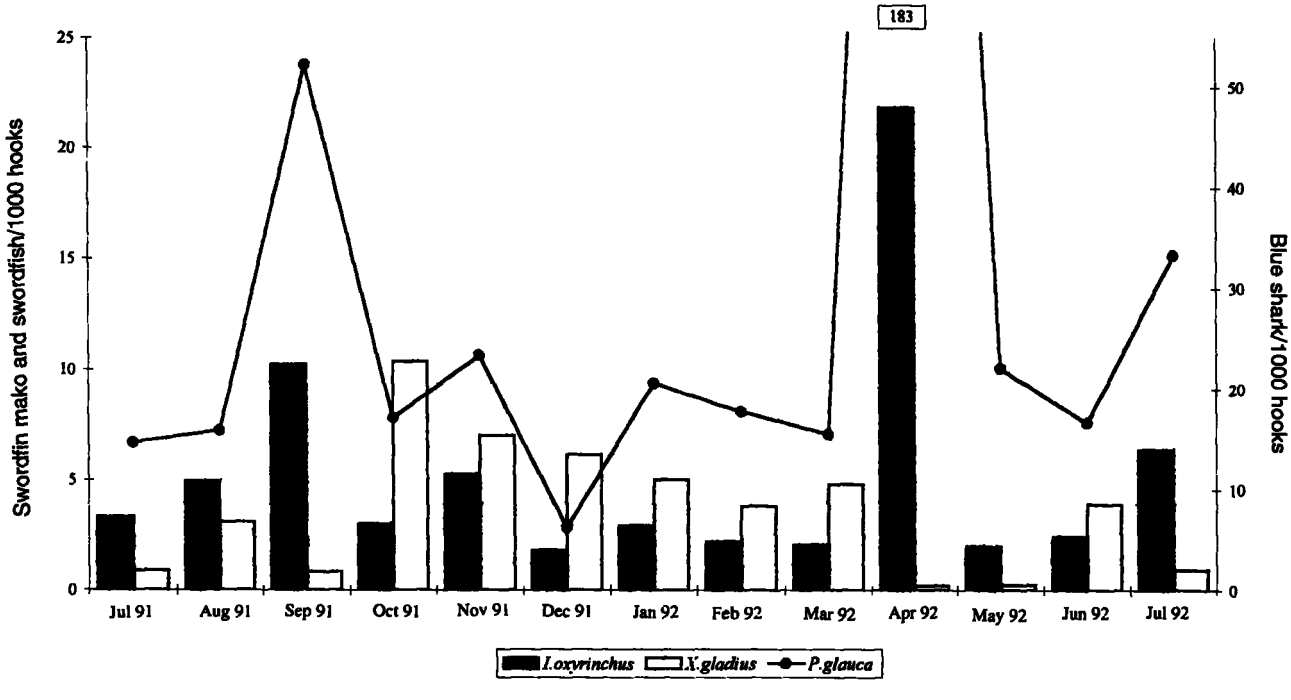


**Figure 10**

Comparison of longline catch rates (number of fish/1000 hooks) of the shortfin mako shark and swordfish (left "y" axis) and of the blue shark (right "y" axis) by month.

age class 4 (sector 4). The minimum size corresponded to age class 0 in all sectors.

Maximum size decreased during March–May (see Fig. 6, A and B). In June and July there was a possible entry of newborn fish (65 cm) with the same birth size as that suggested by Compagno (1984). Mean size decreased during October–November. These changes in size distribution suggest a movement of the largest and mean-size shortfin mako sharks out of the study area. For an area just north of the one studied, Mejuto[2] showed a large increase in catch rate during the last quarter of the year, which could be attributed partially to entry of fish coming from our study area.

## Blue shark

The abundance of this species in longline fishing has been mentioned by several authors (Bigelow and Schroeder, 1948; De Metrio et al., 1984; Muñoz-Chápuli, 1985; Stevens, 1990; Mejuto[2]). In the present study the proportion of blue sharks, compared with swordfish, was half that estimated by Garcés and Rey (1983) for an area that included our five sectors. However, it was greater than the proportion obtained by Rey and Alot (1984) in the western Mediterranean and very similar to that calculated by Mejuto[2] for the area just north of our study region. The number of fish landed increased northward and was greater than the number estimated by De Metrio et al. (1984) in the Mediterranean.

The temporal distribution of fish was also different for the Mediterranean (De Metrio et al., 1984) and for the northeastern Atlantic (Mejuto[2]). As in the case of shortfin mako sharks, the highest catch rates correlated with reductions in swordfish catch rates, i.e. April and September (Fig. 10).

The overall sex ratio (1 male:0.71 females) was inverse to that found by Rey and Alot (1984) in the Mediterranean. The latitudinal distribution of sexes was inverse to that estimated by Stevens (1990) off southwest Great Britain and Portugal and to that presented by Nakano et al. (1985) in a similar latitude in the central north Pacific.

Using Pratt (1979) and Cailliet et al's. (1983) age estimate, we found that frequency distribution of fish by size of landings in sector 1 showed that mature males were more abundant, whereas in the other sectors a greater proportion of immature fish were observed.

## Bigeye thresher shark

The relatively frequent occurrence of this species noted by Muñoz-Chápuli (1985) contrasted with the low numbers observed in our study, with the low

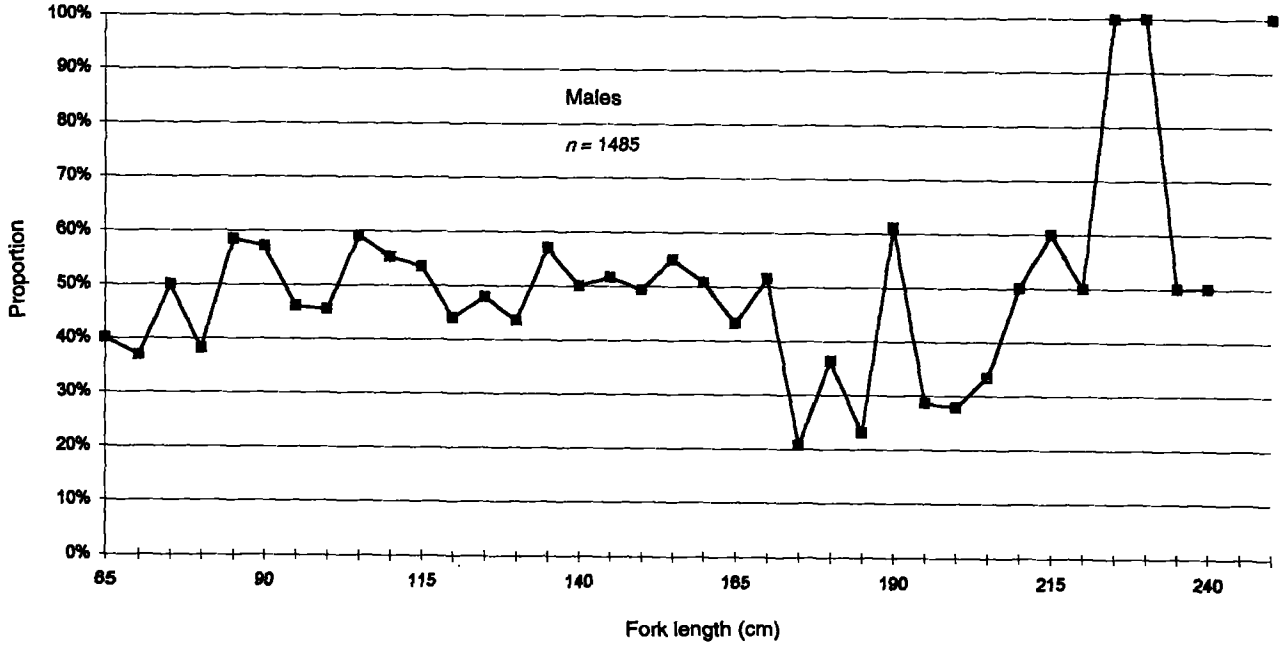


**Figure 11**

Proportion of male shortfin mako sharks in landings by size group (grouped by 5 cm FL).

numbers noted by Moreno and Morón (1992a) in the same area, and with the low numbers noted by Stillwell and Casey (1976) in the northwestern Atlantic. The sexual segregation hypothesized by Muñoz-Chápuli (1984) in this area, i.e. males distributed northward and females southward, was opposite that of our findings. Moreno and Morón (1992a) mentioned that most fish caught during the fall were pregnant females, whereas in this study mostly mature males from the longline fishery and mostly females from the gillnet fishery were recorded during the same period.

Most males in all sectors were adults (>276 cm TL, Moreno and Morón, 1992a). Most females would be have been considered mature in every sector according to Gubanov's (1979) first maturity size (>310 cm TL), but only in sector 5 according to Moreno and Morón's (1992a) criteria (340 cm TL). The largest fish was recorded in sector 5, a 432-cm-TL female, in September 1991, which, nevertheless, did not exceed the maximum for the species (460 cm TL, Nakamura, 1935).

Size distributions by month showed a greater proportion of immature males during the July–September period, whereas mature fish predominated the rest of the year. During January–June and October–December most females were around maturity size limit (300 cm TL, Gubanov, 1979).

Most births occur during fall and winter according to Moreno and Morón (1992a), and as these authors have suggested, sector 5 could be a breeding area. A pregnant female was recorded in September 1991, in sector 5, carrying only one pup. However, no newborn fish were recorded, according to birth sizes reported by Bigelow and Schroeder (1948), Bass et al. (1975), Gruber and Compagno (1981), and Moreno and Morón (1992a).

### Common thresher shark

The scarcity of this species in the present study disagrees with observations of Muñoz-Chápuli (1985). The relative abundance of common thresher sharks found in sector 5 was similar to that presented by Moreno et al. (1989) for the same area. The maximum number during spring agreed with the number observed in California (Cailliet and Bedford, 1983) but did not coincide with the peak reported by Moreno et al. (1989) during fall in this area.

The sex ratio for this species in the area studied (1 male:2 females) differed greatly from estimates by Holts (1988) on the west coast of the United States (1 male:1 female). Moreno et al. (1989) noted the absence of males in May, which suggests sexual segregation during the reproduction period. A mature male was recorded in May at 330 cm TL, which represents the lower limit of maturity for males according to Cailliet et al. (1983).

Only one female was recorded below size of first maturity (260 cm TL, established by Gubanov, 1972; Cailliet and Bedford, 1983; Cailliet et al., 1983). Moreno et al. (1989) pointed out the probable existence of a breeding area close to the Strait of Gibraltar during spring time. The record of a 425-cm-TL pregnant female, with four full-term pups in May, supports this theory.

### Scalloped hammerhead shark

According to sex and length data obtained from sectors 1, 3, and 5, the overall sex ratio (1 male:0.83 females) differed from the ratio observed by Muñoz-Chápuli (1984) in the same area (1 male:6 females).

If we follow Compagno's (1984) first maturity size criteria (256 cm TL for males, 304 cm TL for females), only 6% of males and 4% of females landed would be considered mature in our study area. Muñoz-Chápuli (1984) observed many pregnant females in the area throughout the year, but the lowest size recorded in our study (114 cm TL) was much greater than birth size (50–60 cm TL, Compagno, 1984). Moreover, the lack of mature females contradicts the assessment that the study area is a breeding area, as suggested by Muñoz-Chápuli (1985).

## Conclusions

Sharks, because of their low reproduction rate and late sexual maturity, are extremely sensitive to fishing pressure (Holden, 1973, 1974, 1977). The vulnerability of shark populations as bycatch of some tuna and tunalike fishing is comparable to that of marine mammals (Burke and Francis, 1990). In recent years several cases of overexploitation in shark fisheries (Cailliet and Bedford, 1983; Holts, 1988; Vas, 1990; Hanan et al., 1993) and the effect of other fishing activities (recreational fisheries, the routine procedure of discarding sharks after removal of fins) on shark populations (Casey and Hoey, 1985; Stevens, 1992) has been described.

A lack of fishery statistics about sharks is commonplace all around the world. Du Buit (1989) commented on the complete absence of knowledge about most biological factors influencing shark populations off the coast of France and on the difficulty in sampling most of these migratory species.

Our study shows the importance of shark landings in the Atlantic swordfish longline fishery and points out the large number of immature fish involved.

Shortfin mako may be the shark species most affected by current fishing procedure despite the fact that the most common species caught is blue shark. As Casey and Kohler (1992) suggested with reference to the shortfin mako shark population in western north Atlantic, this species has a continuous distribution throughout the central and northeastern Atlantic Ocean, preferentially in the high production area of Saharian Bank (sector 3).

As it has been shown in this study, sharks greatly affect and are greatly affected by swordfish fishing. Therefore, the management of this fishing industry should be reoriented to multispecies models in which the effect of bycatch and the economic implications of bycatch should be included in the management models for a proper approach to the present situation in the industry.

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# Monophyly and intrarelationships of the family Pleuronectidae (Pleuronectiformes), with a revised classification

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**Abstract.**—A cladistic analysis of interrelationships for 53 (of 59) pleuronectid species was performed by using 106 morphological and osteological characters. The analysis resulted in 128 equally parsimonious cladograms (heuristic search, 403 steps, consistency index=0.33, retention index=0.79). A 50% majority-rule consensus cladogram indicated that only five of 47 resolved nodes were observed in less than 100% of the cladograms. These five nodes are restricted to interrelationships within one subfamily. The Pleuronectidae is monophyletic according to ten synapomorphies. In addition, five subfamilies were defined: Hippoglossinae, Eopsettinae, Lyopsettinae, Hippoglossoidinae, and Pleuronectinae. The largest subfamily, the Pleuronectinae, was further subdivided into four tribes: Psettichthyini, Isopsettini, Microstomini, and Pleuronectini. The interrelationships established within Pleuronectidae provide a strong foundation for a simplified yet phylogenetically informative taxonomic nomenclature at the genus-group level. The following genera are reclassified: *Atherestes* and *Reinhardtius* to *Reinhardtius*; *Errex*, *Glyptocephalus*, and *Tanakius* to *Glyptocephalus*; *Embassichthys*, and *Microstomus* to *Microstomus*; *Hypsopsetta* and *Pleuronichthys* to *Pleuronichthys*; and *Kareius* and *Platichthy* to *Platichthys*. To preserve the monophyletic status of *Eopsetta*, *E. exilis* was reassigned to the genus *Lyopsetta* (Lyopsettinae). The genus *Pleuronectes* (as defined by Sakamoto in 1984) was found to be polyphyletic. Monophyly of this genus is established by revising it to include only five species; *Pleuronectes glacialis*, *P. pinnifasciatus*, *P. platessus*, *P. putnami*, and *P. quadrituberculatus*. Other species, formerly placed in *Pleuronectes*, are now reclassified to *Isopsetta*, *Limanda*, *Parophrys*, *Psettichthys*, and *Pseudopleuronectes*. The monophyletic status of *Limanda* (six species) is uncertain because of unresolved relationships between these species and other taxa in the tribe Pleuronectini.

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The Pleuronectidae (*sensu* Chapleau and Keast, 1988) contains 59 nominal species of right-eyed flatfishes distributed in marine waters of the Northern Hemisphere. As presently composed, this family excludes the subfamilies Poecilopsettinae, Samarinae, Rhombosoleinae, and Paralichthodinae, formerly included in Norman (1934). It contains many commercial species that have long been harvested in coastal seas off Europe, North America, and Asia. Species such as the Petrale sole (*Eopsetta jordani*), Pacific halibut (*Hippoglossus stenolepis*), American plaice (*Hippoglossoides platessoides*), and Dover sole (*Microstomus pacificus*), to name but a few, are valued for their large size and excellent meat (Hart, 1973; Scott and Scott, 1988). In total, there are over 36 species of flatfish monitored by the Food and Agricultural Organization of the United Nations, with a total annual catch of 256,353 metric tons (t) in 1995 (FAO, 1997). Nearly one half (18) of these species are classified within the Pleuronectidae (FAO, 1997). Total annual commerical harvest of Pacific halibut (*Hippoglossus stenolepis*) was estimated at 25,968 t in 1995 a decrease from 40,584 t in 1985 (FAO, 1997). A similar situation has been observed in witch flounder (*Glyptocephalus cynoglossus*) for which 19,537 t was harvested in 1995 as compared to 30,074 t in 1985 (FAO, 1997). With few exceptions, this decline in annual harvest is observed for most pleuronectid species (FAO, 1997). The commercial popularity of pleuronectid species, coupled with a need to manage these renewable resources, strongly emphasizes the necessity for a better understanding of relationships within this group, as well as an informative taxonomic nomenclature that will provide a framework for management policy. Variation in life history traits are observed at many phylogenetic levels. Populations of the American plaice (*Hippoglossoides platessoides*) are recorded to have age of maturity ranging from 3 to 15 years (Roff, 1981). Within the family, variation in maximum length ranges from 220 mm in *Dexistes rikuzenius* (Sakamoto, 1984b) to over 2500 mm in *Hippoglossus stenolepis* (Hart, 1973). An hypothesis of species interrelationships can be used as a framework to assess phylogenetic constraint on life history traits versus a species' ability to respond to changing environmental conditions (Brooks and McLennan, 1991). An assessment of

phylogenetic constraint versus environmental influence could provide a more informed understanding of observed changes in life history traits.

The objectives of this study are to clarify the monophyletic status of the Pleuronectidae, to offer an hypothesis of relationships within the group based on adult morphology, and to establish a phylogenetically informative nomenclature. To attain these objectives, a reassessment of morphological evidence in the literature and new morphological characters were compiled in a matrix analyzed within a cladistic framework. A new classification based on the phylogenetic information is offered.

## Historical classification and diagnosis of Pleuronectidae

The Pleuronectidae was regarded by early ichthyologists to represent all known flatfishes (Norman, 1934). For example, Cuvier (1816) subdivided the Pleuronectidae into five subfamilies: Hippoglossinae, Pleuronectinae, Platessinae, Soleinae, and Cynoglossinae; as did Jordan and Goss (1889) who also added the subfamilies: Samarinae and Oncopterinae. Changes to the early classification in flatfish focused on revisions that accommodated new species without a complete revision of the entire scheme. Newly discovered species, thought to represent distinct morphological groups, were classified into new subgroups; but original species, and those that did not have special morphologies, were to remain within the Pleuronectidae. Thus, the Pleuronectidae became a "garbage" group.

Jordan and Evermann (1898) raised flatfishes to the suborder Heterosomata with two distinct families: Pleuronectidae and Soleidae. The Pleuronectidae, with three subfamilies: Hippoglossinae, Pleuronectinae, and Psettinae, were characterized by "a more or less distinct preopercular margin (i.e. not hidden by the skin and scales of the head); eyes large, well separated; mouth moderate or large; teeth present" (Jordan and Evermann, 1898). The Soleidae were subdivided into two subfamilies, Soleinae and Cynoglossinae, and were characterized by "an adnate preopercular margin, hidden by the skin and scales of the head; eyes small, situated close together; mouth very small, much twisted; teeth rudimentary or wanting" (Jordan and Evermann, 1898).

Regan (1910) proposed a new classification that raised the Heterosomata to the level of order with two suborders: Psettodoidea and Pleuronectoidea. Within the second suborder, the Pleuronectidae now contained three subfamilies; Pleuronectinae, Samarinae, and Rhombosoleinae. The family was characterized by "having eyes on right side of head, nerve of left eye always dorsal, olfactory lamellae slightly raised, parallel without central rachis and eggs without oil globules" (Regan, 1910).

This classification was adopted by Norman (1934), who incorporated minor revisions from Regan (1920, 1929) and Jordan (1923). The Pleuronectidae, at this point containing five subfamilies (Pleuronectinae, Samarinae, Rhombosoleinae, Poecilopsettinae, and Paralichthodinae) were characterized by Norman (1934) as "having eyes on the right side; optic chiasma monomorphic, the nerve of the left eye always dorsal; dorsal fin extending forward on the head at least to above the eye; all the fin-rays articulated; pelvic of from 3 to 13 rays; mouth usually terminal, with the lower jaw more or less prominent; maxillary without a supplemental bone; palatines toothless; lower edge of urohyal deeply emarginate, so that the bone appears forked; preoperculum with free margin; nasal organ of blind side usually near edge of head, but sometimes nearly opposite that of ocular side; vertebrae never fewer than 30; on each side a single post-cleithrum; ribs present; egg without an oil-globule in the yolk." Later classifications removed the genera *Brachypleura* and *Lepidoblepharon* from the Pleuronectidae and placed them in the Citharidae (Hubbs, 1945) but essentially agreed with the classification proposed by Norman (1934).

Nelson (1984) listed the Poecilopsettinae, Rhombosoleinae, Samarinae, and Pleuronectinae as subfamilies in Pleuronectidae on the basis of two characteristics: eyes almost always dextral and no oil globule in yolk of egg. Sakamoto's (1984a) hypothesis of pleuronectid intrarelationships assumed that the Pleuronectinae, Samarinae, Rhombosoleinae, Poecilopsettinae, and Paralichthodinae were monophyletic because both eyes were on right side of the body, optic nerve of the left eye was always dorsal, preopercle had a free margin and fin rays were without spines. Hensley and Ahlstrom (1984), in a review of flatfish classification, indicated that the evidence for monophyly of Pleuronectidae (*sensu* Norman, 1934) was not convincing. The diagnostic characters reviewed in Norman (1934) were found to be plesiomorphic for the order or had distributions that were unknown for many pleuronectiform taxa (Hensley and Ahlstrom, 1984).

Subsequent cladistic analysis of major taxa within the order supported the hypothesis that the Pleuronectidae was not monophyletic and suggested that the subfamilies Pleuronectinae, Samarinae, Rhombosoleinae, and Poecilopsettinae should be elevated to the family level (Chapleau and Keast, 1988; Chapleau, 1993). This new interpretation of taxonomic ranks in right-eyed flounders was recognized

by Hensley (1993) and in part by Nelson (1994). Species in Samarinae of Nelson (1984) and *Paralichthodes algoensis* were classified to Samaridae (Nelson, 1994). The subfamilies Pleuronectinae, Rhombosoleinae, and Poecilopsettinae, remained in Pleuronectidae. Nelson (1994) argued that without a comprehensive understanding of monophyly for some major groups it is difficult to provide an accurate revision of the nomenclature within the order. Although this approach is an obvious attempt to minimize unnecessary changes to the nomenclature, it does not reflect the understanding that only species in Pleuronectinae possess a bothoid caudal-fin complex that clearly distinguishes these 59 north temperate species as being closely related to Bothidae, Paralichthyidae, Scophthalmidae, and *Brachypleura* (Hensley and Ahlstrom, 1984; Chapleau, 1993). The Poecilopsettinae, Rhombosoleinae, and Samaridae do not have this caudal-fin complex and are phylogenetically related to Achiridae, Soleidae, and Cynoglossidae (Chapleau, 1993). Given that Pleuronectinae is the nominotypical subgroup, it is correct to reclassify it to Pleuronectidae. For the species of Poecilopsettinae, and Rhombosoleinae, it is a misrepresentation of the present cladistic framework to classify them in Pleuronectidae when the order level phylogeny (Chapleau, 1993) suggests a relationship with Samaridae, Achiridae, Soleidae, and Cynoglossidae. Therefore, only the 59 nominal species of Pleuronectinae are considered in this study and classified as Pleuronectidae (*sensu* Chapleau and Keast, 1988).

Two tribes in Pleuronectinae (*sensu* Norman, 1934), the Hippoglossini and Pleuronectini, were classified on the basis of jaw morphological characters (Nelson, 1984). The Hippoglossini identified by "mouth large and symmetrical; maxillae extending to or behind pupil of eyes; teeth well developed on both sides of jaws, contained ten genera (e.g. *Atherestes, Eopsetta, Hippoglossoides, Hippoglossus, Lyopsetta, Psettichthys*, and *Reinhardtius*)." The Pleuronectini were identified by "mouth small and asymmetrical; maxillae usually not extending to pupil of eye; teeth chiefly on blind-side of jaw and contained 16 genera (e.g. *Embassichthys, Glyptocephalus, Hypsopsetta, Isopsetta, Lepidopsetta, Limanda, Liopsetta, Microstomus, Parophrys, Platichthys, Pleuronectes, Pleuronichthys*, and *Pseudopleuronectes*)" (Nelson, 1984). Although this classification was effective in identifying two morphological types within Pleuronectinae (*sensu* Norman, 1934), it was not based on an examination of interrelationships within the group, nor did it accurately identify natural groups. The characters defining Hippoglossini were all plesiomorphic for the order and the characters defining the Pleuronectini were also observed in many lineages closely related to the Pleuronectinae (*sensu* Norman, 1934).

The 59 nominal species in this group had been historically classified in as many as 28 genera, many of which were monotypic. This nomenclature was established prior to any understanding of phylogeny and reflected the morphological diversity within Pleuronectidae. The number of genera used in identifying pleuronectid species would presumably be used to accommodate new species as they were discovered. However, the alpha taxonomy for this group has been well established, and only one new species of Pleuronectidae, *Microstomus shuntovi* Borets, 1983, has been described in the latter half of this century. Intuitively, a simplified and more informative nomenclature with fewer monotypic genera would seem appropriate.

There are few published studies that have dealt with phylogenetic relationships among pleuronectid taxa. The most extensive examination of interrelationships and classification within Pleuronectidae (*sensu* Norman, 1934) was established by Sakamoto (1984a). This phenetic hypothesis of interrelationships among 77 species was not aimed at defining relationships within an evolutionary framework; nor was it aimed at determining taxonomic structure on the basis of natural groups. Sakamoto (1984a) concluded his study with a reclassification of several genera within the Pleuronectinae (*sensu* Norman, 1934). In revision, the species of *Eopsetta* and *Lyopsetta*, as well as *Cleisthenes* and *Hippoglossoides*, were reclassified into *Eopsetta* and *Hippoglossoides*. *Glyptocephalus zachirus* became *Errex zachirus*. All species of *Isopsetta, Parophrys, Lepidopsetta, Limanda, Pseudopleuronectes, Pleuronectes*, and *Liopsetta* were regrouped under the genus *Pleuronectes*. Finally *Paralichthodes algoensis*, previously classified in its own subfamily, Paralichthodinae (Nelson, 1994), was placed within the Pleuronectinae on the basis of overall similarity and the presence of the first neural arch, a symplesiomorphy for the order (Hensley and Ahlstrom, 1984).

Chiu (1990) examined the relationships among four glyptocephaline species (formerly classified in *Glyptocephalus* and *Tanakius*). The results of this phenetic analysis of body shape were similar to Sakamoto's (1984a) results with respect to the relationships between *Glyptocephalus cynoglossus, G. stelleri*, and *G. zachirus*. The limited scope of this analysis does not provide adequate information to infer relationships beyond these three species.

Sakamoto's (1984a) nomenclatural changes and classification were adopted in the American Fisheries Society checklist for flatfish species (Robins et

al., 1991). The adoption of this reclassification was a recognition of the first and only study that attempted to define intrarelationships in the Pleuronectidae (*sensu* Norman, 1934). This new classification has not been widely accepted (Wheeler, 1992; Rass, 1996). It is argued here that because the Pleuronectidae used by Sakamoto (1984a) was determined to be polyphyletic (Chapleau, 1993) and given the phenetic nature of the analysis, it is unlikely that the nomenclatorial revisions summarized in that work represent natural groups.

The dubious nature of this most recent reclassification (i.e. Sakamoto, 1984a), the uninformative nature of the previous classification (i.e. Norman, 1934), and the commercial importance of this group require that a more comprehensive examination of pleuronectid intrarelationships be based on natural groups. A cladistic analysis based on structural variation within Pleuronectidae, in contrast with characters observed in closely related outgroups will establish an hypothesis of genealogical descent (Wiley, 1981).

## Outgroup hypothesis for Pleuronectidae

Relationships within the order reveal that only the Pleuronectidae (*sensu* Chapleau and Keast, 1988) have a caudal skeletal complex, synapomorphic with taxa belonging to the Paralichthyidae, Scophthalmidae, *Brachypleura*, and Bothidae (Chapleau, 1993). These taxa have been identified as the bothoid lineage within Pleuronectiformes (Hensley and Ahlstrom, 1984). This lineage is supported in one of 18 equally parsimonious trees observed in a cladistic analysis for the order (Chapleau, 1993). The other taxa formerly in Pleuronectidae (Samaridae, Rhombosoleidae, and Poecilopsettidae) were placed in a clade that included the soles Achiridae, Soleidae, and Cynoglossidae (Chapleau, 1993). *Paralichthodes algoensis* was not included in Chapleau's (1993) cladistic revision but has recently been determined to be the sister lineage to these other taxa formerly in Pleuronectidae (Cooper and Chapleau, 1998). Consequently, the most likely outgroup for Pleuronectidae would be represented by species within the bothoid lineage.

There is a wide range of morphological types within the bothoid lineage for which the intrarelationships are not resolved (Chapleau, 1993). In the absence of synapomorphies to determine the sister relationship of Pleuronectidae with other bothoid taxa, a comparison of jaw structure can be used to determine the most likely candidates. It is assumed that the outgroup for the Pleuronectidae should have large symmetrical jaws and pointed teeth. Within Pleuronectiformes, the evolutionary trend for jaw structure and feeding strategy may be considered unidirectional. Symmetry of jaw and dentition found in piscivorous flatfishes, like Psettodidae and Citharidae (de Groot, 1971), is considered to be the plesiomorphic condition. The osteological characters observed in these two taxa are most similar to the generalized acanthopterygian structure (Yazdani, 1969). Taxa with symmetrical jaw structure are hypothesized to have given rise to groups with more specialized dentition types and jaw asymmetry, as observed in the Achiridae, Soleidae, and Cynoglossidae (Yazdani, 1969; Chapleau, 1993), but the reverse situation is not indicated in any study of relationships.

Within subgroups of Pleuronectiformes, the same evolutionary trend is assumed to occur. Left-eyed flounders within the bothoid lineage have large, nearly symmetrical jaws for piscivory, or a more specialized, asymmetrical jaw structure that accommodates capture of benthic prey (Yazdani, 1969; de Groot, 1971). Likewise, the Pleuronectidae contains both piscivores with nearly symmetrical jaws, *Hippoglossus stenolepis* and *Reinhardtius hippoglossoides,* as well as more specialized predators with asymmetrical jaws, such as *Glyptocephalus stelleri* (de Groot, 1971). Assuming that evolutionary trends in pleuronectid jaw structure are consistent with trends observed in the order, the ancestral pleuronectid would have near symmetrically developed jaws. The bothoid family, Paralichthyidae, appears to be one of the most plesiomorphic groups of left-eyed flounders and is chosen as the outgroup for the Pleuronectidae. In addition, *Psettodes* and *Lepidoblepharon* are also chosen as secondary outgroups. These assumptions are only valid if the Pleuronectidae is monophyletic. If Pleuronectidae is not monophyletic, then multiple outgroup taxa with either symmetrical or asymmetrical jaw structures may account for the variation observed within the Pleuronectidae.

## Materials and methods

Fifty-three of 59 pleuronectid species were examined. Five outgroup taxa, chosen from the families Psettodidae (*Psettodes* sp.), Citharidae (*Lepidoblepharon ophthalmolepis*), and Paralichthyidae (*Citharichthys arenaceus*, *Paralichthys lethostigmus*, and *P. squamilentus*) were also examined. The following cleared and stained specimens were dissected and examined for osteological characters. Nomenclature follows the conclusions of this analysis with the previous classification of Sakamoto (1984a) indicated in

parentheses. Changes in species-group nomenclature recognize gender status of the genus (Eschmeyer, 1990) as specified by the International Code of Zoological Nomenclature, article 31 (Ride et al., 1985). Institutional abbreviations follow Leviton et al. (1985). Length, in mm, is standard length (Hubbs and Lagler, 1970). Radiographs for all specimens, as well as radiographs of the specimens listed in Leipertz (1987), were also examined.

**Psettodidae** *Psettodes* sp. Bennet; ANSP 145394, 65 mm. **Citharidae** *Lepidoblepharon ophthalmolepis* Weber; AMS I.20118-012, 122 mm. **Paralichthyidae** *Citharichthys arenaceus* Evermann and Marsh; USNM 00203510, 69 mm. *Paralichthys lethostigmus* (Jordan and Gilbert); ANSP 143209, 90 mm. *Paralichthys squamilentus* Jordan and Gilbert; ANSP 150694, 50 mm. **Pleuronectidae** *Acanthopsetta nadeshnyi* Schmidt; USNM 77122, 89 mm. UW 22792, 224 mm; *Cleisthenes* (=*Hippoglossoides*) *herzensteini* (Schmidt); USNM 051441, 85, 89 mm. *Cleisthenes* (=*Hippoglossoides*) *pinetorum* Jordan and Starks; UMMZ 159566, 76 mm. *Clidoderma asperrimum* (Temminck and Schlegel); not examined. *Dexistes rikuzenius* Jordan and Starks; UMMZ 159662, 122 mm. *Eopsetta grigorjewi* (Herzenstein); UMMZ 159590, 66, 88 mm. *Eopsetta jordani* (Lockington). NMC 81-1015, 68 mm. *Glyptocephalus cynoglossus* (Linnæus); NMC 77-1087, 89, 114 mm. *Glyptocephalus kitaharai* (Jordan and Starks); UMMZ 141741, 139 mm. *Glyptocephalus stelleri* (Schmidt); UMMZ 159566, 125 mm. *Glyptocephalus* (=*Errex*) *zachirus* Lockington; NMC 65-0211, 95 mm; NMC 81-1027, 133 mm. *Hippoglossoides dubius* Schmidt; not examined. *Hippoglossoides elassodon* Jordan and Gilbert; NMC 61-0117, 71, 82 mm. *Hippoglossoides platessoides* (Fabricius); NMC 80-0601, 31, 61, 63, 77 mm; ROM 504CS, 73 mm; ROM 786CS, 70, 83, 87, 90 mm. *Hippoglossoides robustus* Gill and Townsend; ANSP 105133, 110 mm. *Hippoglossus hippoglossus* (Linnæus); ARC 8808487, 148 mm. *Hippoglossus stenolepis* Schmidt; NMC 61-0072, 100 mm; UW 22743, 54, 56, 67 mm. *Isopsetta* (=*Pleuronectes*) *isolepis* (Lockington); UMMZ 63214, 119, 123 mm. *Lepidopsetta* (=*Pleuronectes*) *bilineata* (Ayres); NMC 61-0050, 51 mm; NMC 81-1027, 56 mm. *Lepidopsetta* (=*Pleuronectes*) *mochigarei* Snyder; UMMZ 159575, 113 mm. *Limanda* (=*Pleuronectes*) *aspera* (Pallas); NMC 66-0016, 156 mm. *Limanda* (=*Pleuronectes*) *ferruginea* (Storer); NMC 80-0217, 102, 107 mm; ROM 560CS, 49 mm. *Limanda* (=*Pleuronectes*) *limanda* (Linnæus); MNHN 1959-560, 119 mm; *Limanda* (=*Pleuronectes*) *proboscidea* Gilbert. USNM 268496, 141 mm; UW 22742, 98, 115 mm. *Limanda* (=*Pleuronectes*) *punctatissima* (Steindachner); HUMZ 93958, 135 mm. *Limanda* (=*Pleuronectes*) *sakhalinensis* Hubbs; HUMZ 60455, 138 mm. *Lyopsetta* (=*Eopsetta*) *exilis* (Jordan and Gilbert); NMC 60-0501, 111, 115 mm. *Microstomus achne* (Jordan and Starks); UMMZ 159434, 145 mm. *Microstomus* (=*Embassichthys*) *bathybius* (Gilbert); UW 22791, 167 mm. *Microstomus kitt* (Walbaum); FMNH 35527, 135 mm. *Microstomus pacificus* (Lockington). NMC 81-1027, 109 mm. *Microstomus shuntovi* Borets; not examined. *Parophrys* (=*Pleuronectes*) *vetula* Girard; FMNH 97128, 97, 128 mm; NMC 81-1121, 39, 61, 66, 68 mm; NMC 85-0025, 53, 67 mm. *Platichthys* (=*Kareius*) *bicoloratus* (Basilewsky); UMMZ 159667, 117 mm. *Platichthys flesus* (Linnæus); ANSP 93141, 78 mm. *Platichthys stellatus* (Pallas); NMC 61-0044, 53, 85, 90 mm. *Pleuronectes glacialis* Pallas; NMC 62-0352, 72 mm. *Pleuronectes pinnifasciatus* (Kner) Steindachner and Kner. HUMZ 75681, 150 mm. *Pleuronectes platessus* (Linnæus); ANSP 93145, 66, 88 mm. *Pleuronectes putnami* (Gill); ROM 23214, 28 mm, ROM 556CS, 104, 110 mm. *Pleuronectes quadrituberculatus* Bean; USNM 064042, 85 mm. *Pleuronichthys coenosus* Girard; not examined. *Pleuronichthys cornutus* (Temminck and Schlegel); UMMZ 159618, 91 mm. *Pleuronichthys decurrens* Jordan and Gilbert; CAS 23703, 58 mm. *Pleuronichthys* (=*Hypsopsetta*) *guttulatus* Girard; NMC 74-0242, 64 mm. *Pleuronichthys ocellatus* Starks and Thompson; CAS 82189, 105 mm. *Pleuronichthys ritteri* Starks and Morris; CAS 11403, 46 mm. *Pleuronichthys verticalis* Jordan and Gilbert; CAS 34728, 83 mm. *Psettichthys melanostictus* Girard; NMC 62-2158, 58, 63 mm. *Pseudopleuronectes* (=*Pleuronectes*) *americanus* (Walbaum); ANSP 105133, 43, 66 mm; NMC 82-0016, 61, 73 mm; ROM 670CS, 27, 35, 46, 49, 54, 60 mm. *Pseudopleuronectes* (=*Pleuronectes*) *herzensteini* (Jordan and Snyder); UMMZ 159631, 88 mm. *Pseudopleuronectes* (=*Pleuronectes*) *obscurus* (Herzenstein); not examined. *Pseudopleuronectes* (=*Pleuronectes*) *schrenki* (Schmidt); HUMZ 75697, 123 mm. *Pseudopleuronectes* (=*Pleuronectes*) *yokohamae* (Günther); UMMZ 159548, 58, 83 mm; UMMZ 220249, 74 mm; USNM 056359 86 mm. *Reinhardtius* (=*Atheresthes*) *evermanni* (Jordan and Starks); not examined. *Reinhardtius hippoglossoides* (Walbaum); NMC 64-0756, 103, 119 mm. *Reinhardtius* (=*Atheresthes*) *stomias* (Jordan and Gilbert); NMC 65-0262, 97 mm; NMC 66-0022, 39 mm; NMC 80-0073, 80, 117 mm; NMC 80-1024, 119 mm. *Verasper moseri* [Jordan and Gilbert] Jordan and Evermann; USNM 056385, 78 mm. *Verasper variegatus* (Temminck and Schlegel); USNM 056375, 91 mm.

All characters used in the study are described in the Appendix. This list also includes the number of steps and character consistency index (cci) for each character in the analysis. The character matrix

(Table 1), illustrating the distribution of 106 characters for 58 taxa, combines information from the literature (Norman, 1934; Batts, 1964; Amaoka, 1969; Ahlstrom et al., 1984; Hensley and Ahlstrom, 1984; Sakamoto, 1984a) as well as 67 new morphological features observed through examination of cleared and stained material, whole preserved specimens, and radiographs. Morphological states obtained from the literature are indicated by the citation immediately following the italic character description (Appendix). Morphological states based on meristic counts represented the modal value of the sample population. Characters at each node of the cladogram are described and numbered in order of presentation in the text.

Given the unresolved nature of the interrelationships for Pleuronectidae and other bothoid taxa within the order (Chapleau, 1993), the establishment of character polarity by outgroup comparison, as outlined by Watrous and Wheeler (1981) and Maddison et al. (1984), was not possible. Character polarity was determined through a direct examination of states observed in outgroup taxa (Table 1). For each character, the majority state observed in the three bothoid taxa *Citharichthys arenaceus*, *Paralichthys lethostigmus*, and *P. squamilentus* was assumed to represent the plesiomorphic condition. This decision was only overruled if there was heterogeneity in the distribution of states within these three taxa and if both secondary outgroup taxa *Lepidoblepharon ophthalmolepis* and *Psettodes* sp. possessed the alternative state. One exception to this rule is stated in character 82 (Appendix). Character states hypothesized as plesiomorphic for the family are coded as zero (0).

### Heuristic search methods

The matrix was analyzed with all combinations of heuristic search parameters available in PAUP 3.1.1.[1] An exhaustive search of the most parsimonious tree with this many taxa (53) would have required the analysis of an estimated $2.84 \times 10^{82}$ bifurcating trees (Felsenstein, 1978) and is not possible within the current standard of computational time. For these same reasons, a branch and bound search technique proved inadequate to resolve relationships for more than 25 taxa (Forey et al., 1992). A two-step procedure (a sequential addition of taxa to produce a cladogram that minimizes homoplasy followed by the subsequent branch-swapping of this addition tree to search for more parsimonious cladograms) was used to search for the most parsimonious result. The random addition sequence in combination with all of the branch-swapping algorithms was a nonrigorous means of assessing the efficiency of the heuristic methods (Forey et al., 1992). If 50 random replicates give the same set of tree topologies, then it is likely that the maximally parsimonious trees have been found. However, if after 100 replicates shorter cladograms are still being found, then it is likely that more trees remain (Forey et al., 1992).

To minimize confounding effects of local minima, the "keep" option was used on successive searches to allow swapping on nonminimal trees (Forey et. al., 1992). Both the "MULPARS" and "swap on all trees" options were employed during each heuristic search to minimize the effect of plateau (Forey et. al., 1992). All searches assumed that the ingroup was monophyletic, and all uninformative characters were ignored. Character optimization was set for accelerated transformation (ACCTRAN). The five outgroup taxa were not included in the analysis. Instead, ancestral states for all characters were set as zero according to established character polarity to represent a hypothetical outgroup. All most parsimonious trees were saved from each search and combined (without duplication) to establish a 50% majority-rule consensus of the equally parsimonious results. Character analysis, character consistency index (cci), tree statistics, and tree presentations were generated with MacClade version 3.04 (Maddison and Maddison, 1992).

## Results and discussion

### Phylogenetic analysis

The heuristic searches found multiple trees of equal length (Table 2). The most parsimonious trees were found to be 403 steps from a minimum of 131 steps, with a consistency index (ci) of 0.33, excluding uninformative characters, and a retention index (ri) of 0.79. Additional rounds of heuristic search allowed swapping on nonminimal trees up to 410 steps but did not resolve cladograms shorter than 403 steps. The "simple" and "closest" addition sequences were biased by taxa with large numbers of unknown character states. Criteria for establishing the initial tree and the addition of taxa are strongly influenced by unknown character states in these two algorithms. As a result, *Reinhardtius evermanni*, *Clidoderma asperrimum*, *Hippoglossoides dubius*, *Microstomus shuntovi*, *Pleuronichthys coenosus*, and *Pseudopleuronectes obscurus* were not included in the heuristic searches. The "as is" and "simple" addition se-

[1] Swofford, D. L. 1991. PAUP Version 3.1.1. Unpublished software documentation.

**Table 1**

Matrix of 106 morphological characters for 5 outgroup taxa, representing the Psettodidae, Citharidae, and Paralichthyidae and 53 ingroup
Blanks represent the hypothesized ancestral state (state 0). Question marks (?) indicate an unknown state. Character states deemed not

| Character number | 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 |
|---|---|
| Psettodidae | |
| *Psettodes* sp. | ? 1 1 na 1 na na na 1 |
| Citharidae | |
| *Lepidoblepharon ophthalmolepis* | 1 na 1 1 na na na 1 1 1 |
| Paralichthyidae | |
| *Citharichthys arenaceus* | 1 1 2 1 1 1 1 2 1 1 1 |
| *Paralichthys lethostigmus* | 1 1 1 1 1 1 |
| *P. squamilentus* | 1 1 1 1 |
| Pleuronectidae | |
| *Acanthopsetta nadeshnyi* | 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 2 1 1 1 2 1 1 1 1 1 |
| *Cleisthenes herzensteini* | 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 2 1 1 1 2 1 1 1 1 1 1 1 1 1 1 1 |
| *C. pinetorum* | 1 1 ? 1 1 1 1 1 1 1 1 ? 1 1 1 1 2 1 1 1 ? 1 1 ? ? ? 1 1 1 1 |
| *Dexistes rikuzenius* | 1 1 1 1 1 1 1 1 1 1 1 1 1 1 2 1 1 1 2 1 1 1 1 1 1 1 1 |
| *Eopsetta grigorjewi* | 1 1 1 1 1 1 1 1 1 1 1 1 |
| *E. jordani* | 1 1 1 1 1 1 1 1 1 1 ? 1 ? ? ? ? ? ? ? ? ? 1 1 ? ? ? 1 1 |
| *Glyptocephalus cynoglossus* | 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 2 1 1 1 1 1 1 1 1 |
| *G. kitaharai* | 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 |
| *G. stelleri* | 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 2 1 1 1 1 1 1 1 |
| *G. zachirus* | 1 1 1 1 1 1 1 1 1 1 1 1 1 2 1 1 2 1 1 1 1 1 1 1 1 |
| *Hippoglossoides elassodon* | 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 2 1 1 1 2 1 1 1 1 1 1 1 |
| *H. platessoides* | 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 2 1 1 1 2 1 1 1 1 1 1 |
| *H. robustus* | 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 2 1 1 1 2 1 1 1 1 1 1 |
| *Hippoglossus hippoglossus* | 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 |
| *H. stenolepis* | 1 1 1 1 1 1 1 1 1 1 1 1 1 2 1 1 1 1 1 1 1 |
| *Isopsetta isolepis* | 1 1 1 1 1 1 1 1 1 1 1 1 2 1 1 2 1 1 1 2 1 1 1 1 1 1 |
| *Lepidopsetta bilineata* | 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 2 1 1 1 ? 1 1 1 1 1 ? 1 |
| *L. mochigarei* | 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 2 1 1 1 2 1 1 1 1 1 1 1 |
| *Limanda aspera* | 1 1 1 1 1 1 1 1 1 1 1 1 2 1 1 2 1 1 1 2 1 1 1 1 1 1 1 2 |
| *L. ferruginea* | 1 1 1 1 1 1 1 1 1 1 1 2 1 1 2 1 1 1 2 1 1 1 1 1 1 2 |
| *L. limanda* | 1 1 1 1 1 1 1 1 1 1 1 1 1 1 2 1 1 1 2 1 1 1 1 1 1 1 2 |
| *L. proboscidea* | 1 1 1 1 1 1 1 1 1 1 1 2 1 1 2 1 1 1 2 1 1 1 1 1 1 2 |
| *L. punctatissima* | 1 1 1 1 1 1 1 1 1 1 2 1 1 2 1 1 1 1 1 1 1 1 1 1 2 |
| *L. sakhalinensis* | 1 1 1 1 1 1 1 1 1 1 1 2 1 1 2 1 1 1 2 1 1 1 1 1 1 2 |
| *Lyopsetta exillis* | 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 |
| *Microstomus achne* | 1 1 1 1 1 1 1 1 1 1 2 1 1 2 1 1 1 1 1 1 1 |
| *M. bathybius* | 1 1 1 1 1 1 1 1 ? 1 ? 2 1 1 1 2 1 1 2 1 1 1 1 ? 1 1 1 1 1 |
| *M. kitt* | 1 1 1 1 1 1 1 1 1 1 2 1 1 2 1 1 1 1 1 1 1 1 1 1 1 1 |
| *M. pacificus* | 1 1 1 1 1 1 1 1 1 1 2 1 1 2 1 1 1 1 1 1 1 1 1 1 1 1 1 |
| *Parophrys vetula* | 1 1 1 1 1 1 1 1 1 1 1 1 2 1 1 2 1 1 1 2 1 1 1 1 1 1 2 |
| *Platichthys bicoloratus* | 1 1 1 1 1 1 1 1 1 1 1 1 2 1 1 2 1 1 1 1 2 2 1 1 1 1 2 1 1 3 |
| *P. flesus* | 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 2 1 1 1 2 1 1 1 2 2 1 1 2 1 1 3 |
| *P. stellatus* | 1 1 1 1 1 1 1 1 1 1 1 2 1 1 2 1 1 1 2 1 2 2 1 1 1 2 1 1 3 |
| *Pleuronectes glacialis* | 1 1 1 1 1 1 1 1 1 1 1 1 2 1 2 2 1 1 1 2 1 1 1 2 1 1 3 |
| *P. pinnifasciatus* | 1 1 1 1 1 1 1 1 1 1 1 1 1 1 2 2 1 1 1 2 1 1 1 1 2 1 1 3 |
| *P. platessus* | 1 1 1 1 1 1 1 1 1 1 1 1 1 2 1 2 2 1 1 1 2 1 1 1 2 1 1 1 3 |
| *P. putnami* | 1 1 1 1 1 1 1 1 1 1 1 1 1 2 1 2 2 1 1 1 2 1 1 1 2 1 1 1 3 |
| *P. quadrituberculatus* | 1 1 1 1 1 1 1 1 1 1 1 1 1 1 ? 1 2 2 1 1 1 ? 1 1 ? ? ? ? 1 ? 1 1 2 ? 1 ? ? 1 1 2 |
| *Pleuronichthys cornutus* | 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 |
| *P. decurrens* | 1 1 1 1 1 1 1 1 1 1 2 1 1 1 1 1 1 1 1 1 1 1 1 1 1 |
| *P. guttulatus* | 1 1 1 1 1 1 1 1 1 ? 1 1 1 1 1 1 2 1 1 1 |
| *P. ocellatus* | 1 1 1 1 1 1 1 1 1 1 1 2 1 1 1 1 1 1 1 1 1 1 1 1 1 |
| *P. ritteri* | 1 1 1 1 1 1 1 1 1 1 2 1 1 1 1 1 1 1 1 1 1 1 1 1 |
| *P. verticalis* | 1 1 1 1 1 1 1 1 1 1 1 2 1 1 1 1 1 1 1 1 1 1 1 1 |
| *Psettichthys melanostictus* | 1 1 1 1 1 1 1 1 1 1 1 1 2 1 2 1 1 1 2 1 1 1 1 1 |
| *Pseudopleuronectes americanus* | 1 1 1 1 1 1 1 1 1 1 1 1 1 2 2 1 1 1 2 1 1 1 1 2 1 1 2 |
| *P. herzensteini* | 1 1 1 1 1 1 1 1 1 1 1 1 1 1 2 2 1 1 1 2 1 1 1 1 1 1 2 |
| *P. schrenki* | 1 1 1 1 1 1 1 1 1 1 1 1 1 2 1 2 2 1 1 1 2 1 1 1 1 2 1 1 2 |
| *P. yokohamae* | 1 1 1 1 1 1 1 1 1 1 1 1 1 1 2 2 1 1 1 2 1 1 1 1 2 1 1 2 |
| *Reinhardtius hippoglossoides* | 1 1 1 1 1 1 1 1 1 1 1 ? 2 1 1 2 1 1 1 1 1 1 |
| *R. stomias* | 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 |
| *Verasper moseri* | 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 2 1 1 1 1 1 1 |
| *V. variegatus* | 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 2 1 1 1 1 1 1 1 |

taxa representing the Pleuronectidae. Numbers in the matrix represent character state for each morphology as described in the Appendix. applicable due to extreme variation in morphology are coded "na."

| 50 | 51 | 52 | 53 | 54 | 56 | 57 | 58 | 59 | 60 | 61 | 62 | 63 | 64 | 65 | 66 | 67 | 68 | 69 | 70 | 71 | 72 | 73 | 74 | 75 | 76 | 77 | 78 | 79 | 80 | 81 | 82 | 83 | 84 | 85 | 86 | 87 | 88 | 89 | 90 | 91 | 92 | 93 | 94 | 95 | 96 | 97 | 98 | 99 | 100 | 101 | 102 | 103 | 104 | 105 | 106 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 2 | | na | 1 | | | | | | | | | | | | | 1 | | | | | | | | | | | | | 1 | | | | 2 | | 4 | | | | 1 | | ? | | | | | | | | | | | |
| | | | | na | | | | | | | 1 | | | | | | | | | 1 | | 1 | | | | | | | | | 1 | 1 | | | 2 | | 4 | 2 | | | 1 | | 1 | | | | | | | | | | | |
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| | | | | | 1 | | | | | 1 | 1 | | 1 | | | 1 | 1 | | | 2 | | 1 | | | | | 1 | | | | | | 1 | | | 1 | 4 | 2 | | | | 1 | 1 | | | | | | | | | | 1 | | |
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| | 2 | | | | 1 | 1 | | 1 | 1 | 1 | 1 | 1 | 1 | | | 1 | 1 | | 1 | 2 | | 1 | | | | | 1 | | | | | | 1 | | 2 | 1 | 3 | 2 | | | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | | | | | 1 | | |
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| | | | | | 1 | 1 | 1 | | | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | | | | | 1 | | | 1 | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | 1 | | |
| | | | 2 | | 1 | 1 | 1 | | | 1 | 1 | 1 | 1 | 1 | 1 | 1 | | 1 | 1 | 1 | | 1 | | 1 | | 1 | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | 1 | | |
| | 1 | | 2 | | 1 | 1 | 1 | | | 1 | 1 | 1 | 1 | 1 | 1 | 1 | | 1 | 1 | 1 | | 1 | | 1 | | 1 | | | | | | 1 | | | | | | | | | | | | | | | | | | | | | 1 | | |
| 1 | | | 2 | | 1 | 1 | | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | | | 1 | | | | | | 1 | | | | | | | | | | | | | | | | | | | | 1 | | | | |
| 1 | | 1 | 2 | | 1 | 1 | | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | | | 1 | 1 | | | | | 1 | | | | | | | | | | | | | | | | | | | | 1 | | | | |
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| 1 | | 1 | 2 | 1 | 1 | | | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | | | 1 | 1 | | | | | 1 | | | | | | | | | | | | | | | | | | | | 1 | | | | 1 |
| | | 1 | 2 | | 1 | 1 | | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | | | 1 | 1 | | | | | 1 | | | | | | | | | | | | | | | | | | | | 1 | | | | |
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| | 2 | | | | 1 | | | 1 | 1 | 1 | 1 | | | | 2 | 2 | | 1 | 3 | | 1 | | | | 1 | | | | 1 | | | 1 | | | 1 | 2 | 1 | | 1 | 1 | 1 | | | | | | | | | 1 | | | | |
| 1 | 2 | | | | 1 | | | 1 | ? | 1 | 1 | | | | 2 | 2 | | 1 | 2 | | | | | | 1 | | | ? | | | 1 | | | 1 | 2 | 2 | 1 | | | | | | ? | | | | | | 1 | | | | |
| | 2 | | | | 1 | | | 1 | 1 | 1 | 1 | | | | 2 | 2 | | 1 | 3 | | 1 | | | | 1 | | | | 1 | | | 1 | | | 1 | | 1 | | 1 | 1 | 1 | | | | | | | | | 1 | | | | |
| | | | | | 1 | | | 1 | 1 | 1 | 1 | | | | 2 | 2 | | 1 | 2 | | 1 | | 1 | | 1 | | | | 1 | | | 1 | | | 1 | 2 | | | 1 | 1 | 1 | | | | | | | | | 1 | | | | |
| | | 1 | 2 | | 1 | 1 | 1 | | | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 1 | 2 | | | | | 1 | | | | | | 1 | | | | | | | | | | | | | | | | | | | | 1 | | | | |
| | | 1 | 3 | | 1 | 1 | | | | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | | | 1 | 1 | | | | | 1 | | | | | | | | | | | | | | | | | | | | 1 | 1 | 1 | 1 | | 1 | 1 |
| | | 1 | 3 | | 1 | 1 | | | | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | | | 1 | 1 | | | | 1 | 1 | | | | | | | | | | | | | | | | | | | 1 | 1 | 1 | 1 | | 1 | 1 |
| | | 1 | 3 | | 1 | 1 | | | | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | | | 1 | 1 | | | | 1 | 1 | | | | | | | | | | | | | | | | | | | 1 | 1 | 1 | 1 | | 1 | 1 |
| | | | 3 | | 1 | 1 | | | | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | | 1 | 1 | | | | | 1 | | | | | | | | | | | | | | | | | | | 1 | | 1 | 1 | 1 | | 1 | |
| | | | 3 | | 1 | 1 | | | | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 1 | 2 | 2 | 2 | 1 | | | 1 | 1 | | | | | 1 | | | | | | | | | | | | | | | | | | | 1 | | 1 | 1 | 1 | | 1 | |
| 1 | | 1 | 1 | | 1 | 1 | | | | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 1 | 2 | 2 | 2 | 1 | | | 1 | 1 | | | | | 1 | | | | | 1 | | | | | | | | | | | | | 1 | | 1 | 2 | | | 1 | |
| | | | 3 | | 1 | 1 | | | | 1 | 1 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 2 | 2 | 2 | 1 | | | 1 | 1 | | | | 1 | 1 | | | | | | | | | | | | | | | | | | | 1 | | 1 | 1 | | | 1 | |
| | | | ? | | 1 | 1 | | | | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 1 | 2 | 1 | 1 | 2 | 1 | | | 1 | 1 | | | | | 1 | | | | | | | | | | | | | | | | | | | 1 | | 1 | 2 | | | 1 | |
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| 1 | 1 | | | 1 | 1 | | 1 | | | 1 | 1 | | | | 2 | 2 | | | | | | | | | 1 | | | 1 | 1 | 1 | 1 | | 1 | 1 | 1 | | | 2 | | | | | | | | | | | | | | | | 1 | | |
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| 1 | | | | 1 | 1 | | 1 | | | 1 | 1 | | | | 2 | 2 | | | | | | | | | 1 | | | 1 | 1 | | 1 | 1 | 1 | 1 | 1 | | | 2 | | | | | | | | | | | | | | | | 1 | | |
| 1 | | 1 | 1 | 1 | 1 | | 1 | | | 1 | 1 | | | | 2 | 2 | | | | | | | | | 1 | | | 1 | 1 | 1 | 1 | | | 1 | 1 | | | | | | | | | | | | | | | | | | | | 1 | | |
| | 1 | | 2 | | 1 | 1 | 1 | 1 | 1 | | | | | | | | | | | | | 1 | | | | 1 | | | | | | 1 | | | | | | | | | | | | | | | | | | | | 1 | | | | |
| 1 | 2 | 1 | 1 | | 1 | 1 | | | | 1 | 1 | 1 | 1 | | 2 | 2 | | 1 | 2 | 1 | 1 | 1 | | 1 | 1 | 1 | | | | | 1 | | | | | | | | | | | | | | | | | | | | 1 | 1 | 1 | | | 1 | |
| 1 | | 1 | 1 | | 1 | 1 | | | | 1 | 1 | 1 | 1 | | 2 | 2 | 1 | 1 | 2 | 1 | 1 | 1 | | | 1 | 1 | | | | | 1 | | | | | | | | | | | | | | | | | | | | 1 | | | | |
| 1 | | 1 | 1 | | 1 | 1 | | | | 1 | 1 | 1 | 1 | 1 | 2 | 2 | 1 | 1 | 2 | 1 | 1 | 1 | | | 1 | 1 | | | | | 1 | | | | | | | | | | | | | | | | | | | | 1 | | | | |
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**Table 2**

Heuristic search results for an analysis of 106 characters for 53 ingroup taxa.

| Addition sequence | Branch-swapping algorithm | Tree length (steps) | Number of trees found | Cumulative total of unique trees |
|---|---|---|---|---|
| as is | tbr | 403 | 112 | 112 |
| as is | spr | 403 | 80 | 112 |
| as is | nni[1] | 405 | 16 | 128 |
| closest | tbr | 403 | 16 | 128 |
| closest | spr | 403 | 16 | 128 |
| closest | nni | 403 | 16 | 128 |
| simple | tbr | 403 | 112 | 128 |
| simple | spr | 403 | 16 | 128 |
| simple | nni[1] | 409 | 48 | 128 |
| random[2] | tbr | 403 | 128 | 128 |
| random[2] | spr | 403 | 128 | 128 |
| random[2] | nni | 403 | 128 | 128 |

[1] Trees found by this method were not of minimum length and not added to the total number of trees observed.
[2] One hundred replicates for each random addition sequence.

quences using the "nearest neighbour interchange" branch-swapping were the only combinations that did not find trees with 403 steps (Table 2). The results with 100 "random" addition replicates were not different from those observed with the three other methods (Table 2). This nonrigorous test suggests that heuristic search combinations were effective in finding all of the most parsimonious cladograms.

A quantitative estimate of data decisiveness (Goloboff, 1991) is not possible for an analysis of 53 taxa which requires calculation of mean length for all possible cladograms. However, a generalized statement of data decisiveness suggests that data for this analysis are decisive. "Data are strongly decisive if one or more cladograms explaining them is very much shorter than others, and only weakly decisive if all possible cladograms are not very different for each other in length" (Forey et al., 1992). In total, only 128 unique cladograms trees were observed (Table 2), which represents a minute fraction of possible trees, and only a slightly larger fraction of those actually examined during the search. Assuming that all trees of 403 steps were found, there must be many trees that have more than 403 steps. Although the frequency distribution of trees with number of steps cannot be determined, it is assumed that the number of trees with more than 403 steps must increase dramatically given that the maximum number of steps is 1384.

The majority-rule consensus of these trees (Fig. 1) illustrates clades observed in 50% or more of the 128 results. Clades found in less than 100% of the trees are indicated in parentheses as the percent of trees observed at this node. Only 5 of 47 resolved nodes were observed in less than 100% of the trees and only 2 were observed in less than 75% of the trees. Examination of character distribution in the tree reveals the homoplastic nature of many characters used in the analysis. This is reflected by the low consistency index (ci=0.33) observed in the 128 most parsimonious cladograms (Rohlf, 1982).

Low consistency index is expected in studies of interrelationships for large numbers of taxa (Sanderson and Donoghue, 1989). The expected consistency index for a study of 53 taxa would be 0.14 with an equation of linear regression derived from 60 previous cladistic studies (Sanderson and Donoghue, 1989). This consistency index suggests that there is less homoplasy describing the interrelationships of the Pleuronectidae than in other studies of this size. The retention index (ri=0.79) indicates that homoplasy is occurring at terminal nodes and not internal nodes, which, in turn, suggests that relationships at the level of subfamily, tribe, and genera are not based purely on homoplastic morphologies (Forey et al., 1992) and that the strength of this analysis can be used to determine relationships at this level. The retention index also suggests that this analysis is not effective at determining relationships near terminal ends, such as interrelationships among species within a genus. Consequently, the character analysis is restricted to the level of subfamily and tribe, and intragenera analysis will be explored only for relationships well corroborated by uniquely derived character states.

## Monophyly of the Pleuronectidae

Ten synapomorphies define the Pleuronectidae. Distributions of these states were also surveyed in the literature for taxa within the bothoid lineage (Hensley and Ahlstrom, 1984) and basal lineages within Pleuronectiformes (Chapleau, 1993).

1 Ocular-side frontal articulated with mesethmoid. Outgroup taxa with ocular-side prefrontal separating frontal from mesethmoid. Distribution of this structure within other pleuronectiform taxa reveals that the frontal on the ocular side is not articulated with the mesethmoid in Psettodidae, Citharidae, Paralichthyidae, Taeniopsettinae, and some genera of Bothinae (*Arnoglossus, Psettina, Asterorhombus, Japonolaeops, Laeops, Komoharaia, Neolaeops,* and *Chascanopsetta)* and is observed to be in contact with the mesethmoid only in the Bothinae genera (*Parabothus,*

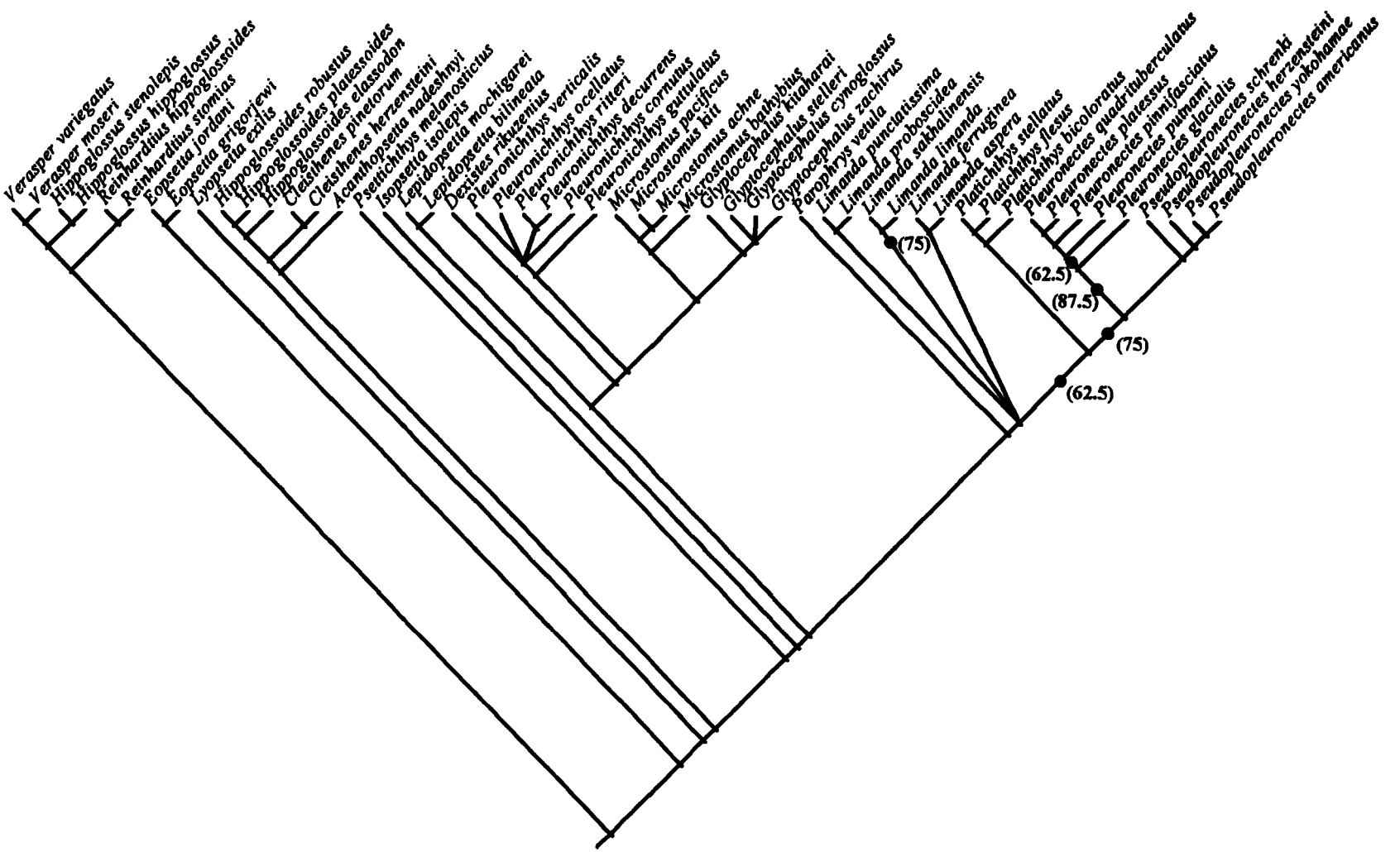


**Figure 1**

Fifty-percent majority-rule consensus tree from 128 equally parsimonious cladograms (404 steps, ci=0.33, ri=0.79) in an analysis of 106 characters, for 53 ingroup taxa and one hypothetical outgroup. All nodes were observed in 100% of the trees unless indicated in parentheses.

*Engyprosopon, Tosarhombus, Crossorhombus,* and *Bothus* [Amaoka, 1969]).

2 Ocular-side preorbital sensory canal absent, with exceptions only in *Reinhardtius hippoglossoides* and *Acanthopsetta nadeshnyi*. In the bothoid group, as well as in the Citharidae and Psettodidae, this sensory canal is present (Amaoka, 1969).

3 Ventral margin of metapterygoid flattened (Fig. 2, B–D), with exception in *Reinhardtius stomias*, which has a distinct curvature along the ventral margin of this bone. Outgroup taxa also possess this ventral curvature of the metapterygoid (Fig. 2A).

4 First and second basibranchials loosely joined by cartilage with exceptions observed in *Eopsetta grigorjewi, Isopsetta isolepis, Limanda ferruginea, L. punctatissima, Parophrys vetula, Psettichthys melanostictus,* and *Reinhardtius stomias* in which basibranchials are sutured. Outgroup taxa also have a suture between first and second basibranchials (Fig. 3A).

5 Second and third basibranchial loosely joined by cartilage (Fig. 3, B–D) with exceptions in *Limanda punctatissima* and *Psettichthys melanostictus*. Outgroup taxa have a suture between second and third basibranchials (Fig. 3A).

6 Posteriormost abdominal vertebrae lack haemapophysis (Fig. 4C), with exceptions in *Eopsetta grigorjewi, Microstomus achne, M. kitt, M. pacificus,* and *Reinhardtius stomias* in which haemapophysis are present (Fig. 4D). Outgroups have fused parapophysis forming a haemal arch on the posteriormost abdominal vertebrae (Fig. 4, A and B).

7 Accessory processes on caudal vertebrae absent (Fig. 5, B and C), with exceptions in *Hippoglossus hippoglossus, H. stenolepis, Microstomus bathybius, Pleuronichthys decurrens, P. guttulatus,* and *P. ritteri*. Outgroups have accessory processes on ventral surface of centrum for all caudal vertebrae (Fig. 5A).

8 Ocular-side infraorbital bones present with exception in *Microstomus bathybius*. Outgroup taxa, except *Psettodes*, do not have infraorbital bones on the ocular side. *Psettodes* has four infraorbital bones on the ocular side. Presence of infraorbital bones in Pleuronectidae, although not unique in comparison with all outgroup taxa, is likely a reversal in the bothoid lineage and synapomorphic for the family.

9 Oil globules in egg absent, with exceptions of one oil globule found in *Pleuronichthys cornutus, P. guttulatus,* and *P. ritteri* (Ahlstrom et al., 1984). Outgroups have at least one oil globule (Ahlstrom et al., 1984). Distribution of this character was not confirmed in the specimens used for this analysis; however the source for this information (Ahlstrom et al., 1984) confirms this distribution in 46 of the 59 pleuronectid species.

10 Olfactory laminae are parallel without a central rachis, with exception in *Reinhardtius evermanni* and *R. stomias*. As in the outgroup, species of *Reinhardtius* have laminae that radiate from a central rachis (Norman, 1934). Distribution of this structure was not confirmed in this analysis. Historically, this structure has been used to diagnose the Pleuronectinae (*sensu* Norman, 1934) and appears to be unique in flatfishes. There has not been any evidence to suggest that this occurs in any other flatfish species.

Exceptions in distribution of these ten synapomorphies do not have a common phylogenetic pattern and do not corroborate exclusion of any of the 53 species examined in this analysis. The exceptions suggest independent cases of reversed characters (reversals) for either the species or their immediate ancestors, and these will be discussed in the context of species interrelationships within the Pleuronectidae. It is noted that *Reinhardtius stomias* has four exceptions to the ten synapomorphies in Pleuronectidae. The most parsimonious explanation places this species in the Hippoglossinae on the basis of seven additional synapomorphies. Other characters (48, 77, 83, and 104) appear to be synapomorphies for the Pleuronectidae. However, distribution of these characters was examined in only the 53 ingroup taxa and in the five outgroup taxa used for this analysis. This limited survey is not sufficient to provide a full understanding of the distribution of these character states within the order. Therefore these character states are not presented as synapomorphies for the family and are only presented in a phylogenetic context within Pleuronectidae. Future analysis examining higher-level relationships within Pleuronectiformes should include these morphological characters.

## Intrarelationships of the Pleuronectidae

The phylogenetic analysis reveals various monophyletic lineages within the Pleuronectidae, four of which illustrate the interrelationships of five newly defined subfamilies: Hippoglossinae, Eopsettinae, Lyopsettinae, Hippoglossoidinae, and Pleuronectinae (Fig. 6). These subfamilies are separated by a gradation of characters (11 to 22) such that the first three, Hippoglossinae, Eopsettinae, and Lyopsettinae, contain species with a large proportion of plesiomorphic

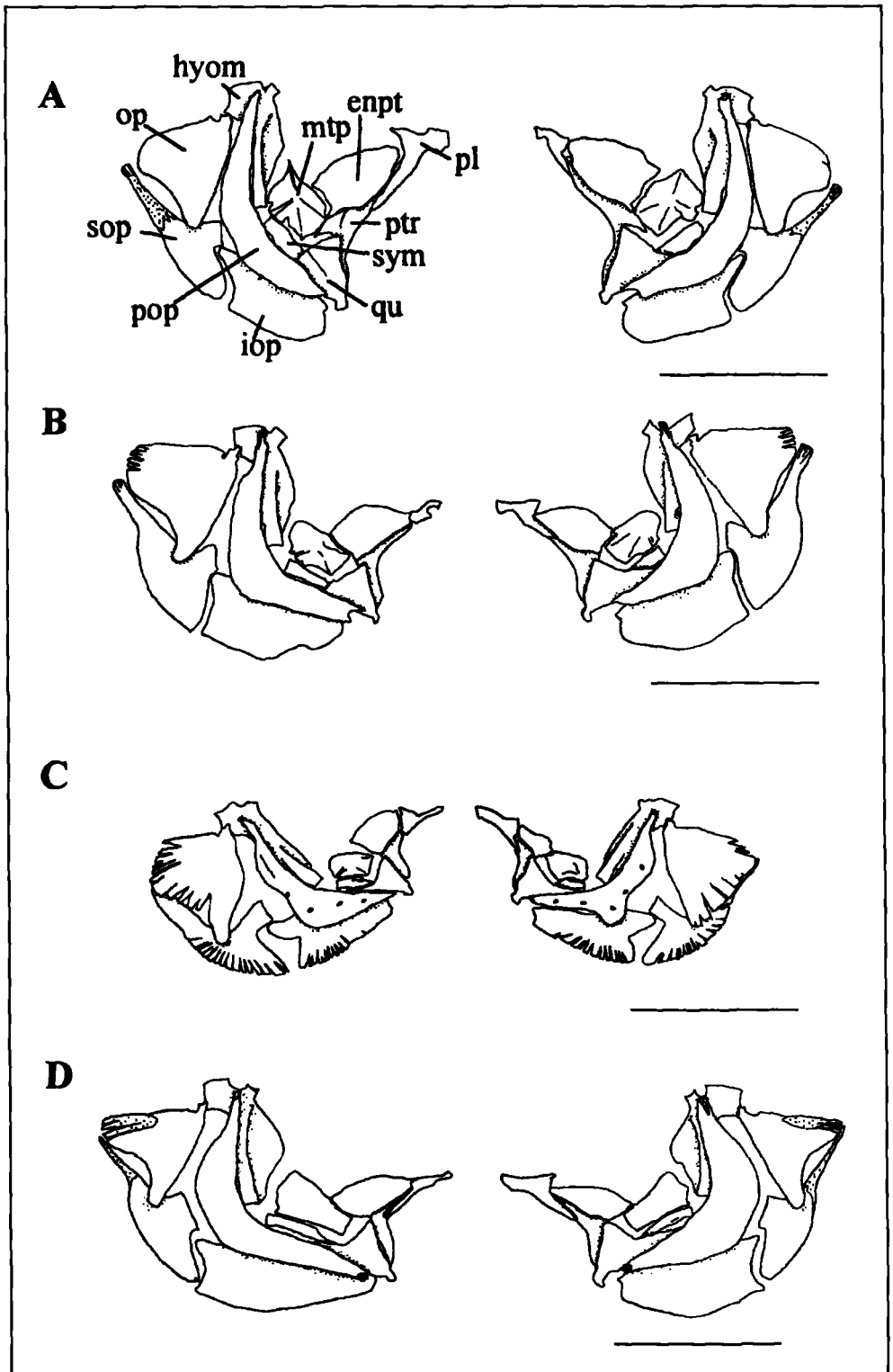


**Figure 2**

Lateral aspect of suspensorium. (Left) ocular side; (right) blind side. (**A**) *Paralichthys lethostigmus*, ANSP 143209; (**B**) *Verasper moseri*, USNM 056385; (**C**) *Microstomus pacificus*, NMC 81-1027; (**D**) *Limanda ferruginea*, NMC 80-0217. enpt = entopterygoid; hyom = hyomandibular; iop = interoperculum; mtp = metapterygoid; op = operculum; pl =palatine; pop = preoperculum; ptr = pterygoid; sop = subopercular; sym = symplectic; qu = quadrate. Scale bars are 10 mm.

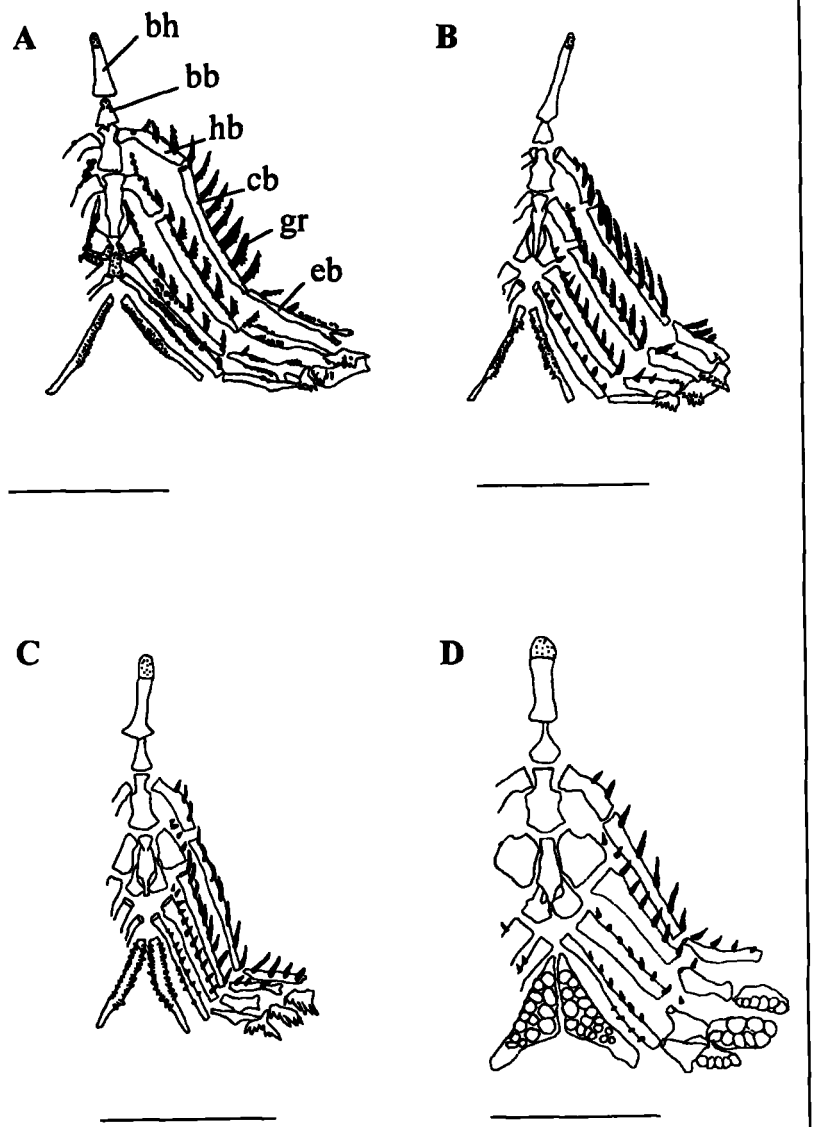


**Figure 3**

Dorsal aspect of branchial apparatus. (**A**) *Paralichthys lethostigmus*, ANSP 143209; (**B**) *Lyopsetta exilis*, NMC 60-0501; (**C**) *Limanda ferruginea*, NMC 80-0217; (**D**) *Pleuronectes putnami*, ROM 556. bb=basibranchial; bh = basihyal; cb = ceratobranchial; eb = epibranchial; gr = gill raker; hp = hypobranchial. The fourth basibranchial is cartilagenous and illustrated in only Fig. 3A. Scale bars are 10 mm.

character states. As a result, interrelationships within these groups are supported by few synapomorphies. Serving as successive outgroups (Stiassny and de Pinna, 1994), the position of these three subfamilies determines the polarity and relationships within the Hippoglossoidinae and the diversified Pleuronectinae.

The first lineage (I) distinguishes Hippoglossinae from all other pleuronectid taxa. The second lineage (II) contains all species classified in Eopsettinae, Lyopsettinae, Hippoglossoidinae, and Pleuronectinae. This second lineage is supported by two synapomorphies (Fig. 6): ocular-side pterosphenoid and prootic join to form the dorsal margin of anterior prootic foramen (11, Fig. 7, B and C); and first epibranchial not bifurcated at its distal end (12, Fig. 3, C and D).

Exceptions to the distribution of these two characters are observed in Pleuronectinae and *Verasper*

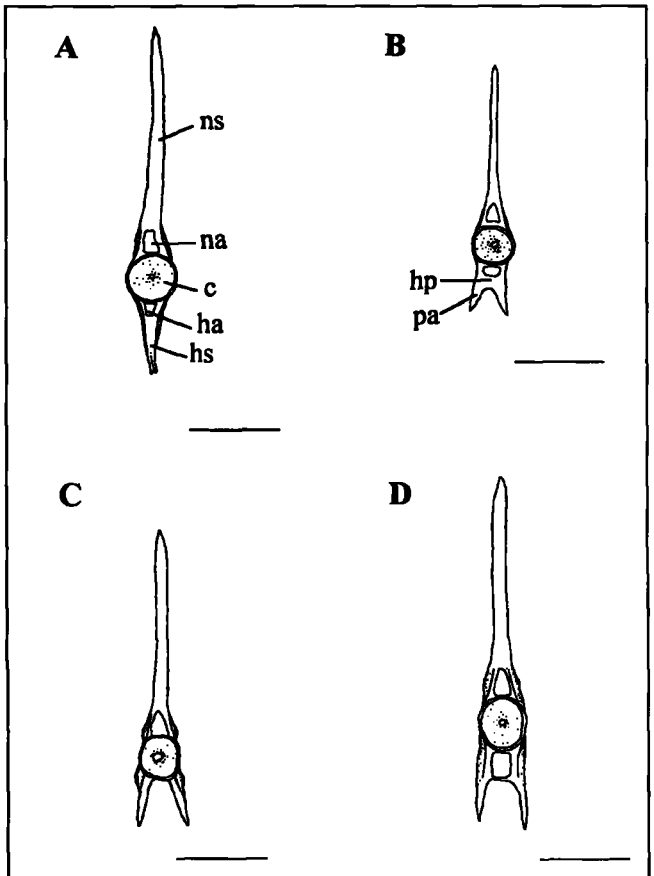


**Figure 4**

Cranial aspect of abdominal vertebrae. (**A**) *Lepidoblepharon ophthalmolepis*, AMS I.20118-012; (**B**) *Paralichthys lethostigmus*, ANSP 143209; (**C**) *Hippoglossoides robustus*, ANSP 105133; (**D**) *Microstomus kitt*, FMNH 355327. c = centrum; ha = haemal arch; hp = haemapophysis; hs = haemal spine; na = neural arch; ns = neural spine; pa = parapophysis. Scale bars are 5 mm.

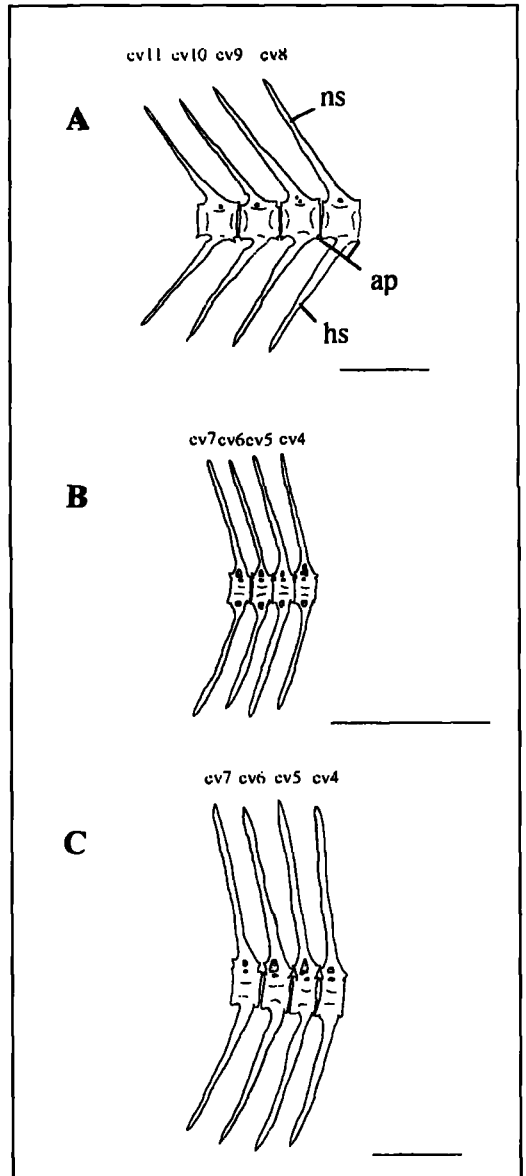


**Figure 5**

Lateral aspect of caudal vertebrae. (**A**) *Lepidoblepharon ophthalmolepis*, AMS I.20118-012; (**B**) *Pleuronectes platessus*, ANSP 93145; (**C**) *Parophrys vetula*, FMNH 97128. ap = accessory process; hs = haemal spine; ns = neural spine. Number represents position of vertebrae from cranial end. Scale bars are 5 mm.

(Hippoglossinae). The pterosphenoid and prootic do not unite to form the dorsal margin of the anterior prootic foramen (Fig. 7A) in the following pleuronectine species: *Glyptocephalus cynoglossus*, *G. stelleri*, *G. zachirus*, *Limanda ferruginea*, *L. proboscidea*, *L. punctatissima*, *Platichthys stellatus*, *Pleuronichthys guttulatus*, and *Pseudopleuronectes americanus*. *Verasper variegatus*, not classified in this second lineage, has the dorsal margin of this foramen formed by the pterosphenoid and prootic on both ocular and blind side. The first epibranchial is bifurcated in the pleuronectine species *Dexistes rikuzenius*, *Limanda aspera*, *L. limanda*, *L. sakhalinensis*, *Glyptocephalus*, *Microstomus*, and *Pleuronichthys*. Both species of *Verasper* were observed to have a bifurcated first epibranchial. The pattern of these exceptions is similar in these two characters, but the analysis did not indicate an alternative topology that would exclude any of the previously mentioned species, or include *Verasper* within the second lineage. The pattern does suggest that these exceptions are instances of reversal or convergence and may determine phylogeny within these other groups.

The third pleuronectid lineage (III) indicates a common ancestor for Lyopsettinae, Hippoglossoidinae,

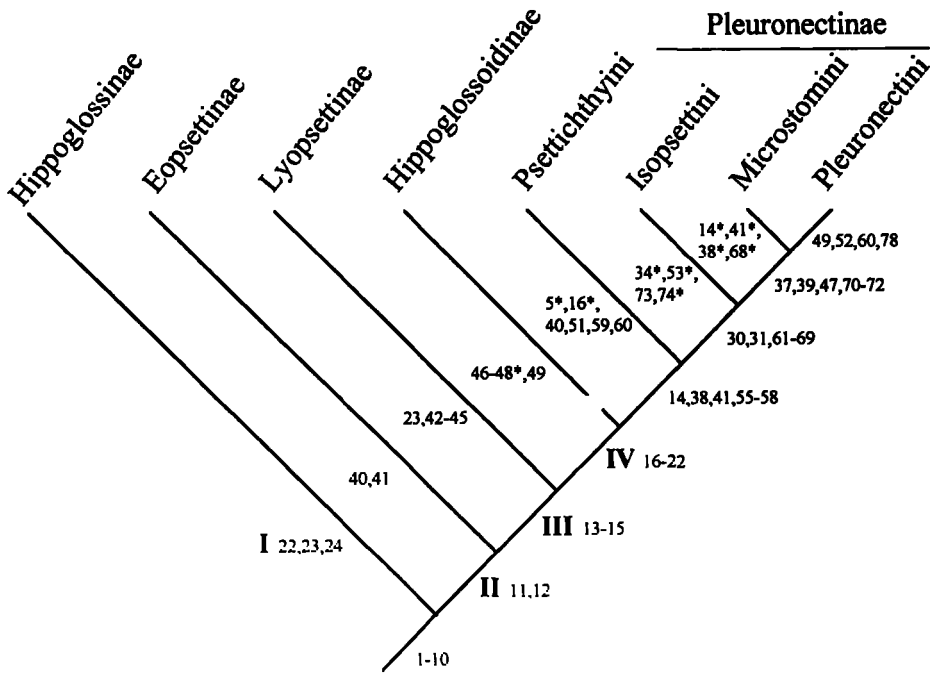


**Figure 6**

Intrarelationship for subfamilies and tribes in Pleuronectidae. Numbers correspond to characters in text. Asterisk represent character state reversal.

and Pleuronectinae. Three synapomorphies defining this lineage (Fig. 6) are spines absent on gill rakers (13, Fig. 3, C and D); anterior margin of upper orbit complete with an overlap between mesethmoid and prefrontal of the blind side (14, Fig. 8, C and D); and first anal pterygiophore broadly thickened (15).

Exceptions to the distribution in these synapomorphies are found in Pleuronectinae and Hippoglossinae. The anterior margin of the upper orbit is incomplete in *Microstomus achne, M. bathybius, M. kitt, M. pacificus, Pleuronectes pinnifasciatus, Pseudopleuronectes americanus, P. herzensteini*, and *P. yokohamae. Reinhardtius stomias,* which also has the derived state for this character, is excluded from this third lineage. The first anal pterygiophore is not thickened in *Microstomus achne, M. bathybius, M. kitt*, and *M. pacificus*, whereas in *Hippoglossus* and *Verasper* (Hippoglossinae) the first anal pterygiophore is broadly thickened.

The fourth lineage (IV) includes all species of Hippoglossoidinae and Pleuronectinae. The sister relationship between these two subfamilies is determined by seven synapomorphies (Fig. 6): dentition of uniform size (16, Fig. 9, B–D); interorbital process reduced or completely absent (17, Fig. 10, B, D, and E); hyomandibula broadened anteriorly (18, Fig. 2D); dentition on third epibranchial absent (19, Fig. 3, C and D); bony plates absent on branchial arches (20, Fig. 3, C and D); two rows of teeth present on fourth ceratobranchial (21, Fig. 3, C and D); and dorsoposterior margin of operculum fimbriated (22, Fig. 2, B–D).

Exceptions to these character distributions are found in only two species of *Hippoglossoides* and in Microstomini. *Hippoglossoides platessoides* and *H. robustus* have larger anterior teeth (16) that were historically termed as "canines" (Norman, 1934). *Glyptocephalus kitaharai, G. zachirus, Microstomus achne, M. kitt, M. pacificus*, and all species in *Pleuronichthys* have an interorbital process (17, Fig. 10C). The anterior margin of the hyomandibular (18) is not broadened in *Glyptocephalus* and *Microstomus* (Fig. 2C). Dentition on the third epibranchial and bony plates on branchial arches are observed in *Pleuronichthys guttulatus*. The number of rows of teeth on the fourth ceratobranchial are reduced to only one in *Glyptocephalus, Platichthys bicoloratus*, and *Pleuronichthys* and are absent in *Limanda punctatissima*. Fimbriation of the operculum (22) is also observed in Hippoglossinae (Fig. 2B) but is absent in the Eopsettinae and Lyopsettinae. This last exception suggests that fimbriation of the operculum may be synapomorphic for Pleuronectidae because only *Eopsetta grigorjewi, E. jordani*, and *Lyopsetta*

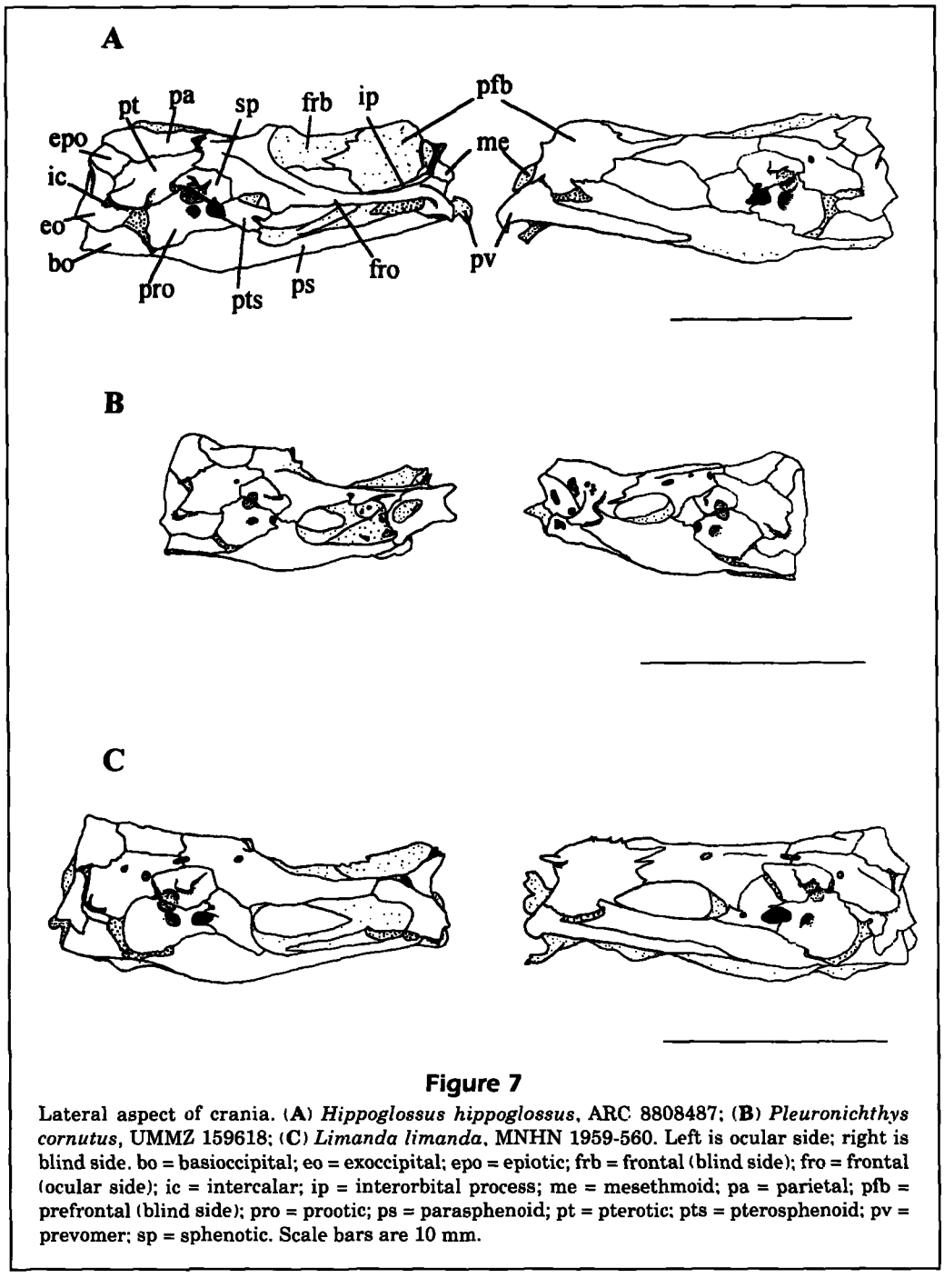


**Figure 7**

Lateral aspect of crania. (**A**) *Hippoglossus hippoglossus*, ARC 8808487; (**B**) *Pleuronichthys cornutus*, UMMZ 159618; (**C**) *Limanda limanda*, MNHN 1959-560. Left is ocular side; right is blind side. bo = basioccipital; eo = exoccipital; epo = epiotic; frb = frontal (blind side); fro = frontal (ocular side); ic = intercalar; ip = interorbital process; me = mesethmoid; pa = parietal; pfb = prefrontal (blind side); pro = prootic; ps = parasphenoid; pt = pterotic; pts = pterosphenoid; pv = prevomer; sp = sphenotic. Scale bars are 10 mm.

*exilis* do not show this condition. This alternative hypothesis would require three evolutionary steps, one more than is presently hypothesized. An equivocal alternative (two steps) would require a single reversal in character 22 to define a monophyletic group of *Eopsetta* and *Lyopsetta*. However, this topology was not observed in any of the 128 most parsimonious trees.

**Subfamily Hippoglossinae** The first pleuronectid lineage is classified as Hippoglossinae, with eight species (6 examined) in four genera: *Clidoderma* (*incertae sedis*), *Hippoglossus*, *Reinhardtius*, and *Verasper* (Fig. 11). This subfamily, as well as the intrarelationships of its species, were observed in all of the most parsimonious cladograms. The Hippoglossinae are hypothesized to be monophyletic ac-

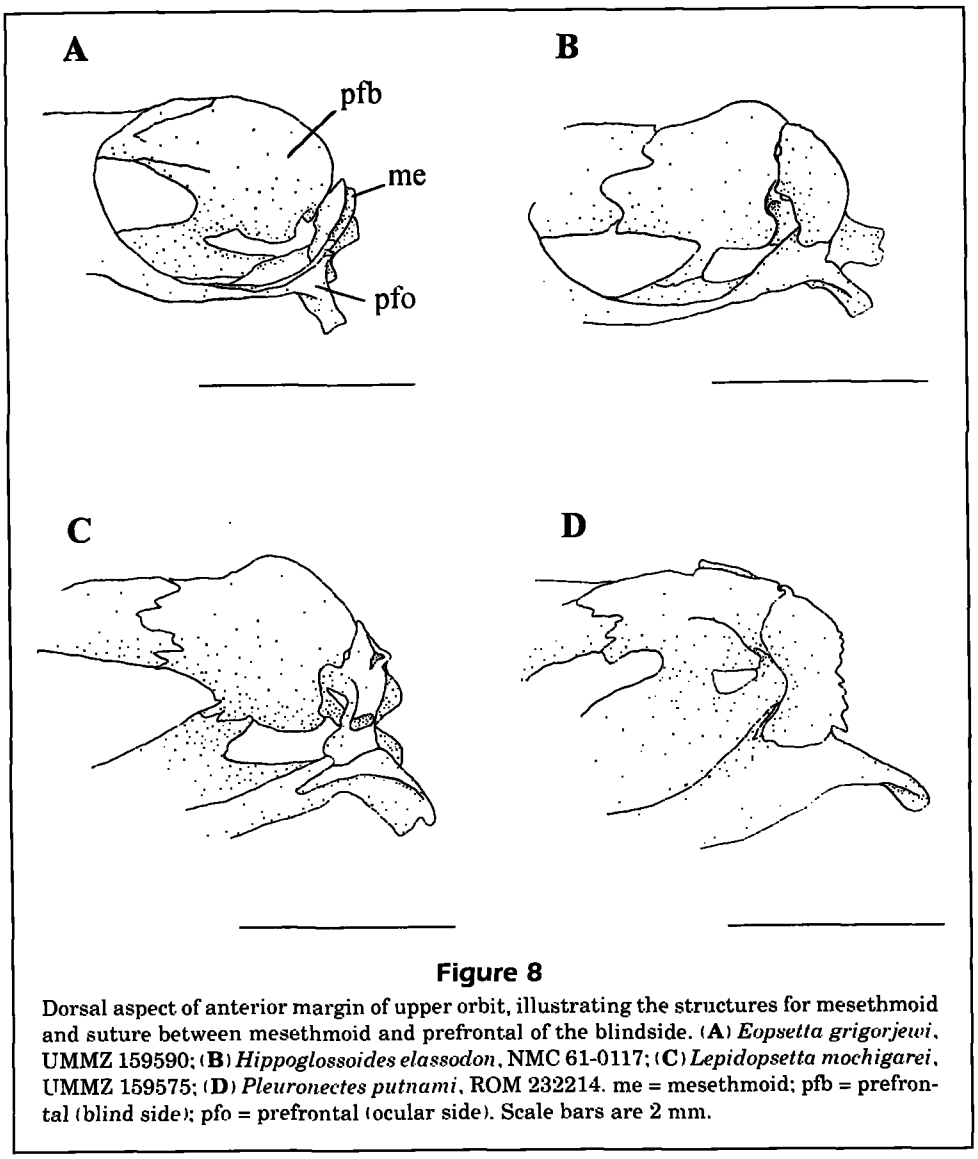


**Figure 8**

Dorsal aspect of anterior margin of upper orbit, illustrating the structures for mesethmoid and suture between mesethmoid and prefrontal of the blindside. (**A**) *Eopsetta grigorjewi*, UMMZ 159590; (**B**) *Hippoglossoides elassodon*, NMC 61-0117; (**C**) *Lepidopsetta mochigarei*, UMMZ 159575; (**D**) *Pleuronectes putnami*, ROM 232214. me = mesethmoid; pfb = prefrontal (blind side); pfo = prefrontal (ocular side). Scale bars are 2 mm.

cording to three synapomorphies (Fig. 6): increase in number of abdominal vertebrae to more than 12 (23); lunate-shaped caudal fin (24); and presence of fimbriation on dorsoposterior opercular margin (22, Fig. 2B). These characters are found to have a high degree of homoplasy within the Pleuronectidae. The fimbriation pattern of the opercular margin (22) appears in all other species of Pleuronectidae, except in *Eopsetta* and *Lyopsetta* that comprise the next two lineages. An increase in the number of abdominal vertebrae (23) is also observed in other subfamilies and the lunate-shaped caudal fin (24) is not observed in all members of this lineage; a reversal is hypothesized for *Verasper*. Monophyletic status of this clade is suspect. The low proportion of derived character states inherent for basal lineages provides little support for monophyly and intrarelationships for these taxa. Analysis of morphological characters that are homoplastic at the familial level, but not so at lower levels of universality, might clarify both the monophyletic status of this subfamily and its intrarelationships.

### Intrarelationships of Hippoglossinae

**Genus *Reinhardtius*** This genus contains three species: *R. hippoglossoides*, *R. evermanni* (not examined), and *R. stomias*, characterized by four synapomorphies (Fig. 11): gill rakers absent on fourth ceratobranchial (21); migrated eye is situated near dorsal midline of cranium, so that it is visible from blind side (25); more than 35 caudal vertebrae (26); and dentary foramen absent on blind side (27).

Homoplasy observed for these characters is observed in unrelated pleuronectid taxa and does not

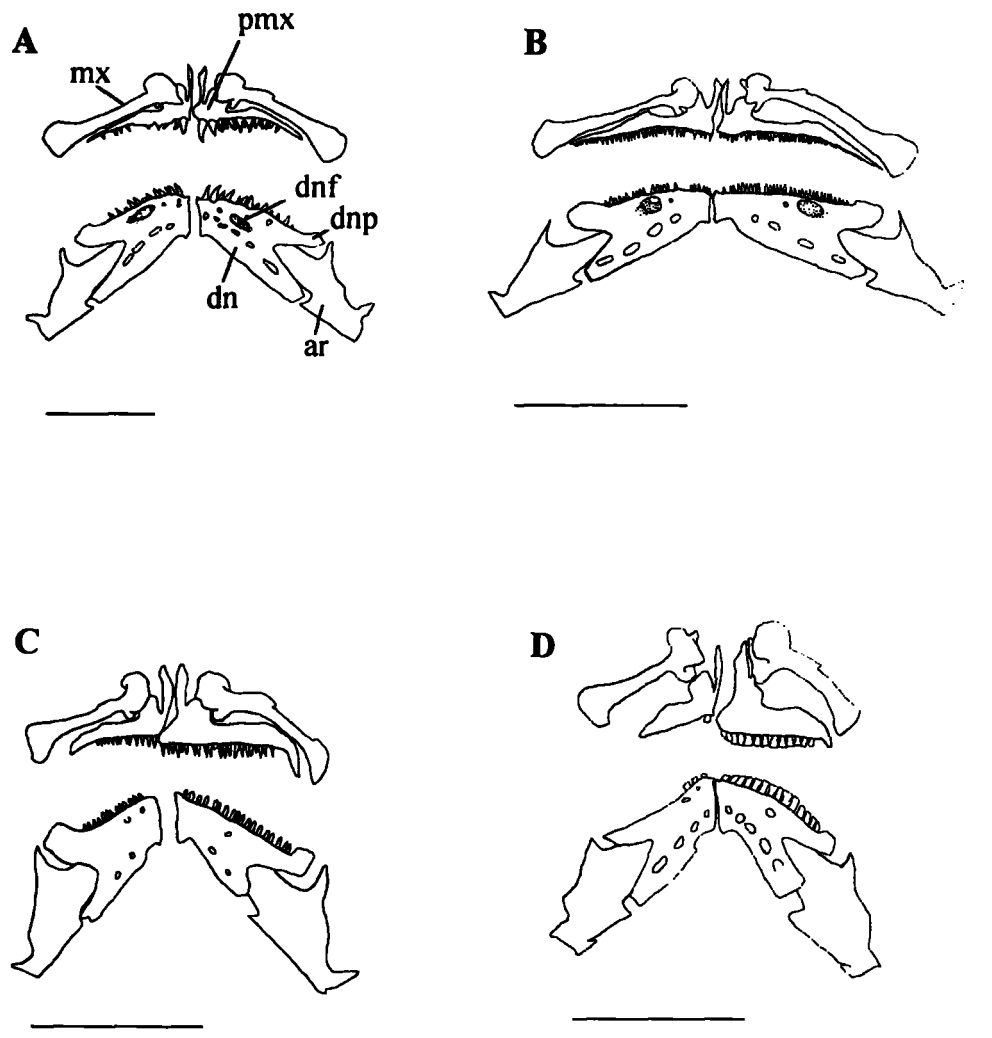


**Figure 9**

Frontal aspect of jaw apparatus. (**A**) *Hippoglossus hippoglossus*, ARC 8808487; (**B**) *Cleisthenes herzensteini*, UMMZ 159566; (**C**) *Isopsetta isolepis*, UMMZ 63214; (**D**) *Pseudopleuronectes schrenki*, HUMZ 75697. ar = articular; dn = dentary; dnf = dentary foramen; dnp = dentary process; mx = maxilla; pmx = premaxillae. Scale bars are 10 mm.

corroborate an alternative hypothesis. The absence of gill rakers on fourth ceratobranchial is observed in *Limanda punctatissima* (Pleuronectinae). The position of the migrated eye in relation to the dorsal midline is a reversal also observed in *Cleisthenes pinetorum* (Hippoglossoidinae). An increase in the number of caudal vertebrae is also observed in *Glyptocephalus* and *Microstomus*, a clade of nine species whose monophyletic status is strongly supported within the Pleuronectinae. Absence of the dentary foramen on the blind side is only observed in four other pleuronectid species including *Hippoglossus hippoglossus*.

*Reinhardtius evermanni* was not examined, but morphological characters reported in the literature suggest monophyly for *R. evermanni*, *R. hippoglossoides*, and *R. stomias*. *Reinhardtius evermanni* also has an increased number of caudal vertebrae, ranging from 37 to 40 (Sakamoto, 1984a). *Reinhardtius evermanni* and *R. stomias* share two unique structures: olfactory lamellae that radiate from a central rachis; and jaw and pharyngeal teeth with barbed tips (Norman, 1934). If these structures are considered synapomorphic within the genus, then *Reinhardtius evermanni* and *R. stomias* are sister species, with *R. hippoglossoides* immediately basal to them.

The sister relationship between *Hippoglossus* and *Verasper* is supported by six synapomorphies (Fig. 11):

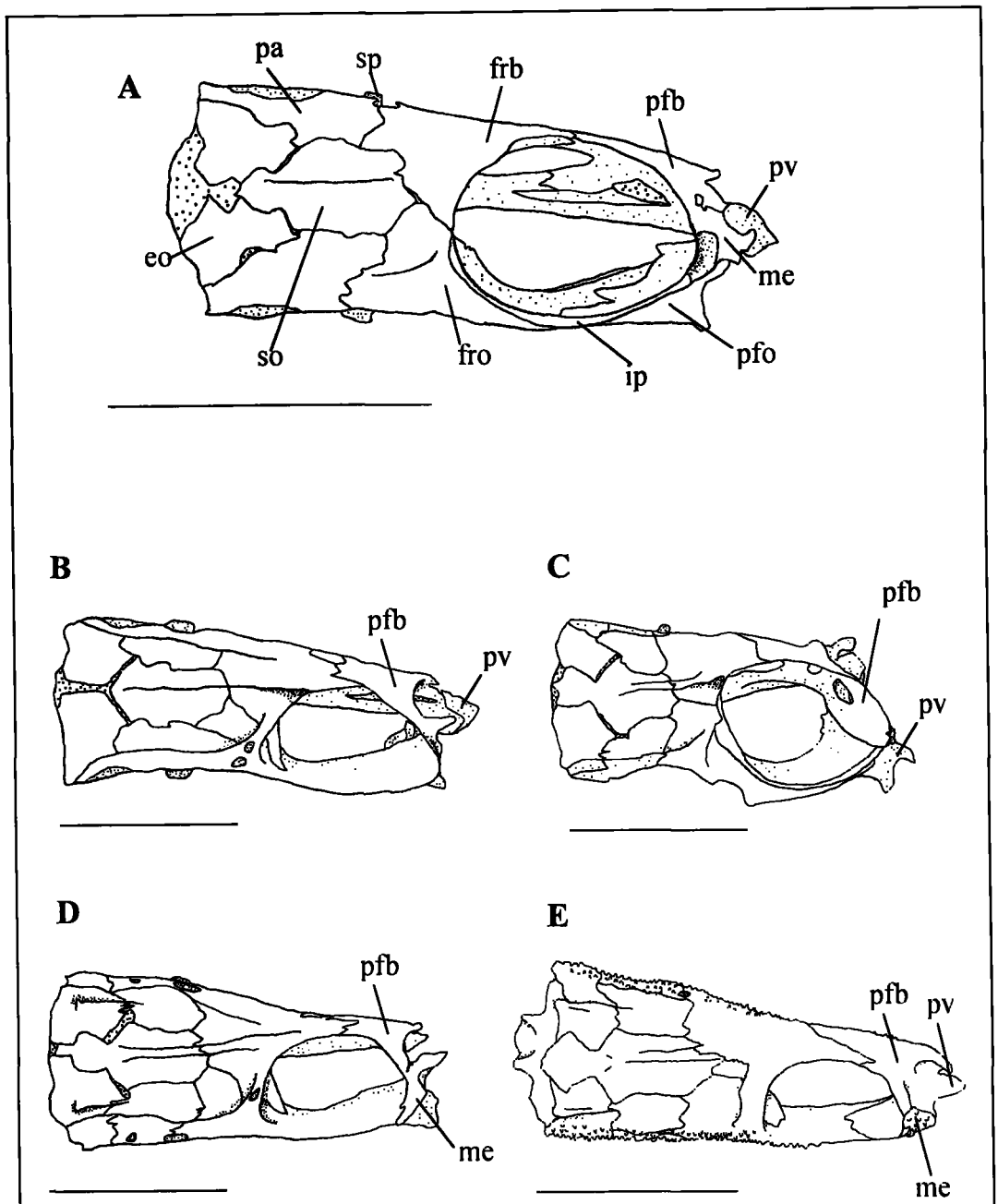


**Figure 10**

Dorsal aspect of crania. (**A**) *Reinhardtius stomias*, NMC 81-1024; (**B**) *Hippoglossoides robustus*, ANSP 105133; (**C**) *Pleuronichthys ocellatus*, CAS 82189; (**D**) *Parophrys vetula*, FMNH 97128; (**E**) *Limanda punctatissima*, HUMZ 93958. eo = exoccipital; frb = frontal (blind side); fro = frontal (ocular side); ip = interorbital process; me = mesethmoid; pa = parietal; pfb =prefrontal (blind side); pfo = prefrontal (ocular side); pv = prevomer; so = supraoccipital; sp = sphenotic. Scale bars are 10 mm.

first anal pterygiophore broadly thickened (15); ocular-side palatine reduced and not articulated with pterygoid (28, Fig. 2B); gill rakers on first epibranchial absent (29) with exception in *Hippoglossus stenolepis*; gill rakers on second and third epibranchials (30, 31) reduced (*Hippoglossus*) or absent (*Verasper*); and gill rakers on first hypobranchial reduced (32).

These states are homoplastic in other lineages of the Pleuronectidae. Thickening of the first anal pterygiophore (15) unites taxa in the third pleuronectid lineage. Reduction of the palatine on the ocu-

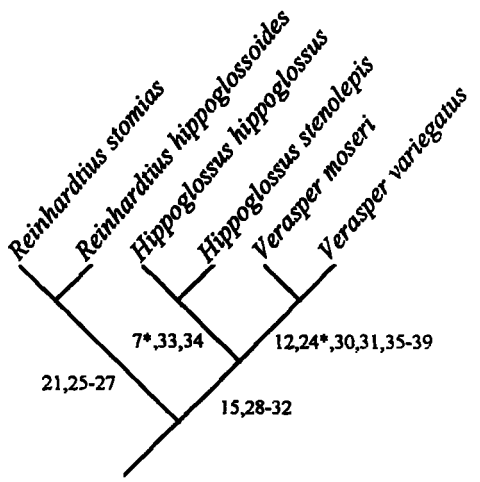


**Figure 11**
Intrarelationships of Hippoglossinae. Numbers correspond to characters in text. Asterisk represents character state reversal.

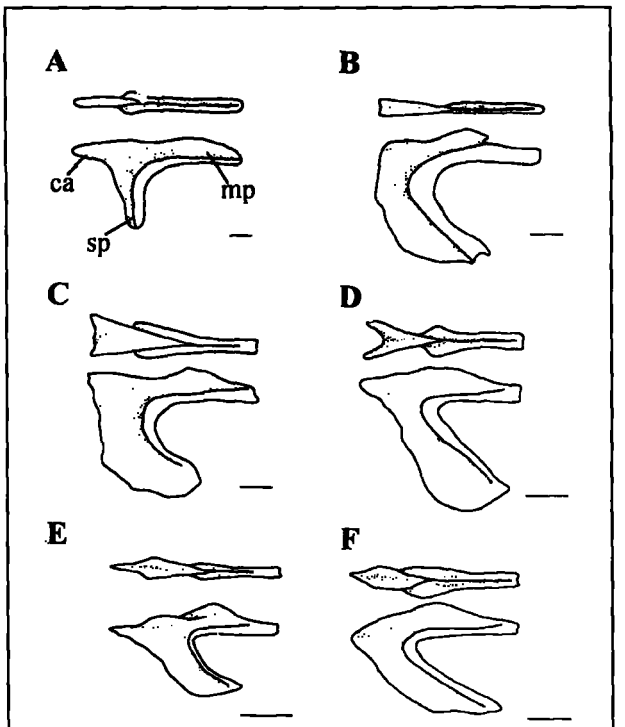


**Figure 12**
Dorsal (above) and lateral (below) aspects of urohyal (modified from Sakamoto, 1984a). (**A**) *Reinhardtius hippoglossoides* (**B**) *Hippoglossus stenolepis* (**C**) *Verasper variegatus* (**D**) *Pseudopleuronectes herzensteini* (**E**) *Glyptocephalus kitaharai* (**F**) *Dexistes rikuzenius*. ca = cardiac apophysis; mp = main part; sp = sciatic part. Scale bars are 2 mm.

lar side (28, Fig. 2, B and C) also defines the lineage uniting *Glyptocephalus*, *Microstomus*, and *Pleuronichthys* within the Pleuronectinae. Absence or reduction of gill rakers on first, second, and third epibranchials (29, 30, 31) is found to define basal lineages within the Pleuronectinae, whereas reduction of gill rakers on the first hypobranchial is observed in only some species of *Pleuronichthys* and *Platichthys bicoloratus*.

**Genus *Hippoglossus*** This genus contains two species: *H. hippoglossus* and *H. stenolepis* and is monophyletic with three synapomorphies (Fig. 11): presence of subdivisions in hypural and parahypural plates, an autapomorphy for the genus (33); presence of accessory processes on ventral margin of caudal vertebrae (7, Fig. 5A), a reversal for the family; and metapterygoid articulated with the blind-side entopterygoid (34, Fig. 2C). Only *Microstomus bathybius* and three species of *Pleuronichthys* have accessory processes on the caudal vertebrae. The metapterygoid is also articulated with the entopterygoid of the blind side in *Reinhardtius hippoglossoides* and species within Pleuronectinae.

**Genus *Verasper*** This genus, containing *V. moseri* and *V. variegatus* is monophyletic with nine synapomorphies (Fig. 11): presence of a large foramen between mesethmoid and blind-side prefrontal (35), autapomorphic for *Verasper*; first epibranchial bifurcated (12); caudal fin is rounded (24), a reversal in this subfamily; gill rakers absent on both second and third epibranchials (30, 31); gill rakers reduced on second hypobranchial (36); sphenotic process not forming dorsal margin of hyomandibular socket (37, Fig. 7, B and C); groove present along supraoccipital crest for insertion of pterygiophores (38, Fig. 10, C–E); and cardiac apophysis of urohyal bifurcated (39, Fig. 12C).

Many character states found within *Verasper* are also observed in the Pleuronectinae, but the strength of the hypothesis placing *Verasper* within Hippoglossinae exceeds the characters mentioned above and illustrates the convergent evolution of these structures.

**Genus *Clidoderma*** *C. asperrimum* was not available for analysis. This species has modified scales on the ocular side to form distinct bony tubercles very similar to those observed in *Platichthys*. However, this unique species appears to be more closely related to *Verasper* than to *Platichthys* (Norman, 1934). This species has subsymmetrical jaws and a mix of pointed and bluntly conical teeth, not uniform in length, set in multiple rows on both upper and lower jaws. These features are plesiomorphic for the fam-

ily and only exclude *Clidoderma* from the fourth pleuronectid lineage. This species has 14 abdominal vertebrae found to be synapomorphic for Hippoglossinae; it also has a thickened first anal pterygiophore suggesting a common ancestry with *Hippoglossus* and *Verasper*. A rounded caudal fin, observed in *Verasper* is also observed in *Clidoderma*. Phylogenetic position of this species could be further ascertained by an examination of the accessory processes on caudal vertebrae, the palatine structure, and the structure of gill rakers on first, second, and third epibranchials.

**Subfamily Eopsettinae** The Eopsettinae consists of *E. grigorjewi* and *E. jordani*. This analysis defines this subfamily with two synapomorphies (Fig. 6): presence of gill rakers on fourth epibranchial (40); and a single row of teeth on lower jaw (41). Gill rakers on the fourth epibranchial are observed in *Cleisthenes herzensteini*, *C. pinetorum* (Hippoglossoidinae), and *Psettichthys melanostictus* (Psettichthyini). The number of rows of teeth on the lower jaw were found to be much more homoplastic. The latter feature was also observed in *Reinhardtius hippoglossoides*, *Verasper moseri*, and *V. variegatus* (Hippoglossinae) as well as in many species of the Pleuronectinae.

**Genus *Eopsetta*** This genus was described in Norman (1934) by a number of plesiomorphic characters. The presence of distinct canines on the upper jaw was suggested in Norman (1934) as diagnostic for *Eopsetta*. However, distribution of this character in the Pleuronectidae is not well defined. Members of the Hippoglossinae also have teeth of irregular lengths (16, Fig. 9A). The longer teeth can also be interpreted as canines in these species. From this analysis, data supporting monophyly of *Eopsetta* are not conclusive, but no other interpretation is available owing to insufficient information.

**Subfamily Lyopsettinae**

**Genus *Lyopsetta*** This lineage contains only *L. exilis*. Its position as a monotypic lineage within the Pleuronectidae is determined by five derived character states (Fig. 6): 12 to 14 abdominal vertebrae (23); barbed teeth present on dentaries and premaxillae (42); supratemporals on both ocular and blind sides are jointed at anterior ends of their bifurcation (43, 44, Fig. 13B); and presence of scales on eye surfaces (45).

These structures are also distributed within other pleuronectid taxa. An increase in abdominal vertebrae is found in Hippoglossinae, some species of Hippoglossoidinae, and in two separate lineages of Pleuronectinae. Barbed teeth are also observed in *Reinhardtius*. Bifurcation of the supratemporals is also observed in *Reinhardtius hippoglossoides*, *Cleisthenes*, *Hippoglossoides*, *Glyptocephalus cynoglossus*, *G. stelleri*, *G. zachirus*, *Microstomus pacificus*, *Limanda aspera*, and *Pleuronectes platessus*. Presence of scales on the eye surfaces is also found in *Reinhardtius stomias*, *Acanthopsetta nadeshnyi*, *Dexistes rikuzenius*, *Glyptocephalus kitaharai*, and *Microstomus*. The distribution of these character states within the family does not indicate an alternative hypothesis of relationships between *Lyopsetta exilis* and other pleuronectid taxa.

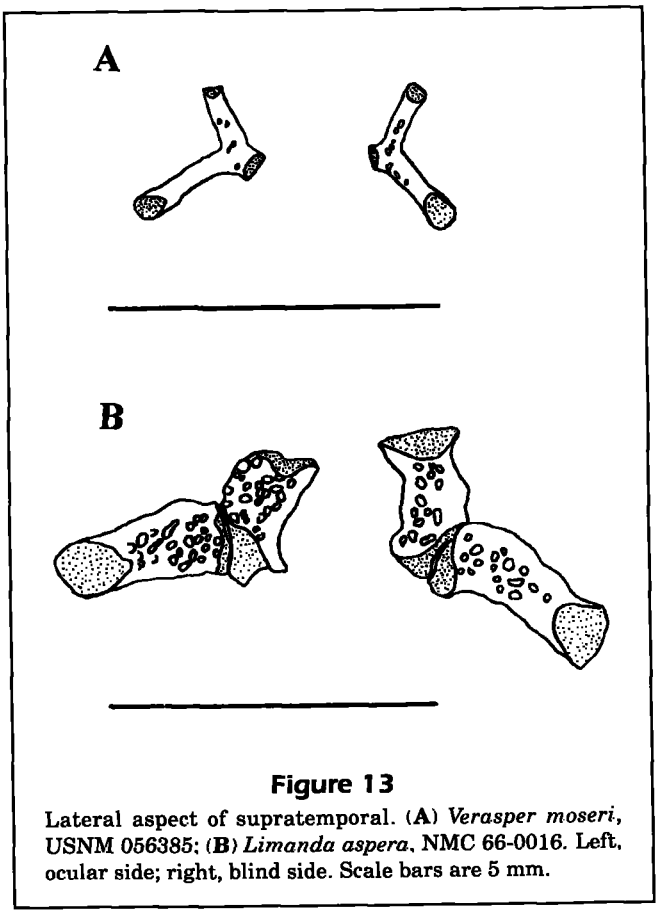


**Figure 13**
Lateral aspect of supratemporal. (**A**) *Verasper moseri*, USNM 056385; (**B**) *Limanda aspera*, NMC 66-0016. Left, ocular side; right, blind side. Scale bars are 5 mm.

**Subfamily Hippoglossoidinae** This subfamily contains seven species (6 examined) in three genera: *Acanthopsetta, Cleisthenes,* and *Hippoglossoides*. This group is characterized by four synapomorphies (Fig. 6): absence of supraoccipital plate extending posteroventrally between epiotics (46, Fig. 10B); pterosphenoid and prootic of blind side join to form dorsal margin of anterior prootic foramen (47, Fig. 7, B and C); pterosphenoid of blind side is reduced and does not form posterior margin of orbit (48, Fig. 7B), a reversal, except in *Cleisthenes;* and two uniform rows of teeth present on fifth ceratobranchial (49).

Distribution of these states within other pleuronectid taxa indicates a degree of homoplasy for these characters but does not refute the monophyly of Hippoglossoidinae. The supraoccipital plate is also absent in *Microstomus* (Microstomini). Pterosphenoid and prootic of the blind side are also united to form the dorsal margin of the anterior prootic foramen in *Verasper variegatus* and in most species of the Pleuronectinae. Reduction of the blind-side pterosphenoid is also observed in *Pleuronichthys* (Microstomini) and may be a reversal within the Pleuronectidae. Two rows of uniform teeth are also present in *Dexistes rikuzenius* (Microstomini) and the Pleuronectini.

### Intrarelationships of Hippoglossoidinae

**Genus *Acanthopsetta*** *A. nadeshnyi* is the sister species to *Cleisthenes* and *Hippoglossoides* (Fig. 14). Placement of *A. nadeshnyi* as a distinct lineage within Hippoglossoidinae is supported by two structures not present in other Hippoglossoidinae: sensory canal on ocular-side preorbital present (2); and presence of scales on eye surfaces (45). The presence of a sensory canal on the ocular-side preorbital is a reversal for the family that also occurs in *Reinhardtius hippoglossoides*. Scales present on the surface of each eye have a more homoplastic distribution as they are found in *Reinhardtius stomias, Lyopsetta exilis, Dexistes rikuzenius, Glyptocephalus kitaharai*, and *Microstomus*.

The sister relationship between *Cleisthenes* and *Hippoglossoides* is supported by three synapomorphies (Fig. 14): ocular-side supratemporal jointed at anterior end of bifurcation (43, Fig. 13B); nasal bones of the blind side are absent (50); and more than seven infraorbital bones on ocular side (51).

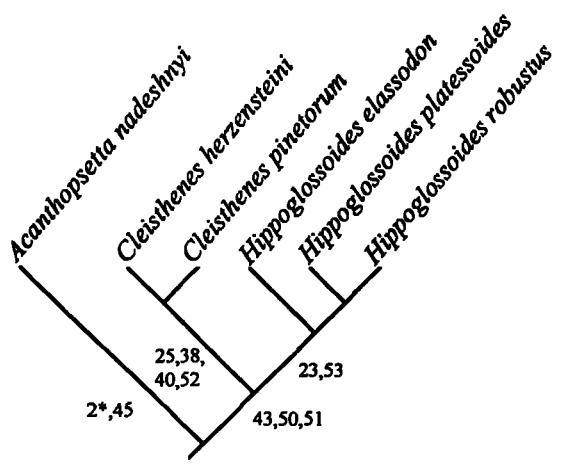


**Figure 14**

Intrarelationships of Hippoglossoidinae. Numbers correspond to characters in text. Asterisk represents character state reversal.

These morphological states are not unique within the family. The bifurcation of the supratemporal is observed in *Lyopsetta exilis* on both ocular and blind side, but not all species of *Cleisthenes* and *Hippoglossoides* have the supratemporal bifurcation on the blind side. The absence of nasal bones on the blind side and number of infraorbitals are shared with some species in the Pleuronectinae, the latter being also observed in *Hippoglossus stenolepis*.

**Genus *Cleisthenes*** This genus contains two species, *C. herzensteini* and *C. pinetorum*, and is diagnosed by four synapomorphies (Fig. 14): migrated eye is near dorsal midline (25); gill rakers on fourth epibranchial present (40); a double crest or groove present on supraoccipital and blind-side frontal (38, Fig. 10, C–E); and crest extending from supraoccipital to blind side reduced (52, Fig. 10, D and E).

These morphological characters are distributed within other pleuronectid taxa but are not observed in any other Hippoglossoidinae. The position of the migrated eye is also observed in *Reinhardtius*. Presence of gill rakers on the fourth epibranchial has a limited distribution in *Eopsetta grigorjewi, E. jordani*, and *Psettichthys melanostictus*. The double crest on the supraoccipital and blind-side frontal is recurrent throughout the family but unique within Hippoglossoidinae. The reduced crest on the blind-side frontal is also observed in *Reinhardtius stomias, Pleuronichthys verticalis*, and Pleuronectini.

**Genus *Hippoglossoides*** This genus contains 4 species: *H. dubius* (not examined), *H. elassodon, H. platessoides*, and *H. robustus*, defined by two synapomorphies (Fig. 14). The structure of the anterior margin of the mesethmoid is complex but consistent in *Hippoglossoides*. In this genus, the "thin plate" structure of the mesethmoid (53, Fig. 8B) is distinct in relation to other members of Hippoglossoidinae who have a thickened triangular-shaped mesethmoid (Fig. 8C), or the plesiomorphic structure of an open canal found in *Cleisthenes pinetorum* (Fig. 8A). In addition, there are 12 to 14 abdominal vertebrae (23), an increase from 11 or fewer in other taxa. The interrelationships within *Hippoglossoides* are not fully resolved by this analysis. *Hippoglossoides dubius* has 13 abdominal vertebrae (Norman, 1934; Sakamoto, 1984a) and is assumed to have common ancestry with other species of *Hippoglossoides*.

### Subfamily Pleuronectinae

The Pleuronectinae is the largest subfamily within the Pleuronectidae with 40 species (38 examined in

this analysis). Seven synapomorphies define this group as monophyletic (Fig. 6): absence of a dentary fossa (55, Fig. 9, C and D); and absence of ceratohyal foramen (56) are both autapomorphic for Pleuronectinae; mesethmoid and blind-side prefrontal are sutured but without a foramen between these bones (14, Fig. 8D); a double supraoccipital crest forms a groove for insertion of anterior dorsal-fin pterygiophores (38, Fig. 10, C–E); a single row of teeth on lower jaw (41); intercalar in contact with basioccipital (57, Fig. 7C); and presence of a posterior extension of supratemporal branch of the lateral line (58).

Some of these character states are not found in all pleuronectines, but the occurrence of these states at basal lineages and their predominance within the Pleuronectinae indicates that the absence of these synapomorphies within the subfamily are instances of evolutionary reversal. For example, the presence of a supratemporal branch (58) is observed in 11 pleuronectine taxa and is hypothesized to arise at this node with two secondary losses observed in more advanced lineages within Microstomini and Pleuronectini.

**Intrarelationships of Pleuronectinae** The Pleuronectinae is classified into 4 tribes: Psettichthyini, Isopsettini, Microstomini, and Pleuronectini (Fig. 6). Branchial structure and characters associated with jaw asymmetry determine the interrelationships of these tribes.

**Tribe Psettichthyini Genus *Psettichthys*** Monotypic with only *P. melanostictus*, this lineage is unique within the Pleuronectinae, having six distinct characters (Fig. 6): dorsal fin rays are elongated beyond dorsal-fin membrane, an autapomorphy for the species (59); second and third basibranchials are sutured (5, Fig. 3A), a reversal within Pleuronectidae; teeth are not uniform in length (16); greater than seven infraorbital bones (51); gill rakers on fourth epibranchial present (40); and one row of teeth on upper jaw (60).

These morphological states are shared with taxa both within and prior to the Pleuronectinae. This evidence clearly positions Psettichthyini as a basal tribe of the Pleuronectinae. A suture between the second and third basibranchials is observed elsewhere only in *Limanda punctatissima*. Tooth length is uniform in other pleuronectine taxa. An increase in infraorbital number is observed in two other pleuronectine species, *Lepidopsetta bilineata* and *Pleuronichthys decurrens*, as well as in *Cleisthenes, Hippoglossoides*, and *Hippoglossus stenolepis*. The presence of gill rakers on the fourth epibranchial is found elsewhere only in *Cleisthenes* and *Eopsetta*. A single row of teeth on the upper jaw is observed in all species of the Pleuronectini, and in *Glyptocephalus* and *Microstomus*.

The second lineage contains the newly defined tribes Isopsettini, Microstomini, and Pleuronectini. Taxa within this lineage are characterized by 11 synapomorphies (Fig. 6): one gill raker at proximal base of second and third epibranchials (30, 31, Fig. 3D); blind-side premaxilla protruding past the sagittal axis at its symphysis with that of ocular side (61, Fig. 9, C and D); ocular-side premaxilla much longer than that of blind side (62, Fig. 9, C and D); ventral posterior curvature on blind-side premaxilla is present (63, Fig. 9, C and D); asymmetry in space between dentary and articular such that blind-side space is larger than on ocular side (64, Fig. 9, C and D); dorsoposterior process of ocular-side dentary larger than its blind-side counterpart (65, Fig. 9C); teeth on both ocular-side premaxilla and dentary reduced (66, 67, Fig. 9, C and D); epiotic processes present (68, Fig. 10, D and E); and ocular-side entopterygoid larger than that of blind side (69, Fig. 2, C and D).

Distribution of these character states is not without exceptions or homoplasies. Reduction of gill rakers on the second epibranchial was not observed in *Limanda* (Fig. 3C), and a reduction of gill rakers on the third epibranchial was not observed for *Pleuronectes quadrituberculatus*. These reductions are homoplastic in *Hippoglossus* and *Verasper* (Hippoglossinae).

The third lineage indicating a sister relationship between the tribes Microstomini and Pleuronectini, is based on six synapomorphies (Fig. 6): within this lineage there is an evolution of dentition, from pointed or bluntly conical teeth to incisorlike or even molariform teeth with uniform cutting edges (70); sphenotic process positioned high on sphenotic (37, Fig. 7, B and C); urohyal with strongly bifurcate cardiac apophysis (39, Fig. 12, D–F); blind-side pterosphenoid and prootic form dorsal margin of anterior prootic foramen (47, Fig. 7, B and C); medial margin of fifth ceratobranchial slightly curved (71, Fig. 3C); and teeth on fifth ceratobranchial bluntly pointed (72, Fig. 3C).

Exceptions to the distribution of character states within the third lineage are observed in few species and appear to be cases of reversal. They do not contradict the sister relationship between Microstomini and Pleuronectini. The sphenotic process is not positioned high on the sphenotic in *Glyptocephalus*. A strongly bifurcated cardiac apophysis on the urohyal was not found in *Limanda punctatissima, Pleuronichthys ritteri, P. ocellatus*, and *Parophrys vetula*. These two morphological characters are homoplastic in *Verasper* (Hippoglossinae). The sphenotic forms the dorsal margin of the anterior prootic foramen on the blind side (47, Fig. 7A) in *Limanda ferruginea, L. proboscidea, Microstomus achne, M. kitt, Glypto-*

*cephalus cynoglossus, G. stelleri, G. zachirus*, and *Pleuronichthys guttulatus*. However, the blind-side pterosphenoid and prootic uniting to form the dorsal margin of the anterior prootic foramen is homoplastic in Hippoglossoidinae and *Verasper variegatus* (Hippoglossinae). The medial curvature of the fifth ceratobranchial is not observed in *Microstomus, Glyptocephalus*, and *Pleuronichthys,* and teeth on the fifth ceratobranchial are sharply pointed in *Microstomus bathybius, Pleuronichthys*, and *Lepidopsetta.*

**Tribe Isopsettini Genus *Isopsetta*** The tribe Isopsettini is monotypic with *Isopsetta isolepis*. Four character transformations identify the lineage (Fig. 6): blind-side metapterygoid is not articulated with entopterygoid (34, Fig. 2A); anterior margin of mesethmoid forming an open canal (53, Fig. 8A); haemal spines of anteriormost caudal vertebrae broadly attached to centrum (73, Fig. 5B); and epiotics are sutured along dorsal posterior margin of skull (74).

Three of these four character states are reversals within the Pleuronectinae. The absence of an articulation between the blind-side metapterygoid and entopterygoid is a reversal of the structure observed in the Psettichthyini and in most species of Microstomini and Pleuronectini, except *Lepidopsetta, Pleuronichthys guttulatus, Limanda aspera*, and *L. ferruginea*. The open canal on the anterior margin of the mesethmoid is a reversal that is also observed in the pleuronectines, *Glyptocephalus, Microstomus*, and *Pleuronichthys* (except *P. verticalis*), and in *Cleisthenes pinetorum* (Hippoglossoidinae). Epiotics sutured along the dorsal posterior margin are observed only in one other pleuronectid species, *Microstomus pacificus*, and the broad attachment of haemal spines to the anteriormost caudal vertebrae is a reversal recurrent throughout the family, indicating a homoplastic structure with a complex distribution. Despite the reversals noted for this lineage, placement of Isopsettini within Pleuronectinae is supported by the eight synapomorphies for Pleuronectinae and the 11 derived morphological characters for the second lineage in Pleuronectinae.

**Tribe Microstomini** The tribe Microstomini contains 19 species (17 examined) classified in five genera: *Lepidopsetta, Dexistes, Pleuronichthys, Glyptocephalus*, and *Microstomus* (Fig. 15). Although the placement of this tribe within the Pleuronectinae is supported by 25 character transformations presented for monophyly and intrarelationships of the subfamily, the status of this tribe, as well as its intrarelationships, are determined mostly by character reversals. The monophyly of this tribe is characterized by four character transformations. All are reversals within the Pleuronectinae (Fig. 6): suture between mesethmoid and blind-side prefrontal is either incomplete or complete with a small foramen present (14, Fig. 8, A–C); single crest on supraoccipital (38, Fig. 10, A and B); lower jaw with multiple rows of teeth (41); and reduced or absent process on dorsoposterior edge of epiotics (68, Fig. 10, A–C).

The few exceptions to the distribution of these states within Microstomini and the occurrence of these same reversals outside of Microstomini indicate the homoplastic nature of these structures. Multiple rows of teeth on the lower jaw were not observed in *Microstomus* and *Glyptocephalus,* which is homoplastic within Hippoglossinae and recurrent for basal lineages within the family but which has only this one instance of reversal in Pleuronectinae. The absence or reduction of an epiotic crest is a reversal also found in *Pseudopleuronectes herzensteini* and *P. yokohamae.*

**Intrarelationships of Microstomini** Three lineages of Microstomini are defined by 16 character transformations; ten are reversals (Fig. 15).

**Genus *Lepidopsetta*** The first lineage of Microstomini, consists of *Lepidopsetta* containing two species, *L. bilineata* and *L. mochigarei* (Fig. 15). This genus is diagnosed by the presence of demersal eggs (75), a feature observed in only four other pleuronectid species: *Pseudopleuronectes americanus, P. schrenki, P. yokohamae*, and *P. obscurus* (not examined).

The second lineage indicates common descent for *Dexistes, Pleuronichthys, Microstomus*, and *Glyptocephalus*. Four character states unite these genera (Fig. 15): first epibranchial bifurcated at distal end (12, Fig. 3A); cardiac apophysis simple at tip with a bifurcation positioned anteriorly (39, Fig. 12, E and F), except in *Pleuronichthys ocellatus* and *P. ritteri;* intercalar not in contact with basioccipital (57, Fig. 7B), a reversal in Pleuronectinae; and less than seven teeth on ocular-side premaxilla (66).

Exceptions to character states within the second lineage of Microstomini were not congruent and did not provide alternative topologies that either excluded taxa observed to be exceptions to this distribution or included taxa that were homoplastic with these structures. Bifurcation of the first epibranchial is a reversal in the Pleuronectidae. Shape of the cardiac apophysis of the urohyal was observed only in one other pleuronectid, *Limanda aspera*. The intercalar is in contact with the basioccipital in *Glyptocephalus cynoglossus* (57, Fig. 7C). The reduction of teeth on the ocular-side premaxilla (less than 7) is not observed in *Pleuronichthys guttulatus* and *Glyptocephalus*. In *Glyptocephalus*, variation in tooth number on the ocular-side premaxilla ranged from 8 to 16 in *G. zachirus*, but in all species there is a

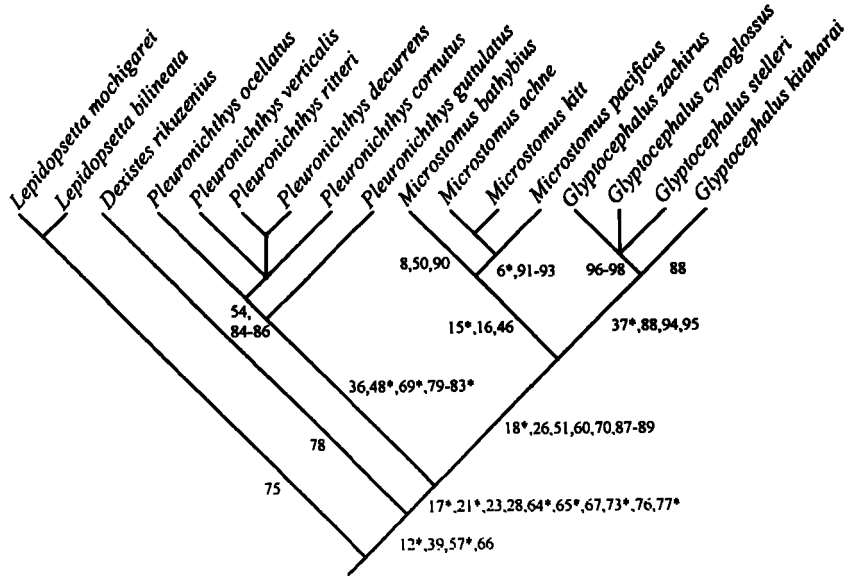


**Figure 15**

Intrarelationships of Microstomini. Numbers correspond to characters in text. Asterisk represents character state reversal.

smaller number of teeth on the ocular-side premaxilla than the number observed in previous lineages of Pleuronectinae (Norman, 1934). *Glyptocephalus cynoglossus* is reported to have 8 to 15 teeth on the ocular-side premaxilla and 17 to 26 on the associated blind-side premaxilla. *G. stelleri* has only seven teeth on the ocular-side premaxilla and 20 to 27 teeth on the blind side. *G. tanakius* has 12 to 14 teeth on the ocular-side premaxilla and 14 to 16 on the blind side, and *G. zachirus* has 12 to 16 teeth on the ocular-side premaxilla and 20 to 27 teeth on the blind side (Norman, 1934).

The third lineage of Microstomini indicates monophyly for *Pleuronichthys, Microstomus*, and *Glyptocephalus*. It is based on ten character transformations, four synapomorphies, and six reversals (Fig. 15). Synapomorphies include increased number of abdominal vertebrae to between 12 and 14 (23); lips thickened or fleshy (76); palatine of ocular side reduced and not attached to pterygoid (28, Fig. 2C); and teeth on ocular-side dentary reduced to fewer than six (67). The reversals are exoccipital and prootic in contact with each other (77, Fig. 7B); presence of an interorbital process (17, Fig. 10C); one row of gill rakers on fourth ceratobranchial (21, Fig. 3, A and B); haemal spine broadly attached to centrum (73, Fig. 5B); space between both ocular- and blind-side dentary and articular equal in size (64, Fig. 9D); and dorsoposterior process of similar size on ocular- and blind-side dentaries (65, Fig. 9D).

Exceptions and homoplasy in this distribution do not support an alternative hypothesis. *Glyptocephalus kitaharai* has only 11 abdominal vertebrae (Sakamoto, 1984a). Reduction of the ocular-side palatine was also observed in *Hippoglossus* and *Verasper* (Hippoglossinae). The exoccipital and prootic are not joined, and secondary reduction of teeth on the dentary of the ocular side are not observed in *Glyptocephalus*. These species all have proportionally fewer teeth on the ocular-side dentary, but the exact number ranges from 11 to 15 in *Glyptocephalus kitaharai* to 10 to 18 in *G. zachirus* (Norman, 1934).

Reversals in this lineage reproduce plesiomorphic states observed prior to the fourth lineage of Pleuronectidae or states that are plesiomorphic within the Pleuronectinae. The contact between exoccipital and prootic, may be a reversal for the family. The lost interorbital process in the fourth pleuronectid lineage is observed (at least partially) in these two pleuronectine genera. The single row of gill rakers on the fourth ceratobranchial is a reversal of the two rows that define the fourth pleuronectid lineage. The broad attachment of the haemal spine to the centrum is a reversal of a narrower attachment defining the fourth pleuronectid lineage. Sym-

metry in the space between dentary and articular, as well as the dentary process, are reversals for Pleuronectinae. These reversals are also observed in some species of the Pleuronectini (Table 1).

The fourth lineage in Microstomini represents the sister relationship between *Microstomus* and *Glyptocephalus*. Eight synapomorphies support this hypothesis (Fig. 15): intestine extending posteriorly into body cavity (87), unique for this lineage; more than 20 caudal-fin rays, an increase from 18 or 19 (88); more than six branched caudal-fin rays (89); 36 to 41 caudal vertebrae, an increase from 25 to 35 (26); less than five infraorbital bones, a reduction from between five and seven (51); teeth incisorlike (70); single row of teeth on upper jaw (60); and hyomandibula without a broad anteroventral margin (18, Fig. 2C).

Exceptions to the distribution of these synapomorphies do not indicate exclusion of any species defined in *Glyptocephalus* or *Microstomus*, nor does homoplasy suggest the inclusion of additional taxa. An increase in caudal-fin rays is only observed in one other pleuronectid, *Pleuronectes platessus*, which usually has 20 caudal-fin rays. An increase in the relative number of branched caudal-fin rays is also observed in *Pleuronichthys decurrens*, *P. ritteri*, and *Pseudopleuronectes yokohamae*. An increase in the number of caudal vertebrae is homoplastic in *Reinhardtius* (Hippoglossinae). A reduction in the number of infraorbital bones is not observed in *Glyptocephalus kitaharai* and *Microstomus pacificus* but is reduced in *Pseudopleuronectes americanus*. The incisorlike tooth structure is unique within Microstomini but is observed in *Parophrys vetula*, *Pleuronectes*, and *Pseudopleuronectes*. A single row of teeth on the upper jaw is also unique within Microstomini but is also observed in *Psettichthys melanostictus* (Psettichthyini) and Pleuronectini. The absence of a broadened hyomandibula is a reversal unique within this lineage of *Glyptocephalus* and *Microstomus*. All other taxa within the fourth lineage of Pleuronectidae have a hyomandibular with a broadened anterior margin (Fig. 2D).

**Genus *Dexistes*** The monotypic genus contains *D. rikuzenius* (Fig. 15). The monotypic status of this species is based on the morphologlical characters examined for intrarelationships of Microstomini and the presence of an ocular-side postocular ridge (78). The latter character has an additional evolutionary step within the sister tribe Pleuronectini, uniting a clade comprising *Limanda*, *Platichthys*, *Pleuronectes*, and *Pseudopleuronectes*.

**Genus *Pleuronichthys*** This genus contains seven species: *Pleuronichthys coenosus* (not examined), *P. cornutus*, *P. decurrens*, *P. guttulatus*, *P. ritteri*, *P. ocellatus*, and *P. verticalis*. This genus is identified by eight character transformations (Fig. 15): presence of villiform teeth, autapomorphic for *Pleuronichthys* (79); large foramen in blind-side prefrontal (80); gill rakers on second hypobranchial reduced to one at proximal base (36); lateral process present on ocular-side frontal (81, Fig. 7B, 10C); 25 or less caudal vertebrae (82); ocular-side pterosphenoid reduced and not forming posterior margin of orbit (83, Fig. 7B); blind-side pterosphenoid is similarily reduced (48, Fig. 7B); and ocular-side entopterygoid similar in size to that of blind side (69, Fig. 2, A and B). *Pleuronichthys coenosus* is assumed to be a member of this genus on the basis of presence of villiform teeth, reduced number of caudal vertebrae (24 to 25), and presence of a lateral process on ocular-side frontal (Sakamoto, 1984a).

There are few exceptions to the distribution of character states within *Pleuronichthys*, and instances of homoplasy do not indicate an alternative hypothesis. The large foramen in the blind-side prefrontal was observed in only one other species, *Glyptocephalus stelleri*. Reduction of gill rakers on the second hypobranchial was not observed in *Pleuronichthys ocellatus*, which has at least two gill rakers on the second hypobranchial. The presence of a lateral process on the ocular-side frontal is also observed in *Microstomus achne*, *M. kitt*, and *M. pacificus*. However, it is not nearly as distinct as that in *Pleuronichthys*. Only *Platichthys flesus*, *P. stellatus*, and *Pleuronectes putnami* (Pleuronectini) have also fewer than 25 caudal vertebrae. Reduction of the ocular-side pterosphenoid is not observed in *Pleuronichthys ritteri*, where the pterosphenoid separates frontal and parasphenoid to form the posterior margin of the orbit. Reduction of the blind-side pterosphenoid is also observed in *Acanthopsetta* and *Hippoglossoides* (Hippoglossoidinae). These two character states are reversals in the Pleuronectidae. The symmetry between ocular-side and blind-side entopterygoids is a reversal of the asymmetrical structure observed prior to the Isopsettini. This reversal only occurs in *Pleuronichthys* and *Glyptocephalus kitaharai*.

The intrarelationships of *Pleuronichthys* are not fully resolved. *Pleuronichthys guttulatus* is the sister species to all other species of *Pleuronichthys* (Fig. 15). Four synapomorphies unite *P. cornutus*, *P. coenosus*, *P. decurrens*, *P. ocellatus*, *P. ritteri*, and *P. verticalis*: dorsal fin originates on blind side of head (84); reduced or absent cartilaginous interspace between blind-side prefrontal and parasphenoid (85, Fig. 7B); mesethmoid forms only part of anterior margin of upper orbit (86); and ocular-side metapterygoid articulated with entopterygoid (54). This last feature is homoplastic because it is also observed in *Reinhardtius hippoglossoides* and *Limanda punctatissima*.

**Genus *Microstomus*** This genus contains five species: *M. achne, M. bathybius, M kitt., M. pacificus,* and *M. shuntovi* (not examined) and is defined by three synapomorphies (Fig. 15): posterior extension of supraoccipital absent (46, Fig. 10B); first anal pterygiophore thin (15); teeth in both upper and lower jaws uniform in length forming a continuous cutting edge (16, Fig. 9D). Descriptions of *Microstomus shuntovi* indicate that this species is very similar to *M. kitt* (Borets, 1983). The teeth are described as "chisel-like" (Borets, 1983), a term that similarly describes teeth in other species of *Microstomus*. An examination of the supraoccipital and the first anal pterygiophore would verify this classification.

Absence of the posterior extension on the supraoccipital has evolved independently in the Hippoglossoidinae. The thin structure of the first anal pterygiophore is a reversal of a thickened structure defining the third lineage. The continuous cutting edge of the teeth is an advanced state, also present in *Glyptocephalus zachirus, Pleuronectes glacialis, P. pinnifasciatus, P. putnami,* and *Pseudopleuronectes schrenki.*

*Microstomus bathybius* is the sister species to *M. achne, M. kitt,* and *M. pacificus* (Fig. 15). This deep-sea species is unique in being the only pleuronectid with a series of infraorbital bones on the ocular side (8). It is the only species of *Microstomus* in which the blind-side nasal bone is absent (50) and is the only pleuronectid in which the anteroventral tip of the pelvis is anterior to the cleithrum (90). The other species of *Microstomus* share four character states (Fig. 15): ocular-side scales with radii completely surrounding the focus (91); margins of interoperculum and subopercular fimbriated (92, 93, Fig. 2C); and haemapophysis present on most posterior abdominal vertebrae (6, Fig. 4D). This last feature is a reversal for Pleuronectidae, and only *Glyptocephalus zachirus* has also a fimbriated subopercular margin.

**Genus *Glyptocephalus*** This genus contains four species: *G. cynoglossus, G. kitaharai, G. stelleri,* and *G. zachirus*. Four synapomorphies are hypothesized at this node (Fig. 15): more than 21 caudal-fin rays (88); cleithra inserted by tip of urohyal (94); presence of two to four pyloric appendages and two or three on upper intestine, an increase from two to three and one on upper intestine (95); sphenotic process positioned low on sphenotic and forming dorsal roof of hyomandibular socket (37, Fig. 7A). This last character is a reversal of that observed in all other Microstomini and Pleuronectini.

*Glyptocephalus kitaharai* is the sister species to *G. cynoglossus, G. stelleri,* and *G. zachirus*. It is unique within this clade and with all other pleuronectids in having 23 caudal-fin rays, the highest number observed in the family (88). The other species are united by three character states (Fig. 15): blind-side nasal bones larger than those of ocular side (96); development of large mucous cavities on blind-side head (97), both characters unique for these three species; and presence of an interpterosphenoid bar (98, Fig. 16), not observed in any other species of *Glyptocephalus* or immediate lineages, but homoplastic in *Hippoglossoides, Acanthopsetta, Psettichthys, Limanda aspera, L. ferruginea, L. proboscidea, L. punctatissima, Pseudopleuronectes americanus, P. yokohamae,* and *Pleuronectes*. The monophyletic status of these three species is in agreement with relationships inferred through an analysis of body shape (Chiu, 1990).

**Tribe Pleuronectini** The tribe Pleuronectini contains 20 species (19 examined). Four synapomorphies define this tribe (Fig. 6): at least two regular rows of teeth on fifth ceratobranchial (49, Fig. 3, C and D); postocular ridge present on ocular side (78); upper jaw teeth in single row (60); and dorsal crest extending anteriorly from supraoccipital to blind-side frontal reduced or absent (52, Fig. 10, D and E).

Exceptions and homoplasy did not indicate an alternative hypothesis for Pleuronectini; all 19 species examined were grouped in all 128 of the equally par-

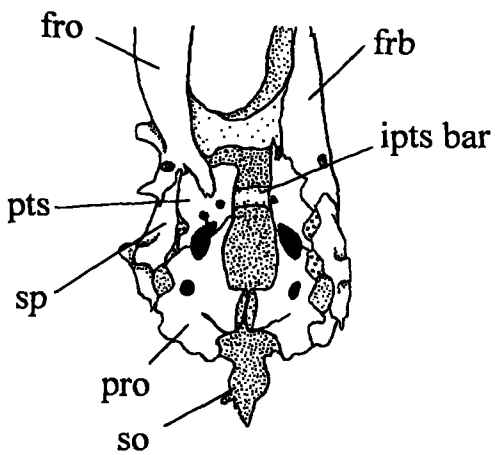


**Figure 16**

Ventral aspect of cranium, *Pleuronectes quadrituberculatus* USNM 064042, with parasphenoid removed to reveal interpteroshenoid bar. frb= frontal (blind side); fro, frontal (ocular side); ipts bar = interpterosphenoid bar; pro = prootic; pts = pteroshenoid; so = supraoccipital; sp = sphenotic. Anterior region of orbit and occipital region have been removed. Scale bar is 10 mm.

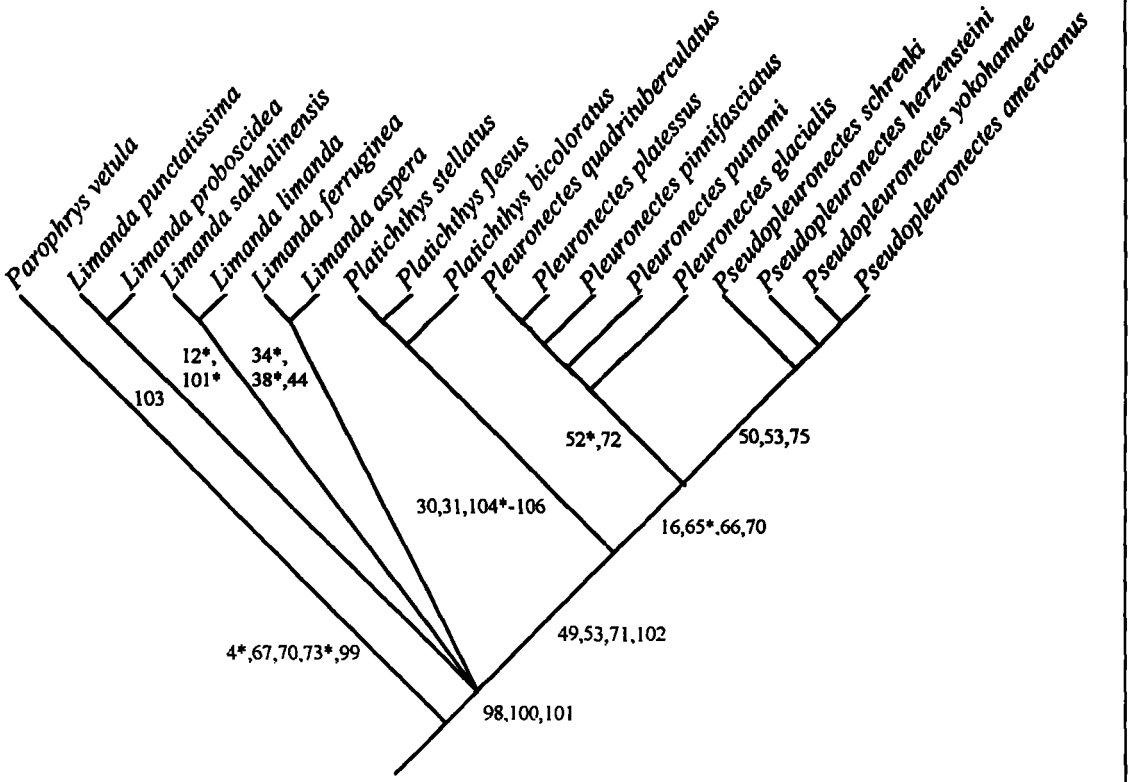


**Figure 17**

Intrarelationships of Pleuronectini. Numbers correspond to characters in text. Asterisk represents character state reversal.

simonious trees. A postocular ridge is observed in only one other pleuronectid taxon, *Dexistes rikuzenius*. A single row of teeth in the upper jaw was also observed in *Psettichthys melanostictus*, *Glyptocephalus*, and *Microstomus*. The structure of the dorsal crest, extending along the supraoccipital and blind-side frontal, was homoplastic within Pleuronectini and in other pleuronectid lineages. *Limanda aspera, Pleuronectes quadrituberculatus, P. glacialis, P. pinnifasciatus*, and *P. putnami* retain a prominent crest. *Pleuronichthys verticalis, Cleisthenes*, and *Reinhardtius stomias* share the reduced morphological character with Pleuronectini.

### Intrarelationships of Pleuronectini

**Genus *Parophrys*** The first lineage in Pleuronectini has only one species, *Parophrys vetula*, which is distinct with five character transformations (Fig. 17): suture between first and second basibranchial (4, Fig. 3A); haemal spines broadly attached to ventral surface of centrum (73), are both reversals within Pleuronectidae; absence of dentary foramen on ocular side (99); reduction of teeth on ocular-side dentary (67) and incisorlike teeth (70, Fig. 9D) are shared with higher lineages within Pleuronectini but are homoplastic, and observed in Microstomini and species of Hippoglossinae.

*Limanda, Platichthys, Pleuronectes*, and *Pseudopleuronectes* represent the second lineage in Pleuronectini and are hypothesized to share an immediate common ancestor on the basis of three synapomorphies (Fig. 17): presence of a blind-side postocular ridge (100); presence of bony prominences on ocular-side postocular ridge (101, Fig. 10E); and presence of an interpterosphenoid bar (98, Fig. 16). The blind-side postocular ridge and bony prominences on the ocular-side postocular ridge are unique within Pleuronectidae. The latter was not observed in *Limanda limanda, L. sakhalinensis, L. aspera, Pseudopleuronectes herzensteini, P. yokohamae*, and *P. americanus*. The presence of an interpterosphenoid bar was not observed in *Limanda limanda, L. sakhalinensis, Pseudopleuronectes schrenki*, and *P. herzensteini* and is homoplastic in *Glyptocephalus cynoglossus, G. stelleri, G. zachirus, Psettichthys, Acanthopsetta*, and *Hippoglossoides*.

The third lineage of Pleuronectini is a clade uniting *Platichthys, Pleuronectes*, and *Pseudopleuronectes*. This result was observed in 80 of 128 (62.5%) trees found by heuristic search and is supported by four morphologies (Fig. 17): bony prominences on blind-side postocular ridge (102, Fig. 10E); a strong medial curvature on fifth ceratobranchial resulting in close approximation or union of ceratobranchials (71, Fig. 3D); an increase of rows of teeth on fifth ceratobranchial from two regular rows to multiple rows of regular length (49, Fig. 3D); and anterior margin of mesethmoid (53) either a thin plate (Fig. 8B) or thickened triangular edge (Fig. 8C).

Exceptions and homoplasy observed in these morphological characters contributed to three alternative topologies for intrarelationships of Pleuronectini (Fig. 18, A–C). Bony prominences on the blind-side postocular ridge were not observed in *Pseudopleuronectes, Pleuronectes platessus*, and *P. quadrituberculatus* and are homoplastic in *Limanda proboscidea* and *L. punctatissima*. Both attributes of the fifth ceratobranchial, the close approximation of the medial margins and the multiple rows of teeth, are not observed in *Pseudopleuronectes*. The thin plate structure of the mesethmoid (Fig. 8B), observed in *Pseudopleuronectes* and *Pleuronectes platessus* is homoplastic in *Dexistes rikuzenius*, *Pleuronichthys verticalis* (Microstomini), and *Hippoglossoides* (Hippoglossoidinae). The thickened triangular edge of the mesethmoid (Fig. 8C) is unique within

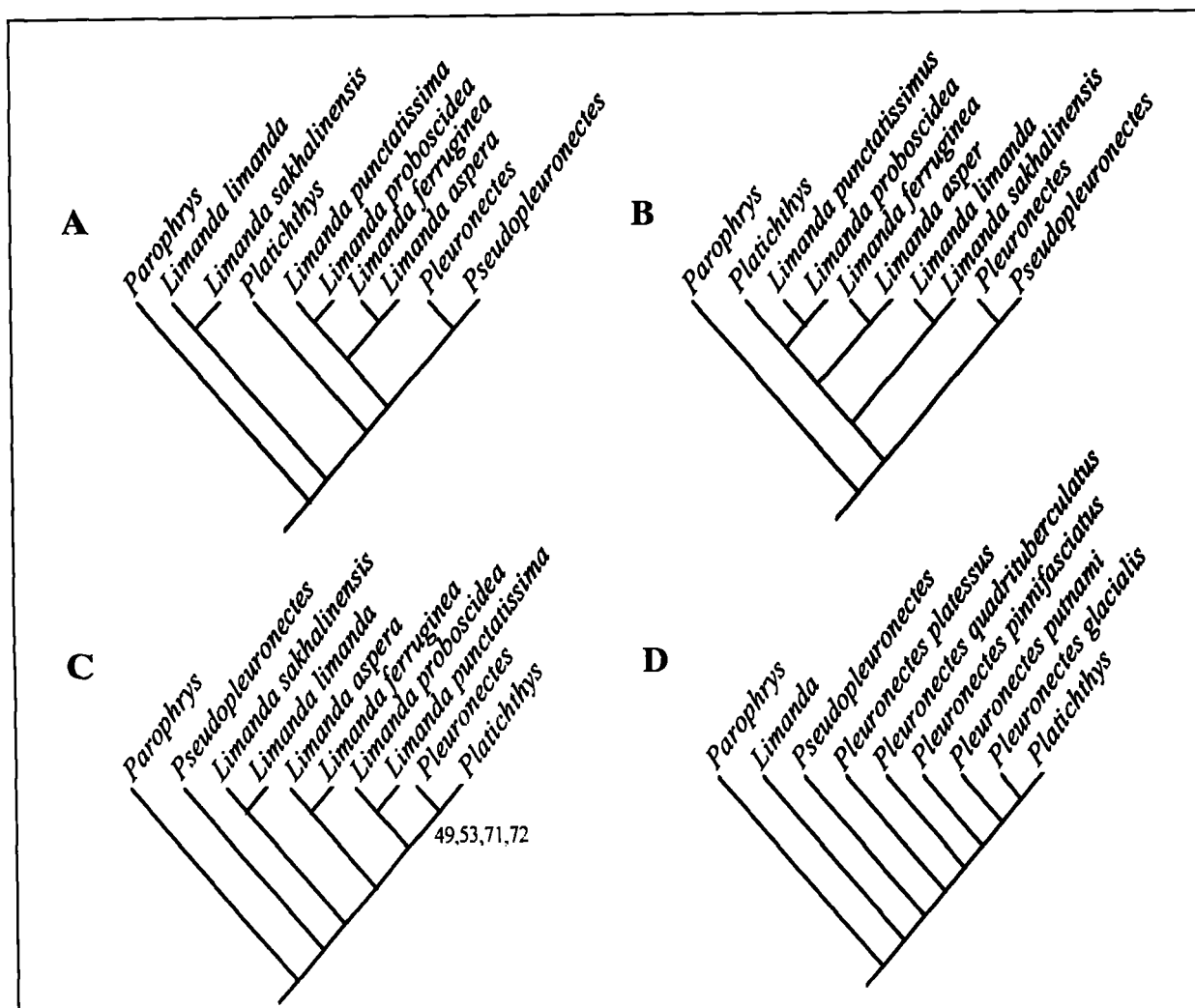


**Figure 18**

Alternative topologies for intrarelationships of Pleuronectini. (**A, B, and C**) Alternative topologies observed for the six species in *Limanda*. Each topology was resolved 16 of the 128 equally parsimonious cladograms. (**D**) Alternative topology for interrelationships in *Pleuronectes* observed in 16 of 128 equally parsimonious cladograms. Numbers correspond to characters in text.

Pleuronectidae but is not observed in *Pseudopleuronectes*, *Pleuronectes platessus*, and *P. quadrituberculatus*. The three alternatives are equally represented in 48 (37.5%) of the most parsimonious results but are not illustrated in the 50% majority-rule consensus tree (Fig. 1). All three alternatives (Fig. 18) maintain monophyly for *Platichthys*, *Pleuronectes*, and *Pseudopleuronectes*, individually. These alternatives place some or all species of *Limanda* as paraphyletic within a *Platichthys*, *Pleuronectes*, *Pseudopleuronectes* clade but do not exclude any species of *Platichthys*, *Pleuronectes*, and *Pseudopleuronectes*. Character states in support of these conflicting nodes illustrate homoplasy observed in *Limanda* (Fig. 18, A–C). Some or all species of *Limanda* are observed to share these character states with the other three genera. However, most of the exceptions and homoplasy observed in these structures fail to illustrate an evolutionary hypothesis that is more convincingly corroborated than the topology presented in the consensus tree (Fig. 1).

The fourth lineage unites *Pleuronectes* and *Pseudopleuronectes*. This clade was observed in 75% of the equally parsimonious trees (Fig. 1) and is supported by four synapomorphies (Fig. 17): less than six teeth on ocular-side maxilla (66, Fig. 9D); teeth incisorlike (70, Fig. 9D); teeth forming a continuous cutting edge (16, Fig. 9D); and dorsoposterior process of dentary similar in size on both ocular and blind sides (65, Fig. 9D), a reversal of the second lineage of Pleuronectinae.

Homoplasy observed in these morphological characters reveals a pattern of parallel evolution between this lineage and the clade formed by *Glyptocephalus*, *Microstomus*, and *Pleuronichthys* (Microstomini). Less than six teeth on the ocular-side premaxilla are also present in these three genera of Microstomini. The presence of incisorlike teeth is also observed in *Parophrys vetula* as well as *Glyptocephalus* and *Microstomus*. A continuous cutting edge found on the teeth has independently evolved in *Glyptocephalus* and *Microstomus*. The symmetrically sized dorsoposterior process of the dentary is not observed in *Pseudopleuronectes herzensteini*, *Pleuronectes platessus*, and *P. quadrituberculatus* and is a reversal that is paralleled in *Glyptocephalus* and *Microstomus*.

Alternative topologies observed in 32 of 128 (25%) trees unite either a monophyletic or paraphyletic *Pleuronectes* with *Platichthys* (Fig. 18, C and D). In *Pleuronectes* and *Platichthys* the mesethmoid has a thickened, triangular anterior margin (53, Fig. 8C). The fifth ceratobranchial has a strong medial curve forming a triangular plate (71, Fig. 3D). The teeth of the fifth ceratobranchial are in multiple rows (49, Fig. 3D), and these teeth are generally rounded or molariform (72, Fig. 3D). Three of these characters (49, 53, 71) are used to define the third lineage of Pleuronectini but notably exclude *Pseudopleuronectes*. The molariform teeth on the fifth ceratobranchial (72, Fig. 3D) are observed in *Pleuronectes* and only in *Platichthys bicoloratus*. The alternative hypothesis, indicating a sister relationship between *Pleuronectes* and *Platichthys*, has the same character support as the hypothesis presented in the consensus tree. However, this topology is parsimonious in only 32 trees and only in conjunction with one of the two alternatives that either position a paraphyletic *Limanda* after *Pseudopleuronectes* (Fig. 18C) or hypothesize a paraphyletic *Pleuronectes* (Fig. 18D). Support for either of these topologies is not well corroborated. Therefore, alternatives to the consensus tree are not as robust to the homoplasy observed in the analysis.

**Genus *Limanda*** Monophyly and intrarelationships of *Limanda* are unresolved by this analysis owing to homoplasy observed in these six species (Fig. 17). *Limanda punctatissima* and *L. proboscidea* are the only two pleuronectid species with bony prominences of the postocular ridge extending anteriorly onto the interorbital bar (103, Fig. 10E). *Limanda aspera* and *L. ferruginea* are united by three morphological characters: the supraoccipital crest not forming a groove for the dorsal-fin pterygiophores (38, Fig. 10, A and B); blind-side metapterygoid not articulated with entopterygoid (34, Fig. 2A), both reversals in Pleuronectini; and supratemporal of the blind side jointed at its anterior bifurcation (44, Fig. 13B). This character state has evolved independently five times in Pleuronectidae as it is also observed in *Cleisthenes herzensteini*, *Hippoglossoides elassodon*, *Lyopsetta exilis*, and *Reinhardtius hippoglossoides*. *Limanda limanda* and *L. sakhalinensis* are monophyletic in 75% of the trees (Fig. 1). Two character states unite these species: first epibranchial is bifurcated (12, Fig. 3A); and bony prominences on ocular-side postocular ridge absent (101). Both of these characters are reversals also observed in *Limanda aspera*. Alternative topologies observed in 32 (25%) other trees, place *Limanda sakhalinensis* and *L. limanda* as paraphyletic taxa in the tribe or as paraphyletic within a clade that unites these two species with *Limanda punctatissima* and *L. proboscidea*.

Although the species of *Limanda* are not resolved as a monophyletic group, they are distinguishable from other members of Pleuronectini. They have reduced dentition on the ocular side but maintain more than six teeth, where as other species of Pleuronectini generally have six or fewer (Norman, 1934). The teeth are bluntly conical or pointed with truncated tips, whereas all other members of this tribe have com-

pressed teeth with an incisorlike shape (Norman, 1934; Sakamoto, 1984a). Both of these tooth structures in *Limanda* are interpreted as synapomorphies for the Pleuronectini. There is little evidence in support for the monophyly of *Limanda*. Only one character state is shared by all six species: presence of gill rakers on second epibranchial (30, Fig. 3C). This character is a reversal of a reduced number of gill rakers defining the second lineage of Pleuronectinae (Fig. 6). There were 16 trees of 403 steps that hypothesized a monophyletic *Limanda* based on three reversals (Fig. 18D), including the presence of gills rakers on the second epibranchial. All 16 topologies were correlated with a hypothetical alternative to the consensus tree (Fig. 18D) such that a monophyletic hypothesis for *Limanda* is not resolved by consensus and is therefore not robust to the homoplasy observed in the analysis. However, the placement of these six species near the base of the second lineage in Pleuronectini and the shared morphological characters mentioned above suggest that a conservative approach to their nomenclature should be considered and that these six species should remain classified as *Limanda* until a more focused phylogenetic analysis is performed.

**Genus *Platichthys*** This genus contains three species: *P. bicoloratus*, *P. flesus*, and *P. stellatus*. It is monophyletic with five synapomorphies (Fig. 17): scales along median fins absent (104), a possible reversal in Pleuronectidae; scales on the body modified to form bony tubercles (105); gill rakers on second and third epibranchial absent (30, 31); and supratemporals on ocular and blind sides are fused to the cranium (106). Absence of gill rakers on the second epibranchial is observed only in the distant lineage *Verasper*. The absence of gill rakers on the third epibranchial also occurs in *Verasper* and *Pleuronectes platessus*. The ocular-side supratemporal fused to the cranium is homoplastic in *Limanda punctatissima*.

**Genus *Pleuronectes*** This genus contains five species: *P. glacialis*, *P. pinnifasciatus*, *P. platessus*, *P. putnami*, and *P. quadrituberculatus*. The monophyly of these five species was observed in 112 of 128 trees (87.5%) and is supported by two synapomorphies (Fig. 17): prominent dorsal crest extending from the supraoccipital to the blind-side frontal (52, Fig. 10, B and C); and presence of molariform teeth on fifth ceratobranchial (72, Fig. 3D). A prominent crest extending from the supraoccipital to blind-side frontal is a reversal within Pleuronectini, that is also observed in *Limanda aspera*. The presence of molariform teeth on the fifth ceratobranchial is only shared with *Platichthys bicoloratus*.

Alternative topologies observed in 16 of 128 trees (12.5%) place species of *Pleuronectes* as paraphyletic with *Platichthys stellatus*, *P. flesus*, and *P. bicoloratus* at the terminal end (Fig. 18D). This topology does not contradict the synonymy of *Liopsetta* (*sensu* Norman) within *Pleuronectes*. It does contradict the classification of *Platichthys*. However, as previously illustrated, the alternative topologies for the intrarelationships within Pleuronectini are based on homoplasy observed in *Limanda* such that the paraphyletic origin in *Pleuronectes* is correlated and observed in the same 16 trees indicating monophyly of *Limanda* (Fig. 18D).

**Genus *Pseudopleuronectes*** This genus contains five species: *P. americanus*, *P. herzensteini*, *P. obscurus* (not examined), *P. yokohamae*, and *P. schrenki*. The monophyletic status of this group is supported by three synapomorphies (Fig. 17): anterior margin of mesethmoid forming a thin plate (53, Fig. 8B); blind-side nasal bone absent (50); and demersal eggs (75). *Pseudopleuronectes obscurus* has character states synapomorphic for the fourth lineage of Pleuronectinae, uniting *Pleuronectes* and *Pseudopleuronectes*. These are the presence of incisorlike teeth forming a continuous cutting edge and close approximation of the fifth ceratobranchials (Norman, 1934). Although teeth on the fifth ceratobranchial are bluntly conical (Norman, 1934), as in *Pseudopleuronectes*, this character state is plesiomorphic at this phylogenetic level. However, presence of a demersal egg in *P. obscurus* (Hensley and Ahlstrom, 1984), is synapomorphic for *Pseudopleuronectes*.

Homoplasy and two exceptions observed in these morphological characters do not corroborate an alternative hypothesis. A clade uniting the four species of *Pseudopleuronectes* examined here, is observed in all 128 equally parsimonious cladograms. The thin plate structure of the mesethmoid is also observed in *Pleuronectes platessus*, and in more distant taxa, *Pleuronichthys verticalis*, *Dexistes rikuzenius*, and *Hippoglossoides*. The absence of a blind-side nasal bone is homoplastic in *Pleuronectes platessus* and *Limanda* (except *L. sakhalinensis*). It is also observed outside of Pleuronectini in *Microstomus bathybius*, *Pleuronichthys* (except *P. guttulatus*), *Cleisthenes*, and *Hippoglossoides*. A demersal egg is not observed in *P. herzensteini* and is homoplastic in *Lepidopsetta*.

## Summary of intrarelationships

The species examined in this analysis (53 of 59), represent the complete range of morphological variation found in the family. The character analysis outlines the characters synapomorphic for clades revealed in the consensus tree (Fig. 1).

The Pleuronectidae can be summarized as comprising large piscivorous species at the basal lineages,

whose jaws and dentition are nearly symmetrical, and species possessing more specialized dentition, jaw structure, and diverse feeding habits at subsequent lineages. The monophyly and intrarelationships of basal lineages in the Pleuronectidae are not supported by a large number of synapomorphies. This is inherent for taxa associated with basal lineages in which the majority of morphological features are plesiomorphic with respect to the ingroup under examination (Stiassny and de Pinna, 1994). However, the position of these basal lineages is key in establishing the polarity of character states for the more advanced taxa in Pleuronectidae.

Homoplasy observed in most of the 106 morphological characters was expected in an analysis containing this many taxa. The alternative topologies within Pleuronectini (Fig. 18) were supported by homoplasy but do not have better character support than the intrarelationships determined through consensus. These alternative topologies are not any less parsimonious than the topologies summarized by the consensus tree. Instead, the limited occurrence of these alternatives indicates that these topologies are not as robust to homoplasy as those summarized in the consensus tree. The taxonomic nomenclature established by the consensus tree is not in contradiction with alternatives. Based on the cladogram, this classification represents the most conservative nomenclature for such a diverse group of pleuronectids.

The interrelationships within most genera cannot be confidently supported, either because of a lack of observed morphological variation (as in *Glyptocephalus, Hippoglossoides*, and *Pleuronichthys*) or because of the large amount of homoplasy occurring at terminal nodes indicated by the low consistency index (ci=0.33) and a high retention index (ri=0.79), as in *Limanda, Pleuronectes*, *Pseudopleuronectes*, and *Platichthys*. In either instance, species interrelationships for these taxa do not warrant a formal description based on synapomorphies from this study. Additional morphological characters, such as the number of dorsal- and anal-fin rays, homoplastic at higher levels of universality may prove informative for species-level relationships. The developmental information summarized in Ahlstrom et al. (1984) has been expanding owing to the commercial popularity of many pleuronectid species (for example Fukuhara, 1988; Markle et. al., 1992). Yet there are still many pleuronectid species for which information of this kind is not yet available. Despite this lack of information across the family, it is certain that these developmental data can also be used in the future to help resolve natural groups among well-documented pleuronectid species.

The phylogenetic limitations of jaw and dental morphological characters is clearly illustrated in the convergent evolution of jaw structures observed between the tribes Microstomini and Pleuronectini. This is most evident in the dentition of *Glyptocephalus*, and *Microstomus,* compared with *Platichthys, Pleuronectes*, and *Pseudopleuronectes,* both of which have single row of incisorlike teeth that sometimes form a continuous cutting edge. However, monophyly for these taxa, based on jaw morphology and dentition, is not supported by other character states observed in the cranial bones and branchial apparatus. These other characters clearly resolve the monophyletic status and intrarelationships of these two groups within each of the two tribes, Microstomini and Pleuronectini. The trend of character reversal, 19 in total (Figs. 6 and 15), observed in Microstomini suggests that some members of this taxon may be positioned at a more basal node in Pleuronectidae prior to the fourth lineage. However, this alternative is not supported in any of the 128 most parsimonious trees. This analysis clearly places Microstomini as a lineage within the Pleuronectinae on the basis of 28 character states that were not reversals.

Six pleuronectid species were not examined in this analysis. They are *Clidoderma asperrimum*, *Hippoglossoides dubius*, *Microtomus shuntovi*, *Pseudopleuronectes obscurus*, *Pleuronichthys coenosus*, and *Reinhardtius evermanni*. These species are classified as members of Pleuronectidae on the basis of morphological characters obtained from the literature. In addition, their phylogenetic position is based on examination of external characters, radiographs, and literature. The *a posteriori* classification of these six species lends support for the functionality of this analysis, such that an individual species can be classified on the basis of uniquely derived features.

## Classification

The objectives for a formal classification of the Pleuronectidae were to recognize large groups within the family and to ensure that only natural groups are represented in the classification. This implied a revision of the established nomenclature. However, changes were minimal and aimed mainly at simplifying the existing nomenclature with its many monotypic genera.

Our results indicate that the Pleuronectidae is monophyletic and can be subdivided into 5 new subfamilies: Hippoglossinae, Eopsettinae, Lyopsettinae, Hippoglossoidinae, and Pleuronectinae. This classification is based on the 50% majority-rule consensus of 128 parsimony trees, obtained through heuristic search (Fig. 1). This is the first classification based on a complete phylogenetic analysis of the group. It

provides a simplified yet phylogenetically informative framework for future studies involving this family.

## Taxonomic list of the Pleuronectidae

Subfamily **Hippoglossinae**
Genus *Reinhardtius* (*R. evermanni*,[2] *R. hippoglossoides*, *R. stomias*)
Genus *Hippoglossus* (*H. hippoglossus*, *H. stenolepis*)
Genus *Verasper* (*V. moseri*, *V. variegatus*)
Genus *Clidoderma* (*C. asperrimum*[2])
Subfamily **Eopsettinae**
Genus *Eopsetta* (*E. grigorjewi*, *E. jordani*)
Subfamily **Lyopsettinae**
Genus *Lyopsetta* (*L. exilis*)
Subfamily **Hippoglossoidinae**
Genus *Acanthopsetta* (*A. nadeshnyi*)
Genus *Cleisthenes* (*C. herzensteini*, *C. pinetorum*)
Genus *Hippoglossoides* (*H. dubius*,[2] *H. elassodon*, *H. platessoides*, *H. robustus*)
Subfamily **Pleuronectinae**
Tribe **Psettichthyini**
Genus *Psettichthys* (*P. melanostictus*)
Tribe **Isopsettini**
Genus *Isopsetta* (*I. isolepis*)
Tribe **Microstomini**
Genus *Lepidopsetta* (*L. bilineata*, *L. mochigarei*)
Genus *Dexistes* (*D. rikuzenius*)
Genus *Pleuronichthys* (*P. coenosus*,[2] *P. cornutus*, *P. decurrens*, *P. guttulatus*, *P. ocellatus*, *P. ritteri*, *P. verticalis*)
Genus *Microstomus* (*M. achne*, *M. bathybius*, *M. kitt*, *M. pacificus*, *M. shuntovi*[2])
Genus *Glyptocephalus* (*G. cynoglossus*, *G. kitaharai*, *G. stelleri*, *G. zachirus*)
Tribe **Pleuronectini**
Genus *Parophrys* (*P. vetula*)
Genus *Limanda*[3] (*L. aspera*, *L. ferruginea*, *L. limanda*, *L. proboscidea*, *L. punctatissima*, *L. sakhalinensis*)
Genus *Platichthys* (*P. bicoloratus*, *P. flesus*, *P. stellatus*)
Genus *Pleuronectes* (*P. glacialis*, *P. pinnifasciatus*, *P. platessus*, *P. putnami*, *P. quadrituberculatus*)
Genus *Pseudopleuronectes* (*P. americanus*, *P. herzensteini*, *P. obscurus*,[2] *P. schrenki*, *P. yokohamae*)

[2] Species not included in analysis, phylogenetic position and classification determined *a posteriori*.
[3] Monophyletic status is uncertain.

The reclassification of several species is necessary to incorporate the new phylogenetic information. The changes to the classification are as follows:

1 *Atherestes evermanni*, *A. stomias*, and *Reinhardtius hippoglossoides* are united within *Reinhardtius* which is the oldest valid genus-group name. *Reinhardtius* (=*Atherestes*) *evermanni* was not examined and its position within the subfamily Hippoglossinae was determined *a posteriori*. Placement of *R. evermanni* within the clade uniting these three species is based on examination of external morphological characters, number of abdominal vertebrae, and the description provided in Norman (1934).
2 The genus *Eopsetta* (*sensu* Sakamoto, 1984a) with *E. exilis*, *E. grigorjewi*, and *E. jordani* is paraphyletic. The revised *Eopsetta* contains *E. grigorjewi* and *E. jordani* whereas *E. exilis*, is reassigned to the genus *Lyopsetta* as in Norman (1934).
3 *Hippoglossoides herzensteini* and *H. pinetorum* (*sensu* Sakamoto, 1984a) are reclassified as *Cleisthenes*, as in Norman (1934). This is a subjective reclassification because interrelationships of these two species within Hippoglossoidinae does not contradict the previous classification. It is based on the monophyletic status of these two species and maintains a hierarchically consistent nomenclature within the family.
4 A number of revisions were made to produce a simplified nomenclature that is hierarchically consistent with the phylogenetic interrelationships. Species of *Hypsopsetta* and *Pleuronichthys* (*sensu* Sakamoto, 1984a) are regrouped under *Pleuronichthys*. The species-group name (*guttulata*) is revised to agree with gender in the genus (i.e. *Pleuronichthys guttulatus*). The species of *Embassichthys* and *Microstomus* (*sensu* Sakamoto, 1984a) are regrouped under *Microstomus*. The species of *Errex*, *Glyptocephalus*, and *Tanakius* (*sensu* Sakamoto, 1984a) are regrouped under *Glyptocephalus*. The species of *Kareius* and *Platichthys* (*sensu* Sakamoto, 1984a) are regrouped under *Platichthys*.
5 The genus *Pleuronectes* (*sensu* Sakamoto, 1984a), with 19 species, is not monophyletic. According to our results *Pleuronectes* comprises only five species: *P. glacialis*, *P. pinnifasciatus*, *P. platessus*, *P. putnami*, and *P. quadrituberculatus*. The species-group name (*platessa*) is revised to correspond with gender in the genus (i.e. *Pleuronectes platessus*). Other species of *Pleuronectes* (*sensu* Sakamoto, 1984a) are reclassified as *Lepidopsetta bilineata*, *L. mochigarei*, *Parophrys vetula*, *Limanda aspera*, *L. ferruginea*, *L. limanda*, *L.*

*sakhalinensis*, *L. proboscidea*, *L. punctatissima*, *Pseudopleuronectes americanus*, *P. herzensteini*, *P. obscurus* (not examined), *P. schrenki*, and *P. yokohamae* on the basis of the oldest valid genus-group name for each species, with the exception of *Pseudopleuronectes schrenki*, and *P. obscurus*, previously classified as *Limanda schrenki* (Sakamoto, 1984b; Hensley and Ahlstrom, 1984) and *Liopsetta obscura* (Norman, 1934), respectively. Sakamoto's (1984a) classification was based on a 100% similarity observed among these 19 species. The new phylogeny is based on 67 additional morphological features that clearly differentiate and classify these 19 species.

6 The reclassification of *Pseudopleuronectes schrenki* is based on its position in all 128 most parsimonious trees, none of which united *P. schrenki* with other taxa exclusive of the three other species in *Pseudopleuronectes*. In addition to the three synapomorphies uniting *Pseudopleuronectes*, the most notable characteristic of *P. schrenki* in observation and in the literature is the presence of incisorlike teeth that form a continuous cutting edge (character 70, Fig. 9D, see also Sakamoto, 1984b). This character defines the fourth lineage of Pleuronectini, uniting *Pseudopleuronectes* and *Pleuronectes*, and excludes the other species of *Limanda* that have teeth with truncated tips or are bluntly conical (70, Fig. 9C). A review of literature describing *Pseudopleuronectes schrenki* (=*Limanda schrenki*) indicates a close relationship with *P. yokohamae* (=*Limanda yokohamae*) (Jordan and Starks, 1906). Norman (1934) synonymized *Limanda schrenki* under *Pseudopleuronectes yokohamae*. Studies dealing with egg characteristics also seem to synonymize *Pseudopleuronectes schrenki* with *P. yokohamae* (Yusa, 1960; Pertseva-Ostroumova, 1961). Recent studies (Sakamoto, 1984b) indicate that *P. schrenki* (=*Limanda schrenki*) is a valid species with similar characteristics to *P. yokohamae* (=*Limanda yokohamae*). Meristic counts of vertebrae, dorsal- and anal-fin rays are overlapping (Sakamoto, 1984a, 1984b). They also have similar dental structure. However, *P. schrenki* has a distinct pattern of bars on the dorsal- and anal-fin rays (Sakamoto, 1984b). Uncertainty surrounding the status of *Pseudopleuronectes schrenki* is also the result of the ineffective use of nomenclature. As illustrated in the above references, the classification of *Pseudopleuronectes yokohamae* as *Limanda yokohamae*, has led to a degree of confusion, further supporting the need to clearly identify natural groups on the basis of uniquely derived features. Although a further analysis is required to clearly assess the taxonomic status of *Pseudopleuronectes schrenki* and *P. yokohamae*, this analysis clearly indicates that neither should be classified as *Limanda*.

7 The reclassification of *Pseudopleuronectes obscurus* is based solely on information available from the literature. This species is confidently placed in the fourth lineage of Pleuronectini and its placement as a species of *Pseudopleuronectes* is supported by one synapomorphy, the presence of a demersal egg. A complete osteological examination of this species may test the validity of this classification.

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# Appendix

## List of characters

1 *Attachment of ocular-side frontal with mesethmoid.* 2 states, 1 step, cci=1.00: frontal of ocular side not in contact with mesethmoid, separated by prefrontal (state 0), frontal of ocular side in contact with mesethmoid (state 1), (see Fig. 104, p. 184 in Amaoka, 1969).

2 *Sensory canal of ocular-side preorbital (Sakamoto, 1984a).* 2 states, 3 steps, cci=0.33: present (state 0), absence (state 1). The presence or absence of a sensory canal in the ocular-side preorbital in the outgroup taxa *Psettodes* sp. could not be determined (state ?). A sensory canal is common in left-eyed flounders, (see Fig. 105, p. 187, in Amaoka, 1969).

3 *Morphology of metapterygoid.* 2 states, 2 steps, cci=0.50: ventral margin concave (state 0, Fig. 2A), observed in *Reinhardtius stomias* and all outgroup taxa. Ventral margin not concave nearly straight (state 1, Fig. 2, B–D).

4 *Articulation between first and second basibranchials.* 2 states, 8 steps, cci=0.13: wedgelike articulation between first and second basibranchial (state 0, Fig. 3A). No wedgelike articulation, first basibranchial loosely attached to second basibranchial by cartilage (state 1, Fig. 3, B–D).

5 *Articulation suture between second and third basibranchials.* 2 states, 3 steps, cci=0.33: wedgelike articulation between second and third basibranchial (state 0, Fig. 3A). No wedgelike articulation, second basibranchial loosely attached to third basibranchial by cartilage (state 1, Fig. 3, B–D).

6 *Haemapophysis through fusion of parapophysis of posterior most abdominal vertebrae (Sakamoto, 1984a).* 2 states, 4 steps, cci=0.25: present (state 0, Fig. 4, A, B, and D), absent (state 1, Fig. 4C).

7 *Accessory processes on ventral side of centrum.* 2 states, 5 steps, cci=0.20: present (state 0, Fig. 5A), absent (state 1, Fig. 5, B and C).

8 *Infraorbitals on ocular side (Sakamoto, 1984a).* 2 states, 2 steps, cci=0.50: absent (state 0), present (state 1). All pleuronectid taxa (except *Microstomus bathybius*) have infraorbital bones on the ocular side. This character state is shared with *Psettodes* and *Paralichthys lethostigmus.* The sensory canal bones are absent in other outgroup taxa examined (*Lepidoblepharon ophthalmolepis*, *Citharichthys arenaceus*, and *Paralichthys squamilentus*), and most taxa within the bothoid lineage, (see Table 6, p. 193 in Amaoka, 1969).

9 *Oil globules in yolk (Hensley and Ahlstrom, 1984).* 2 states, 3 steps, cci=0.33: present (state 0), absent (state 1). All outgroup taxa have at least one oil globule (Hensley and Ahlstrom, 1984).

10 *Morphology of olfactory lamellae (Norman, 1934).* 2 states, 2 steps, cci=0.50: olfactory lamellae radiating around a central rachis (state 0). Olfactory lamellae parallel without a central rachis (state 1).

11 *Morphology of anterior prootic foramen, on ocular side.* 2 states, 8 steps, cci=0.13: sphenotic forms dorsal margin of foramen (state 0, Fig. 7A). Pterosphenoid and prootic join to form dorsal margin of foramen (state 1, Fig. 7, B and C).

12 *Bifurcation of first epibranchial (Sakamoto, 1984a).* 2 states, 5 steps, cci=0.20: distal end of first epibranchial divided into two branches (state 0, Fig. 3, A and B), distal end of first epibranchial simple (state 1, Fig. 3, C and D).

13 *Spines or teeth on gill rakers (Sakamoto, 1984a).* 2 states, 1 step, cci=1.00: present (state 0, Fig. 3, A and B), absent (state 1, Fig. 3, C and D).

14 *Structure of suture between mesethmoid and blind-side prefrontal.* 3 states, ordered, 13 steps, cci=0.15: anterior margin of upper orbit is incomplete, mesethmoid and prefrontal on blind side not completely overlapping resulting in a space between them (state 0, Fig. 8A). Anterior margin on upper orbit is complete, mesethmoid and prefrontal on blind side completely overlapping or sutured with a small foramen present (state 1, Fig. 8, B and C). Same as state 1 but foramen absent (state 2, Fig. 8D). The character state for the mesethmoid and prefrontal is not applicable (na) for the outgroup taxa *Psettodes* sp. and *Lepidoblepharon ophthalmolepis* owing to the morphological differences in this region with respect to the ingroup taxa.

15 *Structure of first anal ptergyiophore.* 2 states, 3 steps, cci=0.33: thin (state 0). Broadly thickened (state 1).

16 *Uniformity of dentition.* 3 states, ordered, 6 steps, cci=0.33: dentition of variable lengths and size (state 0, Fig. 9A). Dentition of near equal or equal length (state 1, Fig. 9, B and C). Uniform dentition as in state 1 but teeth forming a continuous cutting edge (state 2, Fig. 9D).

17 *Development of interorbital process (Sakamoto, 1984a).* 3 states, unordered, 4 steps, cci=0.50: well developed (state 0, Fig. 10, A and C). Middle part absent (state 1). Not developed (state 2, Fig. 10, B, D, and E).

18 *Structure of hyomandibular of both ocular and blind sides.* 2 states, 2 steps, cci=0.50: anterior margin of hyomandibular is not broad (state 0, Fig. 2, A–C). Anterior margin of hyomandibular is flatly broadened (state 1, Fig. 2D).

19 *Dentition of third epibranchial (Sakamoto, 1984a).* 2 states, 1 step, cci=1.00: present (state 0, Fig. 3, A and B), absent (state 1, Fig. 3, C and D).

20 *Bony plates of the branchial arch (Sakamoto, 1984a).* 2 states, 2 steps, cci=0.50: present (state 0, Fig. 3, A and B), absent (state 1, Fig. 3, C and D).

21 *Number of rows of gill rakers on fourth ceratobranchial.* 3 states, unordered, 6 steps, cci=0.33: one row, second row absent or very reduced (state 0, Fig. 3, A and B). Zero rows (state 1). Two rows (state 2, Fig. 3, C and D). *Reinhardtius* may have 1 row of gill rakers on fourth ceratobranchial, but very modified and difficult to distinguish from bony plates.

22 *Fimbriation along posterior dorsal margin of the operculum.* 2 states, 2 steps, cci=0.50: absent (state 0, Fig. 2A), present (state 1, Fig. 2, B–D).

23 *Number of abdominal vertebrae.* 3 states, ordered, 9 steps, cci=0.22: counts for Pleuronectidae taken from Sakamoto (1984a, Table 13). Less than 12 (state 0). Between 12 and 14 (state 1). Greater than 15 (state 2).

24 *Shape of caudal fin.* 2 states, 2 steps, cci=0.50: caudal fin truncate, double truncate or rounded (state 0). Caudal fin lunate or emarginate (state 1).

25 *Position of migrated eye in relation to dorsal midline (Sakamoto, 1984a).* 2 states, 3 steps, cci=0.33: located on side of head (state 0). Near dorsal midline, visible on blind side (state 1).

26 *Increase in number of caudal vertebrae.* 3 states, ordered, 5 steps, cci=0.40: counts for Pleuronectidae taken from Sakamoto (1984a, Table 13). Less than or equal to 35 (state 0). From 36 to 41 (state 1). Greater than 41 (state 2).

27 *Foramen on blind-side dentary just below margin of dentition.* 2 states, 5 steps, cci=0.20: present (state 0), absent (state 1).

28 *Attachment of palatine with ocular-side pterygoid.* 2 states, 2 steps, cci=0.50: palatine and pterygoid attached (state 0, Fig. 2, A and D). Palatine and pterygoid not attached due to a reduction of the posterior ventral arm of the palatine (state 1, Fig. 2, B and C).

29 *Gill rakers on first epibranchial.* 2 states, 2 steps, cci=0.50: present (state 0, Fig. 3, A–D), absent (state 1).

30 *Gill rakers on second epibranchial.* 3 states, ordered, 5 steps, cci=0.40: present (state 0, Fig. 3, B and C). Reduced to just one gill raker at proximal base of epibranchial (state 1, Fig. 3, A and D). Absent (state 2).

31 Gill rakers on third epibranchial. 3 states, ordered, 5 steps, cci=0.40: present (state 0, Fig. 3B). Reduced to just one gill raker at proximal

base of epibranchial (state 1, Fig. 3D). Absence (state 2, Fig. 3C).

32 *Gill rakers on first hypobranchial.* 2 states, 4 steps, cci=0.25: present (state 0, Fig. 3, A–D). Reduced to just one gill raker at distal base of hypobranchial (state 1).

33 *Subdivisions of hypurals or hypurals and parhypurals (Sakamoto, 1984a).* 2 states, 1 step, cci=1.00: absent (state 0), present (state 1). Character states for the caudal skeleton is not applicable (na) for the outgroup taxa *Psettodes* sp. and *Lepidoblepharon ophthalmolepis* owing to the morphological differences in this region with respect to the ingroup taxa.

34 *Articulation of blind-side metapterygiod with entopterygoid.* 2 states, 7 steps, cci=0.14: absent (state 0, Fig. 2, A and B), present (state 1, Fig. 2, C and D). The metapterygoid is articulated to the pterygoid in outgroup taxa (Fig. 2A).

35 *Morphology of mesethmoid and prefrontal on blind side, special type for Verasper.* 2 states, 1 step, cci=1.00: large open foramen absent (state 0). Large open formamen formed between mesethmoid and prefrontal on blind side (state 1), autapomorphy for *Verasper*. The character state for the mesethmoid and prefrontal is not applicable (na) for the outgroup taxa *Psettodes* sp. and *Lepidoblepharon ophthalmolepis* owing to the morphological differences in this region with respect to the ingroup taxa.

36 *Gill rakers on second hypobranchial.* 2 states, 4 steps, cci=0.25: present (state 0, Fig. 3, A and C). Reduced to just one gill raker at distal base of hypobranchial (state 1, Fig. 3, B and D).

37 *Sphenotic process in relation to hyomandibular socket.* 2 states, 3 steps, cci=0.33: process position low on sphenotic to form dorsal roof of socket between sphenotic and prootic (state 0, Fig. 7A). Process is positioned higher on sphenotic and more anteriorly so as not to be associated with socket (state 1, Fig. 7, B and C).

38 *Supraoccipital crest.* 2 states, 7 steps, cci=0.14: single crest (state 0, Fig. 10, A and B). Double crest to form a groove for the insertion of the basal ends of pterygiophores for the dorsal fin (state 1, Fig. 10, C–E).

39 *Cardiac apophysis of urohyal (Sakamoto, 1984a).* 3 states, unordered, 8 steps, cci=0.25: cardiac apophysis is simple or slightly bifurcate at the posterior portion (state 0, Fig. 12, A and B) Cardiac apophysis is simple at tip with bifurcation positioned anteriorly on dorsal edge (state 1, Fig. 12, E and F). Cardiac apophysis is strongly bifurcate at the posterior portion (state 2, Fig. 12, C and D).

40 *Gill rakers on fourth epibranchial.* 2 states, 3 steps, cci=0.33: absent (state 0, Fig. 3, A–D), present (state 1).

41 *Rows of teeth in lower jaw (Norman, 1934).* 2 states, 6 steps, cci=0.17: multiserial or biserial rows of teeth (state 0). Uniserial row of teeth (state 1). The distribution from published accounts of this character was reexamined in the specimens used for this analysis. The state that was observed in these specimens was used if the number of rows was in conflict with the published accounts in Norman (1934).

42 *Barbed teeth (Norman, 1934).* 2 states, 2 steps, cci=0.50: absent (state 0), present (state 1).

43 *Supratemporals on ocular side.* 2 states, 7 steps, cci=0.1: supratemporal in one piece (state 0, Fig. 13A). Supratemporal in two pieces, jointed at anterior bifurcation point (state 1, Fig. 13B).

44 *Supratemporals on blind side.* 2 states, 5 steps, cci=0.20: Supratemporal in one piece (state 0, Fig. 13A). Supratemporal in two pieces, jointed at anterior bifurcation point (state 1, Fig. 13B).

45 *Scales on the surface eyes (Sakamoto, 1984a).* 2 states, 6 steps, cci=0.17: absent (state 0), present (state 1).

46 *Posterior region of supraoccipital.* 2 states, 2 steps, cci=0.50: presence of a flat plate triangular or diamond shaped extending posteriorly from supraoccipital between or overtop epiotics (state 0, Fig. 10, A, and C–E). Absence of posterior extension of supraoccipital (state 1, Fig. 10B).

47 *Anterior prootic foramen on blind side.* 2 states, 8 steps, cci=0.13: sphenotic forms dorsal margin of foramen (state 0, 7A). Pterosphenoid and prootic join to form dorsal margin of foramen (state 1, Fig. 7, B and C). The anterior prootic foramen entirely contained within prootic in outgroup taxa.

48 *Pterosphenoid on blind side.* 2 states, 3 steps, cci=0.33: pterosphenoid reduced, frontal and parasphenoid join to form posterior margin of orbit (state 0, Fig. 7B). Pterosphenoid large forming posterior margin of orbit (state 1, Fig. 7, A and C).

49 *Rows of teeth on fifth ceratobranchial.* 3 states, ordered 4 steps, cci=0.75: irregular single or multiple rows (state 0, Fig. 3A). Regular 2 rows (state 1, Fig. 3, B and C). Regular multiple rows or clustered (state 2, Fig. 3D).

50 *Nasal bone on blind side.* 2 states, 7 steps, cci=0.14: present (state 0), absent (state 1). The presence of a blind-side nasal bone could not be determined (state ?) for the outgroup taxa *Citharichthys arenaceus* either through cleared and stained material or through radiograph.

51 *Number of infraorbital bones on blind side (Sakamoto, 1984a).* 3 states, unordered 9 steps, cci=0.22: from five to seven (state 0). Greater than seven (state 1). Less than five (state 2). The number of infraorbital bones in *Citharichthys arenaceus* could not be determined (state ?) owing to the poor preservation of infraorbital bones for this specimen.

52 *Dorsal crest extending anteriorly from supraoccipital to blind-side frontal.* 2 states, 7 steps, cci=0.14: prominent narrow crest present, angled laterally to ocular side (state 0, Fig. 10, B and C). Reduced of absent crest resulting in a flattened posterior dorsal region on blind-side frontal (state 1, Fig. 10, A, D, and E).

53 *Anterior margin of mesethmoid.* 3 states, unordered, 10 steps, cci=0.30: open canal extending from frontal on ocular side (state 0, Fig. 8A). Thin plate (state 1, Fig. 8B). Closed canal extending from frontal on ocular side or from interorbital process if present. Process extending anteriorly with a triangular shape to make anterior edge thicker (state 2, Fig. 8C). Similar to state 2 but anterior edge reduced to form an irregular edge (state 3, Fig. 8D). The morphology of the mesethmoid in the outgroup taxa, *Psettodes* sp. and *Lepidoblepharon ophthalmolepis* is unlike any observed in the other outgroup taxa or within the ingroup and is coded as not applicable (na).

54 *Articulation of metapterygoid with ocular-side entopterygoid.* 2 states, 3 steps, cci=0.33: absent (state 0, Fig. 2, A–C), present (state 1, Fig. 2D). The metapterygoid is articulated to the pterygoid in outgroup taxa (Fig. 2A).

55 *Dentary fossa for the insertion of Meckel's cartilage on both ocular- and blind-side dentaries.* 2 states, 1 steps, cci=1.00. Present (state 0, Fig. 9, A and B), absent (state 1, Fig. 9, C and D).

56 *Ceratohyal foramen (Sakomoto, 1984a).* 2 states, 1 step, cci=1.00: present (state 0), absent (state 1).

57 *Intercalar in contact with basioccipital.* 2 states, 4 steps, cci=0.25: intercalar not joined to basioccipital (state 0, Fig. 7, A and B). Intercalar and basioccipital in contact (state 1, Fig. 7C).

58 *Posterior extension of supratemporal branch of lateral line (Norman, 1934).* 2 states, 4 steps, cci=0.25: absent (state 0), present (state 1).

59 *Prolongation of anterior dorsal-fin rays (Norman, 1934; Sakamoto, 1984a).* 2 states, 1 step, cci=1.00: absent (state 0), present (state 1).

60 *Rows of teeth in upper jaw (Norman, 1934).* 2 states, 3 steps, cci=0.33: multiserial or biserial rows of teeth (state 0). Uniserial row of teeth (state 1). Character state based on direct observation of materials mantained priority in observations conflicting with Norman (1934).

61 *Asymmetry in medial symphysis of premaxillae.* 2 states, 1 step, cci=1.00: blind-side premaxilla does not protrude past sagittal axis at anterior symphysis with ocular-side premaxilla (state 0, Fig. 9, A and B). Blind-side premaxilla overlaps or protrudes past sagittal axis (state 1, Fig. 9, C and D).

62 *Asymmetry in length of premaxillae.* 2 states, 2 steps, cci=0.50: ocular-side nearly equal or equal to length of blind-side premaxilla (state 0, Fig. 9, A and B). Ocular-side premaxilla shorter than blind-side premaxilla (state 1, Fig. 9, C and D).

63 *Ventral posterior curvature of blind-side premaxilla.* 2 states, 2 steps, cci=0.50: absent (state 0, Fig. 9, A and B), present (state 1, Fig. 9, C and D).

64 *Asymmetry of size of space along ventral margin of dentary and articular.* 2 states, 5 steps, cci=0.20: space nearly the same size (state 0, Fig. 9, A, B, and D). Asymmetrical space, blind side greater than ocular side (state 1, Fig. 9C).

65 *Asymmetry in size of dorsal posterior process of dentary.* 2 states, 5 steps, cci=0.20: symmetrical (state 0, Fig. 9, B and D). Asymmetrical, ocular side greater than blind side (state 1, Fig. 9, A and C).

66 *Reduction of teeth on ocular-side maxilla (Norman, 1934).* 3 states, ordered, 5 steps, cci=0.40: number of teeth on ocular side nearly equal or equal to those on blind side (state 0, Fig. 9, A and B). Ocular-side teeth fewer than blind- side teeth but greater than 6 (state 1, Fig. 9C). Ocular-side teeth fewer than blind-side teeth, less than 6 (state 2, Fig. 9D).

67 *Reduction of teeth on ocular-side dentary (Norman, 1934).* 3 states, ordered 6 steps, cci=0.33: number of teeth on ocular side nearly equal or equal to those on blind side (state 0, Fig. 9, A and B). Ocular-side teeth fewer than blind-side teeth but greater than 6 (state 1, Fig. 9C). Ocular-side teeth fewer than blind-side teeth , less than 6 (state 2, Fig. 9D).

68 *Epiotic process on ocular and blind sides.* 2 states, 3 steps, cci=0.33: process absent in *Microstomus pacificus* or barely evident in *Hippoglossoides* and *Reinhardtius* (state 0, Fig. 10, A–C). Process is clearly evident extending anteriorly from epiotics onto parietals in *Limanda* and *Platichthys* (state 1, Fig. 10, D and E).

69 *Asymmetry in size of entopterygoid.* 2 states, 3 steps, cci=0.3: blind side equal in size to ocular side (state 0, Fig. 2, A and B). Blind side smaller than ocular side (state 1, Fig. 2, C and D).

70 *Shape of teeth (Norman, 1934).* 4 states, ordered 6 steps, cci=0.50: sharply pointed (state 0, Fig. 9, A and B). Bluntly conical or with truncated tips (state 1, Fig. 9C). Incisorlike (state 2, Fig. 9D). Molariform (state 3).

71 *Shape of fifth ceratobranchial.* 3 states, ordered 5 steps, cci=0.40: straight "rod" shaped (state 0, Fig. 3, A and B). Slight curve on medial margin found in *Limanda, Parophrys, Psettichthys, Isopsetta* etc. (state 1, Fig. 3C). Strong curve on medial margin, the ceratobranchials forming or almost forming a triangular plate found in *Pleuronectes* and *Platichthys* (state 2, Fig. 3D).

72 *Dentition profile on fifth ceratobranchial.* 3 states, ordered, 6 steps, cci=0.33: pointed (state 0, Fig. 3, A and B). Bluntly pointed (state 1, Fig. 3C). Rounded or molariform (state 2, Fig. 3D).

73 *Structure of haemal spines in anteriormost caudal vertebrae.* 2 states, 6 steps, cci=0.17: broadly attached both anteriorly and posteriorly to centrum, lateral foramen in haemal arch present (state 0, Fig. 5B). Narrow at base, attached anteriorly to centrum, lateral foramen in haemal arch absent (state 1, Fig. 5, A and C).

74 *Structure of epiotics (Sakamoto, 1984a).* 2 states, 2 steps, cci=0.50: epiotics not joined to each other along dorsal posterior margin of skull (state 0). Epiotics joined (state 1), only observed in *Isopsetta isolepis, Microstomus pacificus.*

75 *Egg type (Hensley and Ahlstrom, 1984).* 2 states, 2 steps, cci=0.50: pelagic egg (state 0). Demersal egg (state 1).

76 *Thickened lips (Norman, 1934).* 2 states, 2 steps, cci=0.50: absent, thin lips (state 0), present, lips thickened (state 1). Taxa in Pleuronectini are also described as having thickened lips (Norman, 1934) but this is not as evident as in Microstomini.

77 *Structure of exoccipital and prootic.* 2 states, 2 steps, cci=0.50: exoccipital and prootic joined (state 0, Fig. 7B). Exoccipital and prootic not joined (state 1, Fig. 7, A and C).

78 *Postocular ridge on ocular side (Norman, 1934).* 2 states, 2 steps, cci=0.50: absent (state 0), present (state 1).

79 *Villiform teeth (Norman, 1934).* 2 states, 1 step, cci=1.00: absent (state 0), present (state 1).

80 *Foramen in blind-side prefrontal.* 2 states, 2 steps, cci=0.50: absent (state 0), present (state 1).

81 *Lateral process on ocular-side frontal.* 2 states, 3 steps, cci=0.33: absent (state 0, Fig. 7, A and C, Fig. 10, A, B, D, and E), present (state 1, Fig. 7B, Fig. 10C).

82 *Decrease in the number of caudal vertebrae.* 2 states, 3 steps, cci=0.33: counts for Pleuronectidae taken from Sakamoto (1984a, Table 13). Greater than 25 (state 0). Less than or equal to 25 (state 1). The polarity established for this character is an exception to the general outgroup comparison methodology. It is apparent that a caudal vertebrae count between 25 and 35 is plesiomorphic for Pleuronectidae and for many taxa within the bothoid lineage. Despite the heterogeneity in *Citharichthys arenaceus* and less than 25 vertebrae observed in *Lepidoblepharon ophthalmolepis* and *Psettodes* sp.; the reduction of caudal vertebrae observed within Pleuronectidae is considered a derived character state.

83 *Pterosphenoid on ocular side* . 2 states, 2 steps, cci=0.50: pterosphenoid reduced, frontal and parasphenoid join to form posterior margin of orbit (state 0, Fig. 7B). Pterosphenoid large and forms posterior margin of orbit (state 1, Fig. 7, A and C).

84 *Position and origin of dorsal fin (Norman, 1934; Sakamoto, 1984a).* 2 states, 1 step, cci=1.00: originating nearly on the median line of head, ancestral (state 0). Originating on blind side (state 1).

85 *Cartilagenous interspace between blind-side prefrontal and parasphenoid.* 2 states, 1 step, cci=1.00: present (state 0, Fig. 7, A and C), reduced or absent (state 1, Fig. 7B).

86 *Mesethmoid in relation to upper orbit (Sakamoto, 1984a).* 3 states, ordered, 3 steps, cci=1.00: completely forms anterior margin of orbit (state 0). Forms only part of anterior margin in orbit (state 1). Does not form part of orbit (state 2).

87 *Extension of intestine into body cavity (Sakamoto, 1984a).* 2 states, 1 step, cci=1.00: absent (state 0), presence (state 1).

88 *Number of caudal-fin rays.* 5 states, ordered, 7 steps, cci=0.57: the number of caudal-fin rays was taken as the modal value for counts in Sakamoto (1984a, Table 18). 18 or 19 (state 0), 20 (state 1), 21 (state 2), 22 (state 3), 23 (state 4).

89 *Degree of caudal-fin ray branching.* 3 states, unordered, 8 steps, cci=0.25: expressed as the number of caudal-fin rays minus the number of branched caudal-fin rays. Six unbranched rays (state 0). Less than 6 unbranched rays (state 1). Greater than 6 unbranched rays (state 2).

90 *Position of ventral anterior tip of pelvis of ocular side in relation to cleithra (Sakamoto, 1984a).* 2 states, 1 step, cci=1.00: pelvis posterior to cleithrum ancestral (state 0), observed in majority of outgroup as well as Pleuronectidae . Pelvis anterior to cleithrum autapomorphy for *Microstomus bathybius* (state 1).

91 *Structure of scales (Batts, 1964).* 2 states, 1 step, cci=1.00: radii extending anteriorly from focus of each scale (state 0). Radii completely surrounding focus of scale (state 1).

92 *Fimbriation along the posterior ventral margin of the interoperculum.* 2 states, 1 step, cci=1.00: absent (state 0, Fig. 2, A, B, and D), present (state 1, Fig. 2C).

93 *Fimbriation along posterior margin of the suboperculum.* 2 states, 2 steps, cci=0.50: absent (state 0, Fig. 2, A, B, and D), present (state 1, Fig. 2C).

94 *Relation of cleithra with urohyal (Sakamoto, 1984a).* 2 states, 1 step, cci=1.00: cleithra not inserted by tip of urohyal (state 0), most common state in bothoid group. Cleithra slightly inserted by tip of urohyal (state 1).

95 *Increase in the number of pyloric appendages on upper intestine (Norman, 1934).* 2 states, 1 step, cci=1.00: two or three pyloric appendages plus one on upper intestine (state 0). Two to four pyloric appendages plus two or three on upper intestine (state 1).

96 *Asymmetry in nasal bones (Sakamoto, 1984a).* 2 states, 1 step, cci=1.00: ocular side larger than blind side with blind side reduced or absent as recorded in character 50 (state 0). Blind side larger than ocular side (state 1). States could not be observed (state ?) in the outgroup taxa *Psettodes* sp., *Citharichthys arenaceus*, and *Paralichthys squamilentus* owing to the poor condition of the specimens around the dorsal anterior margin of the upper eye. A blind-side nasal bone was not observed in radiographs of these specimens prior to clearing and staining.

97 *Mucous cavities on blind side of head (Sakamoto, 1984a).* 2 states, 1 step, cci=1.00: absent (state 0), present (state 1).

98 *Interpterosphenoid bar.* 2 states, 7 steps, cci=0.14: absent (state 0), present (state 1). The interpterosphenoid bar is a medial extension of the pterosphenoid foramen. This morphological character can be observed only from a lateral view, through the pterosphenoid if it is thin, or from a ventral view if the parasphenoid is removed (Fig. 16).

99 *Foramen on ocular-side dentary just below margin of dentition.* 2 states, 11 steps, cci=0.09: present (state 0), absent (state 1).

100 *Post-ocular ridge on blind side.* 2 states, 1 step, cci=1.00: absent (state 0), present (state 1).

101 *Bony prominences along ocular-side postocular ridge.* 3 states, unordered, 4 steps, cci=0.50: bony prominences absent (state 0, Fig. 10D). Many small bony prominences (state 1, Fig. 10E). A series of enlarged prominences on postocular ridge in *Pleuronectes platessus* and *P. quadrituberculatus* (state 2).

102 *Bony prominences along blind-side postocular ridge.* 2 states, 3 steps, cci=0.33: bony prominences absent (state 0, Fig. 10D). Many small bony prominences present (state 1, Fig. 10E).

103 *Bony prominences extending anteriorly onto interorbital bar.* 2 states, 1 step, cci=1.00: prominences not extended anteriorly (state 0). Prominences extending anteriorly onto interorbital bar of the ocular-side frontal (state 1, Fig. 10E).

104 *Scales on median-fin rays (Sakamoto, 1984a).* 2 states, 1 step, cci=1.00: absent (state 0), present (state 1). The presence of scales on median-fin rays in the outgroup taxa *Paralichthys squamilentus* could not be determined (state ?), because it was apparent that all of the scales on this specimen had been lost during clearing and staining.

105 *Bony plates or tubercles on body (Sakamoto, 1984a).* 2 states, 1 step, cci=1.00: absent (state 0), present (state 1).

106 *Supratemporals fused to cranium (Sakamoto, 1984a).* 2 states, 2 steps, cci=0.5: not fused with cranium (state 0). Fused with cranium (state 1).

**Abstract.**—We examined 107 harbor porpoise (*Phocoena phocoena*) carcasses recovered from beaches in Maryland, Virginia, and North Carolina between 1994 and 1996 for evidence of entanglement in fishing gear. Stranded porpoises ranged in length from 102 to 128 cm, indicating that only juvenile porpoises are present in the nearshore waters of the Mid-Atlantic during winter. Of the 40 porpoises for which we could establish cause of death, 25 displayed definitive evidence of entanglement in fishing gear. Evidence of entanglement consisted primarily of line marks from nets; in four cases we were able to determine specifically that porpoises had become entangled in monofilament nets. These mortalities demonstrate the need for a directed observer program for coastal gillnet fisheries in the Mid-Atlantic.

# Documenting the bycatch of harbor porpoises, *Phocoena phocoena*, in coastal gillnet fisheries from stranded carcasses

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Large numbers of harbor porpoises (*Phocoena phocoena*) are killed in United States and Canadian commercial fisheries each year. For example, between 1200 and 2900 harbor porpoises were killed annually between 1990 and 1993 in the Gulf of Maine sink gillnet fishery (Bravington and Bisack, 1996). Porpoises from the Gulf of Maine population have also been killed in gillnet fisheries in the Bay of Fundy, where an estimated 424 and 101 porpoises were taken in 1993 and 1994, respectively (Trippel et al., 1996). Efforts are currently underway to reduce mortality in these fisheries by using a variety of mitigation strategies (Resolve[1]).

Harbor porpoises from the Gulf of Maine and Bay of Fundy are believed to constitute a single population (Palka et al., 1996). The population disperses during winter and some individuals move south to the Mid-Atlantic region (defined here as from New York to North Carolina) (Polachek et al., 1995). Strandings of harbor porpoises have been documented as far south as Florida

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[1] Resolve, Inc. 1996. Final draft of the Gulf of Maine/Bay of Fundy harbor porpoise take reduction team take reduction plan. A consensus document prepared by Resolve, Inc., Washington, DC, 33 p.

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(Polachek et al., 1995), but the southern limit of the range of the species is generally accepted to be Cape Hatteras, North Carolina (reviewed in Palka et al., 1996). Little is known about the distribution and ecology of this harbor porpoise population in winter; even less is known about interactions with commercial fisheries in the Mid-Atlantic region. Porpoises are taken in a variety of gillnet fisheries in this area (Read, 1994; Read et al., 1996), but to date it has not been possible to determine the full extent or nature of incidental catches in the southern portion of the range of this population. The impact of these incidental takes on the Gulf of Maine and Bay of Fundy population, therefore, is unknown.

Current monitoring efforts for estimating the magnitude of porpoise bycatch in gillnet fisheries in the Mid-Atlantic rely on observers placed aboard commercial fishing vessels operating in this region. The majority of these observed trips take place more than three miles from shore; coverage of nearshore commercial fisheries by observers is extremely limited. An alternative source of information on marine mammal mortality in these nearshore fisheries comes from documentation of recovered stranded carcasses. Here we augment current monitoring programs by reporting observations of stranded harbor porpoises that exhibit evidence of entanglement in the Mid-Atlantic region. Our intent is to provide this information to managers of observer programs, so that they may concentrate efforts in times and areas where entanglements have been documented.

## Methods

Porpoises stranded on the beaches of Maryland, North Carolina, and Virginia[2] in 1994, 1995, and 1996 were examined for evidence of entanglement by using the protocol developed by Haley and Read (1993). This protocol is used by personnel in regional stranding networks to assess the carcasses of stranded marine mammals for the presence of physical evidence consistent with entanglement in fishing gear. Physical evidence of entanglement includes impressions of net material in the epidermis, thin lacerations on appendages, and mutilation, including dismemberment and longitudinal cuts along the ventral abdomen into the body cavity (Fig. 1). In general, these observations are indicative of entanglement and death in fishing gear.

Carcasses were examined on the beach by stranding network personnel for fishery interactions and

[2] Carcasses retrieved in New York, New Jersey, and Delaware were not included in this study because comparable data on fisheries interaction were not available for these specimens.

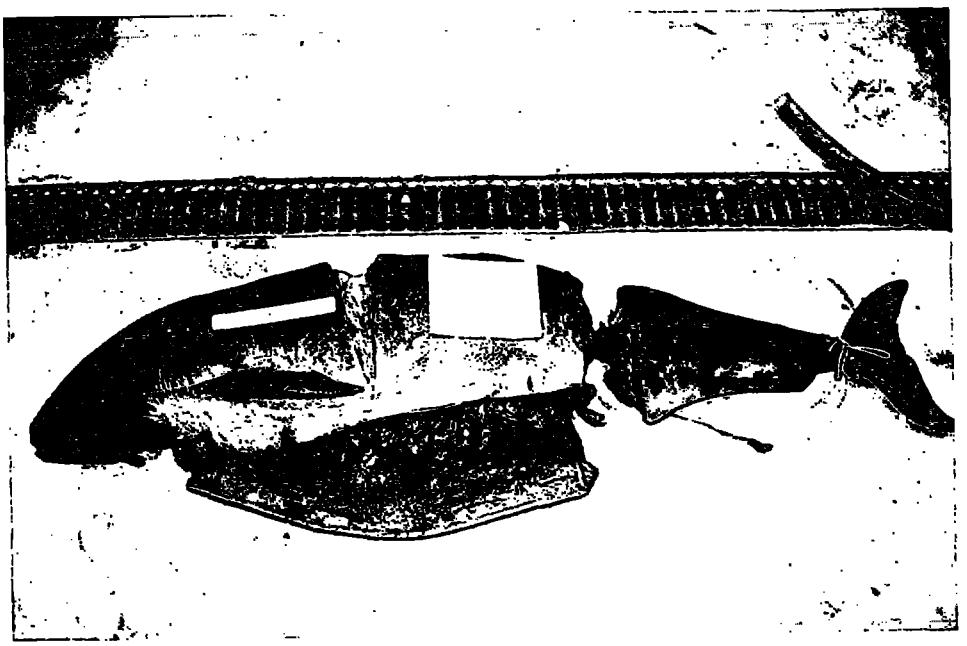

**Figure 1**

Mutilated carcass of a stranded harbor porpoise, *Phocoena phocoena* (MMSC 94-009). Note the net mark encircling the body just anterior to the insertion of the flipper.

were then stored frozen and examined at the Smithsonian Institution (SI) during necropsy workshops in May 1994, November 1995, and October 1996. In all but three specimens, assessments made by stranding network personnel on the beach were compared with independent assessments made at the SI. The determination of entanglement was conservative; an animal was scored as having been entangled only when external lacerations or impressions from net material or when mutilation consistent with entanglement was clearly present. If a carcass was too decomposed to determine cause of death definitively, or if skin was missing from a large proportion of the appendages, it was scored as "CBD" (could not be determined). Read and Murray[3] determined that all porpoises killed in sink gill nets and retrieved by observers exhibited external net marks. Thus, if a carcass could be assessed, but was scored as not having died of entanglement, the animal was assumed to have died of natural causes. Investigators attempted to identify the net type (i.e. monofilament or multifilament) responsible for the entanglement. The condition of the carcass on the SI scale, in which code 1 = alive, code 2 = dead but fresh, code 3 = moderately decomposed, code 4 = severely decomposed, and code 5 = skeletal remains was noted (Geraci and Lounsbury, 1993).

Standard morphometric data (Norris, 1961) were collected and body condition was evaluated as robust (convex epaxial surface and no "neck" evident) or emaciated (concave epaxial surface and "neck" evident) (Kastelein et al., 1997). Testis size and the presence or absence of ovarian scars (Read and Hohn, 1995) were used to determine the sexual maturity of individuals.

A chi-square test (Sokal and Rohlf, 1981) was used to determine whether there was a difference in carcass condition (SI codes 2 and 3) between entangled and nonentangled animals. To determine if there was a difference in body condition (robust or emaciated) in entangled and nonentangled animals, a $G$-test with an adjusted $G$-value for William's correction (Sokal and Rohlf, 1981) was conducted. Two $t$-tests were also used (Sokal and Rohlf, 1981): the first to compare the mean standard lengths of entangled and nonentangled stranded animals; the second to compare the mean standard lengths of stranded entangled animals and 10 nonstranded entangled animals. The standard lengths of the latter set of porpoises were collected by observers working on gillnet vessels off the coasts of Maryland and North Carolina during 1995 and 1996. Only those animals for which we were able to assess evidence of fisheries interaction were included in the statistical analyses; those scored as CBD were excluded from these analyses. Mean standard lengths are reported with associated standard deviations.

[3] Read, A, and K. Murray. 135 Duke Marine Lab Rd., Beaufort, NC 28516. Unpubl. data.

## Results

### Characterization of strandings

We examined 107 harbor porpoise carcasses (Table 1; Fig. 2). We are aware of 17 additional harbor porpoise strandings that occurred between 1994 and 1996 in the Mid-Atlantic but did not include these strandings in our analysis. Fifteen of these 17 carcasses were not examined according to our protocol, and data discrepancies could not be resolved for two others. Of the 107 porpoise carcasses that we included, 104 were examined independently both on the beach and at SI workshops. The remaining three carcasses were examined only on the beach; however, excellent photo-documentation allowed researchers at the SI to confirm the assessments for these three carcasses that had been made on the beach by stranding network personnel.

All harbor porpoise strandings occurred between January and May, with a peak between the months of March and May (Table 2). Fifty-five animals were male, 51 female; the sex of one was unidentifiable

**Table 1**

Summary of harbor porpoises (*Phocoena phocoena*) stranded along the Mid-Atlantic coast (by year and state) and evidence of entanglement. Yes = evidence of fisheries interaction; No = no evidence of fisheries interaction; CBD = evidence of fisheries interaction could not be determined owing to advanced decomposition of carcass.

| Year | State | Total | Yes | No | CBD |
|---|---|---|---|---|---|
| 1994 | NC | 5 | 0 | 2 | 3 |
| | MD | 9 | 4 | 2 | 3 |
| | VA | 39 | 13 | 3 | 23 |
| | Total | 53 | 17 | 7 | 29 |
| 1995 | NC | 7 | 1 | 3 | 3 |
| | MD | 2 | 1 | 1 | 0 |
| | VA | 15 | 0 | 2 | 13 |
| | Total | 24 | 2 | 6 | 16 |
| 1996 | NC | 11 | 2 | 2 | 7 |
| | MD | 3 | 1 | 0 | 2 |
| | VA | 16 | 3 | 0 | 13 |
| | Total | 30 | 6 | 2 | 22 |
| Total | | 107 | 25 | 15 | 67 |

owing to advanced decomposition. The condition of the animals varied: code-3 and code-4 carcasses occurred most frequently in North Carolina and Maryland; the greatest number of code-2 animals was found in Virginia (Table 3; Fig. 3).

We considered 34 animals to be robust and 35 animals emaciated; we could not assess body condition for the remaining 38 animals owing to advanced decomposition. We were able to determine the total standard length of 64 carcasses; 43 were too decomposed to obtain an accurate measurement. Stranded porpoises ranged in length from 102 cm to 128 cm (Mean: 116 ±6 cm; Fig. 4). We were able to assess sexual maturity of 82 porpoises, and all were immature.

### Characterization of fishery interactions

Of the 107 carcasses, we found 15 discrepancies between assessments of fishery interaction made by stranding personnel on the beach and those made at the SI workshops. Fourteen of these carcasses were assessed as entangled on the beach, but at the workshops these carcasses were considered too decomposed to evaluate evidence of entanglement. This deteriorated condition likely resulted from decomposition during transport from the beaches to the SI. Before a final assessment was made, we reviewed photographs and records taken at the initial examination of these 14 carcasses. We concluded from this analysis that four of these porpoises died as a result of entanglement (one of these carcasses, for example, had monofilament net wrapped around it when discovered on the beach). Photographs of ten of these carcasses were inconclusive, therefore, to be conservative, we scored them as "CBD." Another carcass was initially scored on the beach as too decomposed for evaluation, but subsequent assessment at the workshop revealed clear signs of entanglement.

Owing to decomposition of the carcasses, only 40 of the 107 porpoises were assessed for signs of entanglement. Of these, a total of 25 (63%) displayed clear evidence of entanglement (Table 1). Entangled

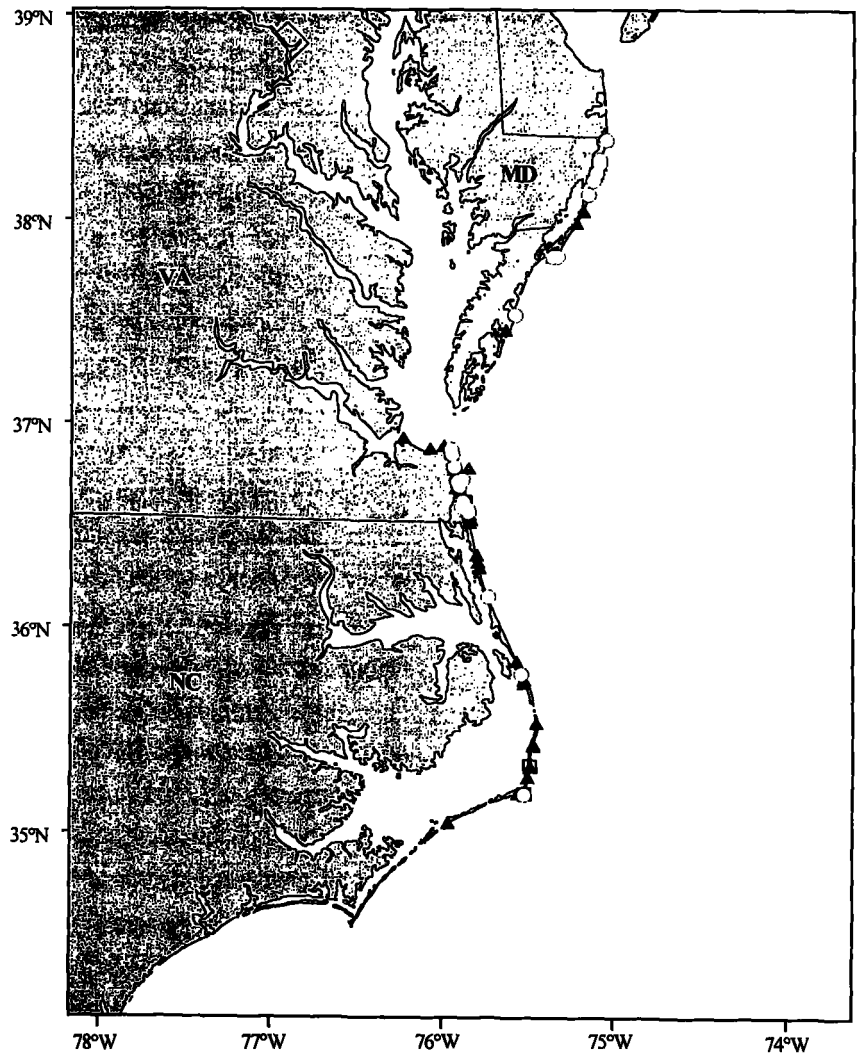


**Figure 2**

Map of the Mid-Atlantic coast showing stranding locations of harbor porpoises, *Phocoena phocoena*, between 1994 and 1996. Open circle = evidence of fishery interaction; open square = no evidence of fishery interaction; closed triangle = evidence of fishery interaction could not be determined due to advanced decomposition of carcass.

**Table 2**

Summary of harbor porpoises (*Phocoena phocoena*) stranded along the Mid-Atlantic coast by month. Yes = evidence of fisheries interaction; No = no evidence of fisheries interaction; CBD = evidence of fisheries interaction could not be determined owing to advanced decomposition of carcass.

| Month | Yes | No | CBD | Total |
|---|---|---|---|---|
| January | 0 | 0 | 1 | 1 |
| February | 2 | 0 | 0 | 2 |
| March | 8 | 7 | 11 | 26 |
| April | 14 | 7 | 39 | 60 |
| May | 1 | 1 | 16 | 18 |
| Total | 25 | 15 | 67 | 107 |

porpoises were observed in all three states between the months of February and May; most ($n$=13) entangled porpoises were found on the beaches of Virginia (Fig. 2; Table 1) in March and April 1994 (Table 2). Twelve entangled animals were male; 13 were female. We were able to positively identify four cases of entanglement in monofilament gill nets.

Nine of the 25 entangled porpoises were fresh (code 2); 14 were moderately decomposed (code 3); two were very decomposed (code 4). The proportion of code-2 and code-3 porpoises in the sample of entangled porpoises was not significantly different from that of nonentangled animals ($\chi^2$=0.82, df=1, $P$=0.36). We were able to assess evidence of entanglement for 93% ($n$=13) of the code-2 animals; 41% ($n$=24) of the code-3 animals; and 9% ($n$=3) of the code-4 animals. Fifteen of the entangled animals were robust, and six were emaciated; four were too decomposed to allow us to determine body condition. The proportion of robust animals in the entangled sample was significantly greater than that in the nonentangled sample ($G_{adj}$=23.51, df=1, $P$<0.001). None of the entangled animals displayed any unusual gross signs of pathology.

The mean total length of entangled animals was 116 ±5 cm (range: 112–128 cm; Fig. 4). The mean total length of entangled porpoises was not significantly different from that of nonentangled animals (116 ±7 cm; $t$=0.396, df=36, $P$=0.69). The mean total length of the entangled stranded animals was significantly less than that of porpoises killed at sea and examined by observers (131 ±14 cm; $t$=2.97, df=9, $P$=0.015).

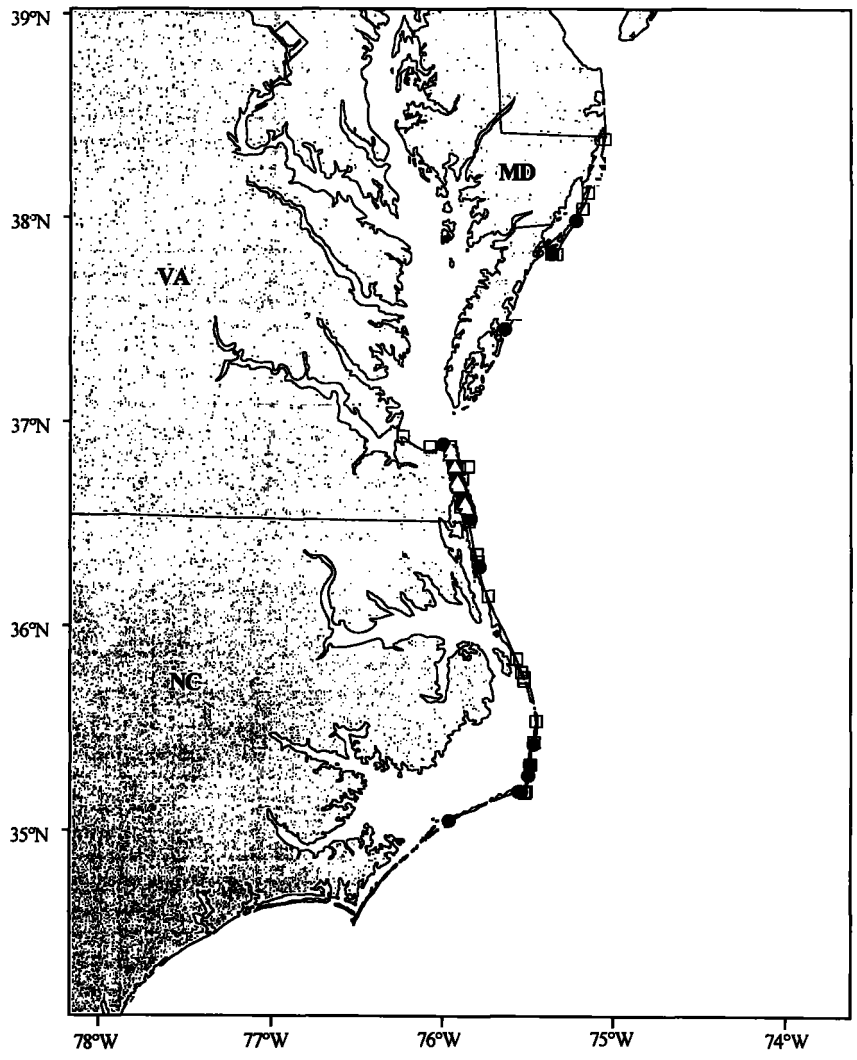


**Figure 3**

Map of the Mid-Atlantic coast showing stranding locations of harbor porpoises, *Phocoena phocoena*, between 1994 and 1996. Open triangle = SI code 2; open square = SI code 3; closed circle = SI code 4.

**Table 3**

Summary of Smithsonian Institution codes to define condition of harbor porpoises (*Phocoena phocoena*) stranded along the Mid-Atlantic coast by state. One animal stranded in Virginia was in code-5 condition. Code 1 = alive; code 2 = dead but fresh; code 3 = moderately decomposed; code 4 = severely decomposed; code 5 = only skeletal remains noted.

| SI Code | NC | VA | MD | Total |
|---|---|---|---|---|
| 2 | 0 | 10 | 4 | 14 |
| 3 | 14 | 37 | 7 | 58 |
| 4 | 9 | 22 | 3 | 34 |
| Total | 23 | 69 | 14 | 106 |

## Discussion

Here we have documented fisheries mortality in stranded harbor porpoises killed in coastal gill net fisheries in the Mid-Atlantic between 1994 and 1996. However, these deaths represent only an unknown proportion of the total number of porpoises killed in nearshore fisheries along the Mid-Atlantic. Many carcasses were too decomposed to determine cause

of death, and our documentation of entanglement was conservative. In addition, it is likely that not all animals entangled in nearshore gill nets reached the beach.

Detailed examination of stranded carcasses can be a useful means of identifying bycatch of harbor porpoises, and other marine mammals, in nearshore gillnet fisheries. This method is not, however, a surrogate for at-sea observer programs that monitor bycatch rates. The gillnet fisheries that operate along the coastal waters of the Mid-Atlantic are diverse, complex, and their activities poorly documented. An observer program is necessary to provide an unbiased estimate of the number of animals killed in these fisheries, so that a complete assessment can be made of this anthropogenic source of mortality.

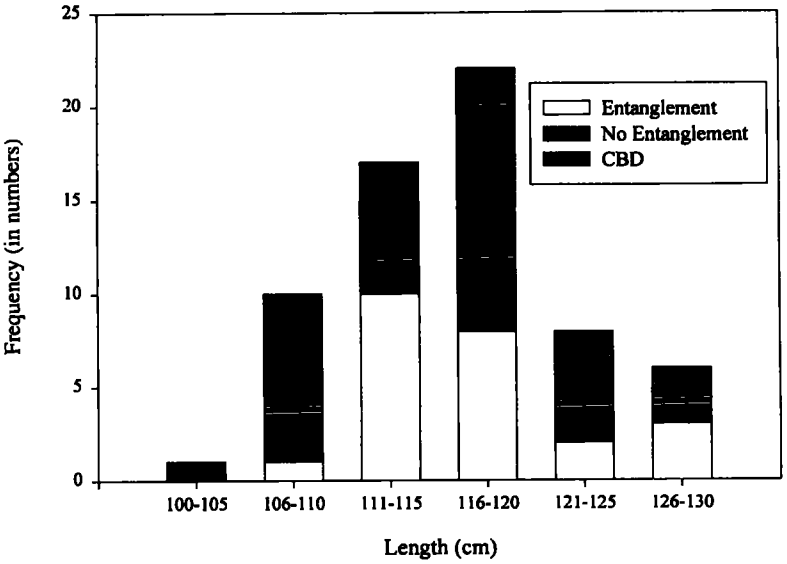


**Figure 4**

Frequency distribution of the lengths of stranded harbor porpoise, *Phocoena phocoena*, carcasses showing evidence of entanglement, no evidence of entanglement, or carcasses for which evidence of entanglement could not be determined owing to advanced decomposition of the carcass.

Accurate assessment of carcasses requires consistent and conservative use of an objective protocol, such as that described by Haley and Read (1993), by trained stranding network personnel. The process of transporting, freezing, and thawing carcasses may obscure subtle evidence of entanglement, so it is important for experienced observers to examine fresh carcasses. At the necropsy workshops, for example, we were unable to assess 14 carcasses that were previously scored as entanglements when examined fresh on the beach.

All stranded porpoises were young and sexually immature. Interestingly, however, both mature and immature porpoises have been taken by gillnet fisheries operating in the Mid-Atlantic. Most of these observed bycatches have been recorded at some distance from shore, suggesting that some age-based segregation occurs in this population during winter. An alternative explanation is that adult porpoises captured in gill nets do not wash ashore. This latter explanation seems unlikely for two reasons. Because of their larger size, carcasses of adults should be more likely to reach shore intact than those of juveniles. In addition, most (17 out of 24) of the observed porpoises taken as bycatch in the Mid-Atlantic were tagged before being discarded; none of these tagged porpoises have subsequently washed up on the beaches. Thus, it appears that only juvenile porpoises are present in the nearshore waters of the Mid-Atlantic during winter.

The proportions of code-2 and code-3 stranded carcasses were not significantly different in the samples of nonentangled and entangled porpoises, indicating that the carcasses of porpoises killed in fisheries were likely originating at similar distances from shore as those animals dying of natural causes. In addition, the lengths of entangled porpoises were similar to those that died from other means. All stranded porpoises, entangled and nonentangled, were from the same segment of the population —young animals in nearshore waters. The distinguishing feature of these two samples is that a larger proportion of the nonentangled animals were emaciated, indicating that they may have died of starvation, whereas most of the entangled animals were in good body condition when they died.

The majority of strandings were reported in Virginia, but this may be due in part to the regular monitoring of beaches in the southern portion of this state. The beaches of Virginia are patrolled frequently by stranding network personnel; therefore stranded porpoises are discovered soon after they appear on the beach. In Maryland beaches are patrolled daily by national and state park personnel. Lower numbers of stranded harbor porpoises in Maryland, therefore, likely reflect lower abundance or different fishing effort and hence fewer strandings in this area. The Outer Banks of North Carolina, by contrast, have not been patrolled frequently, resulting in fewer reports of stranded porpoises. The condition of harbor porpoise carcasses retrieved in North Carolina was poor in relation to those retrieved in

Virginia. Harbor porpoises are small animals and are consumed quickly by scavengers. The National Marine Fisheries Service Beaufort Lab and the University of North Carolina at Wilmington are currently increasing the scope and frequency of beach surveys in the Mid-Atlantic to locate carcasses before they are severely decomposed or scavenged.

We were able to identify the type of net involved in the entanglement of only a small number of animals; therefore at present it is not possible to determine the type of gillnet fisheries in which these porpoises were taken. We assume that all entangled animals were caught in gillnet fisheries operating very close to shore, because the carcasses of porpoises captured farther offshore are not likely to reach the beach intact (see above). Although we could not determine in which fisheries the porpoises were entangled, we can draw attention to patterns of fishing activities that correspond to the time and location of strandings. For example, coastal gillnet fisheries for dogfish (*Squalus* spp.) and American shad (*Alosa sapidissima*) are active during March and April in the Mid-Atlantic, corresponding to the period in which most harbor porpoise strandings occur. A large number of entangled animals stranded in Virginia during the spring of 1994, when the coastal fishery for American shad was operating near the Virginia coast. Records from the state of Virginia indicate that 79 licensed watermen, who individually harvested more than 100 lb of American shad, harvested a total of approximately 387,000 lb of American shad in March and April 1994 (Bower[4]). Both the number of licensed watermen who harvested more than 100 lb of shad and the total harvest decreased dramatically in 1995 and 1996 to 50 and 43 licensed watermen and approximately 161,000 and 235,000 lb, respectively (Bower[4]). We noted a corresponding decrease in the number of stranded harbor porpoises in Virginia in the spring of 1995 and 1996 (Table 1).

Here we have attempted to characterize interactions between nearshore gillnet fisheries and juvenile harbor porpoises in the Mid-Atlantic. The bycatch of harbor porpoises in offshore gillnet fisheries in the Mid-Atlantic is currently monitored closely by a National Marine Fisheries Service observer program and thus can be quantified. Unfortunately, the same is not true for harbor porpoise mortality in the coastal gillnet fisheries. There is a need for a directed observer program for nearshore gillnet fisheries in the Mid-Atlantic to better estimate overall mortality of harbor porpoises owing to fishery interactions in this region. Quantifying this mortality will help in management and conservation efforts for harbor porpoises in the Mid-Atlantic.

[4] Bower, D. Virginia Marine Resources Commission, Newport News, VA 23607. Personal commun.

## Acknowledgments

We would like to thank all the stranding network volunteers in Maryland, Virginia, and North Carolina for their dedicated efforts in collecting harbor porpoise carcasses. We thank Aleta Hohn and two anonymous reviewers for their helpful comments on earlier drafts of this paper. The Smithsonian Institution provided facilities and logistical support for the necropsy workshops. This research was funded by Co-operative Agreements NA57FL0557 and NA67FL0431 from the Northeast Fisheries Science Center to A. J. Read, Purchase Order 43AANF501263 from the Office of Protected Resources, NMFS, to A. J. Read, and Grant N00014-93-1-0640 from the Office of Naval Research to D. A. Pabst.

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# Age, growth, and reproduction of black grouper, *Mycteroperca bonaci*, in Florida waters

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**Abstract.**—We examined 1166 black grouper ranging from 155 to 1518 mm TL collected in South Florida waters from 1994 to 1996. Among all black grouper that we sexed, females ranged from 155 to 1310 mm in length (mean= 696, $n$=834), and males ranged from 947 to 1518 mm (mean=1255, $n$=54). Ages of 927 black grouper ranging from 155 to 1518 mm TL were estimated from thin-sectioned otoliths (sagittae). Marginal-increment analysis of grouper 1–7 years old suggested that a single annulus was formed each year during May–June. Black grouper appear to reach a maximum age of at least 33 years, but ages of fish older than 7 years are unvalidated. Growth of the black grouper in our study was rapid until an age of about 10 years and then slowed considerably. The von Bertalanffy growth equation for black grouper was $TL = 1306.2(1-e^{(-0.169(Age+0.768))})$. Black grouper are protogynous hermaphrodites. We estimated that 50% of the females in the population had reached sexual maturity by 826 mm and an age of 5.2 years. By a length of 1214 mm and an age of 15.5 years, 50% of the females in our sample had transformed into males. The presence of large females in the population suggests that some females may not transform into males. The scarcity of transitional grouper ($n$=1) in our sample suggests that transition occurs quickly. Black grouper appear to spawn yearround, but peak spawning occurs during winter and early spring. Vitellogenic oocytes and oocytes in the final stages of maturation were most common during January–March.

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The black grouper, *Mycteroperca bonaci*, is a large, piscivorous epinepheline serranid that inhabits coral reefs and rocky ledges from North Carolina to Florida, in the Gulf of Mexico, off Bermuda, in the West Indies, and from Central America to southern Brazil (Smith, 1971; Bullock and Smith, 1991). The black grouper supports important commercial and recreational fisheries in South Florida. Commercial landings of the species consistently exceed landings of any other grouper in the Florida Keys. Statewide, the estimated value of Florida black grouper commercial landings has decreased from $2.7 million in 1990 to $1.1 million in 1996 (Florida Department of Environmental Protection Marine Fisheries Information System[1]).

Florida imposes both recreational and commercial regulations on black grouper caught in state waters. There is a recreational minimum size limit of 20 inches (508 mm) total length (TL) and an aggregate daily bag limit of five groupers, including black, yellowfin (*Mycteroperca venenosa*), gag (*M. microlepis*), red (*Epinephelus morio*), yellowmouth (*M. interstitialis*), and scamp (*M. phenax*). The commercial minimum size limit is also 20 inches TL. Federal regulations include a 20-inch minimum size limit and an annual quota for the shallow-water grouper complex, which includes the black grouper. In addition, the activities of commercial longline fishermen east of Cape San Blas, Florida (85°22'W), are restricted to depths greater than 20 fathoms.

Even though the black grouper fishery is regulated in both state and federal waters, little is known about the species' biology, and existing data are inadequate to evaluate the effect of fishing mortality on populations. Like most grouper species, black grouper are protogynous hermaphrodites (García-Cagide and García, 1996). Hermaphroditic species may respond differently to fishing mortality than typical gonochoristic species do, and in some situations, protogynous hermaphrodites may be more sensitive to overfishing than gonochorists (Bannerot et al., 1987). For example, size-selective fishing mortality can greatly skew population sex ratios towards females, which may affect spawning success. In addition, many grouper species form large spawning aggregations that can be easily overfished (Sadovy, 1994). Only Manooch and Mason (1987) have specifically addressed black

[1] Florida Dep. Environmental Protection Marine Fisheries Information System. 1997. Florida Marine Research Inst., Florida Dep. Environmental Protection, 100 Eighth Ave. SE, St. Petersburg, Florida 33701-5095.

grouper life history in South Florida waters, but their study was limited because most of the fish examined were eviscerated and could not be sexed. Consequently, they could not describe sex-specific growth rates, length and age at sexual maturity, length and age at sexual transition, or sex ratios. Furthermore, black grouper often attain much larger sizes than the largest fish aged by Manooch and Mason, who acknowledged that black grouper can probably live longer than the oldest fish they aged (14 years). García-Cagide and García (1996) estimated the length at sexual maturity, the length at transition from female to male, and described seasonal spawning patterns of black grouper captured off Cuba, but they did not estimate ages of the fish they examined. Additional information on growth, maturation, and the length and age at transition are needed to fully assess the status of black grouper stocks. Our article describes growth, length and age at maturity, length and age at sexual transition, dichromatism between the sexes, and seasonal patterns of gonad development. In addition, we used marginal-increment analysis to validate the ages of young black grouper.

## Methods

### Collections

We obtained black grouper from a variety of sources throughout the Florida Keys and Florida's Gulf coast from November 1994 to November 1996. Most of the black grouper in our sample were caught by spear fishermen and landed in the Florida Keys ($n$=733). Commercial hook-and-line and bottom longline black grouper catches were landed and sampled at fish houses in Pinellas County on Florida's Gulf coast ($n$=433). Commercial fishermen captured grouper primarily south of 25°N in depths greater than 37 m, but some catches were made north of 25°N along the Florida Gulf coast to the Florida Panhandle in depths of 37–100 m. Most of the black grouper landed in Pinellas County were caught on or near the Tortugas Banks west of the Florida Keys by commercial longline fishermen, whose operations are restricted by federal regulations to depths greater than 20 fathoms (37 m).

Standard length (SL), fork length (FL), and total length (TL) were measured to the nearest millimeter (mm). Total length was measured following Hubbs and Lagler (1964). Fork length was measured as the center-line length from the tip of the lower jaw to the center of the caudal fin. Unless otherwise indicated, all lengths reported are total lengths. Large grouper were weighed to the nearest 50 grams and smaller grouper were weighed to the nearest gram. Otoliths (sagittae) were removed, rinsed in water, and stored dry until sectioned. Otoliths were weighed to the nearest 0.01 mg. Gonad weight (g) was recorded, and gonad samples for histology were removed from the fish and preserved in 10% buffered formalin; they were later soaked in water for one hour and then stored in 70% ethanol.

We examined most grouper to detect color changes that might be associated with the sex of the fish. All of the fish we examined were dead and had been on ice for several hours to a week. The colors of the pectoral, anal, dorsal, and caudal fins were recorded throughout the year during routine sampling of gonads and otoliths. Only grouper for which we had gonad histology samples were selected for differential color analysis.

### Age and growth

The left sagitta was usually used for age estimation; however, in cases where the left otolith was broken, lost, or damaged during processing, the right otolith was substituted. We prepared most otoliths by using a Buehler Isomet low-speed saw with a diamond blade to cut three or four thin sections to a thickness of approximately 0.5 mm, one of which was through the otolith core. Sections were then mounted on a microscope slide with Histomount. Initially, we prepared some otoliths for age estimation by embedding them in Spurr, a high-density plastic medium (Secor et al., 1992). A 1- to 2-mm-thick transverse section containing the otolith core was cut. The section was mounted on a microscope slide with thermoplastic glue (CrystalBond 509 adhesive) and polished with "wet/dry" sandpaper (grit sizes ranging from 220 to 2,000) until annuli were visible. Sections were then polished on a Buehler polishing cloth with 0.05-μ gamma alumina powder to remove scratches. There was no consistent difference in the quality of either preparation technique. Mounting the sections in Histomount took less time than embedding them in Spurr, so we adopted it as our standard protocol.

Annuli were counted using compound microscopes equipped with transmitted light and dissection microscopes equipped with reflected light. Two independent readers counted annuli on each otolith section three times each, for a total of six counts for each otolith. Thirty-two otoliths were considered unreadable by one or both readers and were discarded from our analysis before the completion of six readings. Annulus counts for individual otoliths often varied among readings. We established criteria for accepting or rejecting individual otoliths by calculating a coefficient of variation:

$$CV = (SD/\bar{X} \times 100),$$

where $SD$ = the standard deviation of counts for a given otolith; and
$\bar{X}$ = the mean annulus count for a given otolith.

After six readings were completed for all otoliths, otoliths for which the CV>12% were again read independently by each reader without knowledge of previous annulus counts. The count with the greatest difference from the mean of all counts was then discarded and replaced with a new count made by the reader whose reading was discarded. This protocol was repeated twice, and if the CV for a given otolith remained >12%, the otolith was rejected from our analysis.

The von Bertalanffy (1957) growth equation $TL_t = L_\infty(1-e^{(-K(t-t_0))})$ was fitted to observed age-length data with nonlinear regression procedures. Age was estimated as the mean of all six annulus counts. We did not attempt to backcalculate the length at which the last annulus was formed because of the variability among annulus counts for most otoliths. Our estimates of length at age thus include some seasonal growth that occurred after the formation of the final annulus. To estimate mean length at age, we rounded all ages to the nearest integer, but in growth and maturity models the mean age was not rounded to an integer and fractional ages were used. Length-weight regressions were calculated by linear regression of $\log_{10}$-transformed data.

## Age validation

Measurements for marginal-increment analysis were made with a digital image-processing system on an axis extending along the sulcal ridge from the otolith's core to the proximal margin of the section. Because many black grouper otoliths were difficult to read, we selected only otoliths for which there was 100% agreement among all readings for marginal-increment analysis. In addition, we restricted measurements to otoliths with from one to seven annuli because it was difficult to measure the more closely spaced outer annuli of older fish. We expressed the distance from the final annulus to the otolith's edge (marginal increment) as a percentage of the distance between the last two annuli formed on the otolith. For all grouper, the distance between the otolith core and the first annulus ($r_1$) was typically much greater than the distance between the first and second annuli ($r_2$–$r_1$). For this reason, we divided the distance between the first and second annuli by the distance between the otolith's core and the first annulus for each otolith measured and then calculated the mean of this number for the entire sample:

$$\frac{\sum_{i=1}^{n}((r_2 - r_1)/r_1)_i}{n} = 0.353. \qquad (SE = 0.0065)$$

We then estimated the expected distance between the first and second annulus for each age-1 black grouper otolith as a function of the distance between the otolith's core and the first annulus. The percent marginal increment for age-1 fish was then calculated as

$$(MI/(0.353 \times r_1)) \times 100,$$

where $MI$ = the marginal increment.

We then plotted the percent marginal increments as a function of capture month for 1995–96, the period during which we made regular monthly collections.

## Reproduction

Histological sections of gonads from 857 black grouper that ranged in length from 155 to 1518 mm were prepared and assessed for reproductive state. Gonad samples were processed histologically with `,Modification of the periodic acid Schiff's (PAS) stain for glycol-methacrylate sections, with Weigert's iron-hematoxylin as a nuclear stain, and with metanil yellow as a counterstain (Quintero-Hunter et al., 1991).

Oocytes were staged and counted from histological preparations at 100× with a compound microscope attached to a digital image-processing system. Four oocyte stages were recognized in black grouper ovaries: primary growth, cortical alveolar, vitellogenic, and oocytes in the final stages of maturation (Wallace and Selman, 1981). The final stages of oocyte maturation included yolk coalescence, germinal vesicle migration, germinal vesicle breakdown, and hydration. At least 300 oocytes per slide were staged and counted in arbitrarily chosen fields, and frequencies were expressed as a percentage of the total count. We counted all oocytes that had at least 50% of their area visible in a field before moving to the next field.

Gonads were classified on the basis of the maturity criteria of Moe (1969). Female grouper were considered sexually mature if ovaries contained vitellogenic oocytes or contained evidence of widespread atresia consistent with gonadal recrudescence. Mature females included Moe's classes 2, 3, and 4.

Monthly median gonadosomatic indices (GSI) were plotted to show seasonal reproductive patterns. Gonadosomatic indices were calculated for 201 sexu-

ally mature female grouper ranging in length from 565 to 1310 mm and for 43 sexually mature male grouper ranging in length from 947 to 1518 mm as

$$GSI = (GW / (TW - GW)) \times 100,$$

where $GW$ = total gonad weight (g); and
$TW$ = total fish weight (g).

We measured the diameters of whole oocytes from six females whose ovaries contained numerous hydrated oocytes. Samples of ovarian tissue that were preserved in 10% formalin were rinsed briefly in water and transferred to 33% glycerin for measurements. Diameters of at least 300 oocytes for each female were measured with a digital image-prossessing system. Only oocytes larger than 0.2 mm in diameter were measured.

We estimated the length at which 50% of the females in the population reached sexual maturity by fitting a logistic function to the percentage of females that were sexually mature and their respective lengths. A similar function was fitted to the percentage of the population made up by females to estimate the length at which 50% of the females in the population transformed into males. The parameter $b$ in Table 1 is the inflection point of the logistic curves and is the estimate of the length or age at which 50% of the females in the population were sexually mature or the length or age at which 50% of the population had undergone transition from female to male. Sometimes distinguishing between the gonads of sexually immature grouper and the regressed gonads of mature fish was difficult, and we eliminated 29 females that ranged in length from 586 to 894 mm from our analysis of maturation because we were uncertain of their maturity. Hunter et al. (1992) recommended that only fish collected early in the spawning season be used to estimate the length at 50% maturity, but because we found evidence of some spawning during most of the year, we included all months in our analysis.

## Results

The 1166 black grouper we examined ranged from 155 to 1518 mm in length. Among black grouper that we sexed, females ranged from 155 to 1310 mm in length (mean=696.3, SD=204.53, $n$=834) and males ranged from 947 to 1518 mm (mean=1254.9, SD=126.19, $n$=54; Fig. 1). Our sample contained 276 grouper that were not sexed, usually because the grouper had been eviscerated at sea by fishermen. The sex ratio of our sample was 1:15.4 (male:female); greatly skewed towards females. Black grouper landed in Pinellas County on Florida's Gulf coast by commercial fishermen were much larger than those landed in the Florida Keys (Fig. 2). The male:female sex ratio of the black grouper we sampled that were landed in the Florida Keys was 1:58.7, and the sex

**Table 1**

The relations between standard length, fork length, and total length, between length and weight, between the percentage of females that were sexually mature and length, and between the percentage of the population made up by females and length of black grouper, *Mycteroperca bonaci*, from South Florida waters. TL = total length (mm), FL = fork length (mm), SL = standard length (mm), WT = whole weight (g), GWT = gutted weight (g), OTOWT = otolith weight (g), and AGE = age (years). The total length range for all length-length regressions was 238–1518 mm and for the length-weight regression was 177–1518 mm; the total weight range for the total weight-gutted weight regression was 467–61,462 g; the age range for the age-otolith weight regression was 1–30.5 years.

| | | | $Y = a+bX$ | | |
|---|---|---|---|---|---|
| $Y$ | $X$ | $n$ | $a$ (1 SE) | $b$ (1SE) | $r^2$ |
| SL | FL | 1,134 | -23.712 (0.6852) | 0.883 (0.0008) | 0.999 |
| SL | TL | 1,141 | -21.611 (0.7743) | 0.858 (0.0009) | 0.999 |
| FL | SL | 1,134 | 27.607 (0.7514) | 1.131 (0.0011) | 0.999 |
| FL | TL | 1,150 | 1.641 (0.5223) | 0.973 (0.0006) | 0.999 |
| TL | SL | 1,141 | 26.186 (0.8757) | 1.164 (0.0012) | 0.999 |
| TL | FL | 1,150 | -1.317 (0.5378) | 1.028 (0.0006) | 0.999 |
| WT | GWT | 638 | 81.519 (12.9253) | 1.056 (0.0014) | 0.999 |
| $\log_{10}$WT | $\log_{10}$TL | 772 | -5.457 (0.0323) | 3.218 (0.0115) | 0.995 |
| | | | $Y = a+b\times\sqrt{X}$ | | |
| OTOWT | AGE | 389 | -0.1026 (0.0036) | 0.1210 (0.0014) | 0.952 |
| | | | $Y = \left(1/\left(1+e^{(a(X-b))}\right)\right)\times 100$ | | |
| % Mature (Females) | TL | 782 | -0.0194 (0.0017) | 826.0 (4.75) | 0.592 |
| % Mature (Females) | AGE | 617 | -1.375 (0.1341) | 5.20 (0.078) | 0.555 |
| % Females | TL | 888 | 0.016 (0.0013) | 1214.4 (5.05) | 0.618 |
| % Females | AGE | 694 | 0.355 (0.0287) | 15.55 (0.382) | 0.551 |

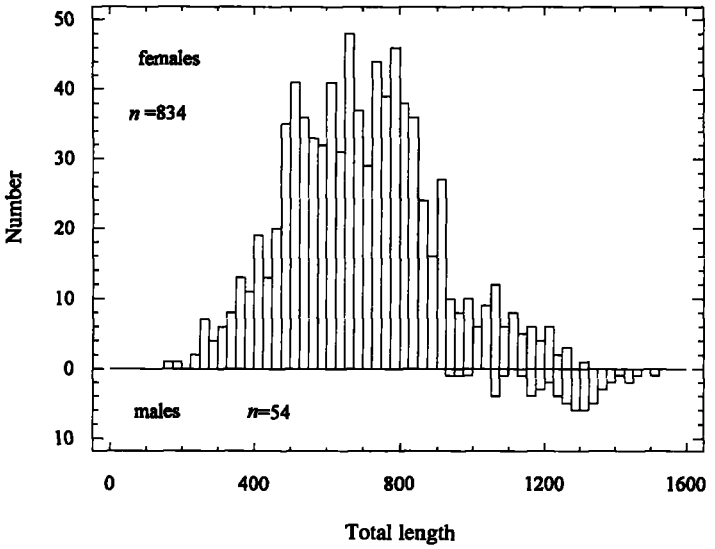


**Figure 1**

Total lengths (mm) of male and female black grouper, *Mycteroperca bonaci*, sampled from South Florida waters during 1994–96.

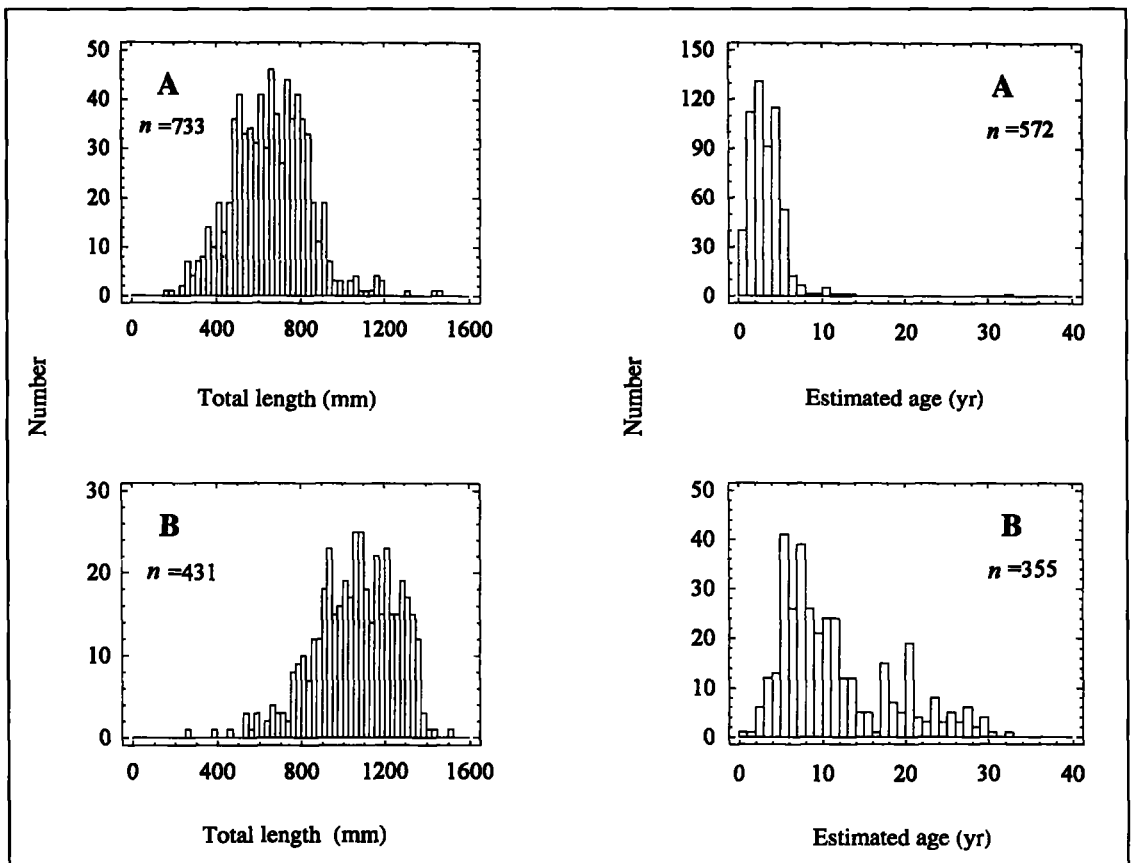


**Figure 2**

Total lengths (mm) and ages (years) of black grouper, *Mycteroperca bonaci*, landed in the Florida Keys (**A**) and in Pinellas County on Florida's Gulf coast (**B**).

ratio of black grouper landed in Pinellas County by commercial fishermen was 1:3.1. The pooled length-weight equation for sexed and unsexed fish and the relations between SL, FL, and TL are presented in Table 1.

## Age and growth

When viewed with reflected light, black grouper otoliths have narrow, opaque (bright) annuli that alternate with broad translucent (dark) zones (Fig. 3, A and B). Proceeding from the otolith's core towards the otolith's proximal margin, these translucent zones become increasingly opaque in appearance as the otolith grows. In the outer portion of the otoliths from older grouper (>10 years old), the dark translucent zones are narrow. In some individuals, the annuli are indistinct and irregular in appearance, which makes age estimation difficult. In older grouper, the annuli become closely spaced near the edge of the otolith, and this also makes age estimation difficult (Fig. 3C). Often otoliths of older grouper (>15 years) were more easily read under transmitted light and compound microscopes; otoliths from younger fish were often more easily read under reflected light. Overall, the otoliths from black grouper are similar in appearance to those of other grouper species we have examined in our laboratory.

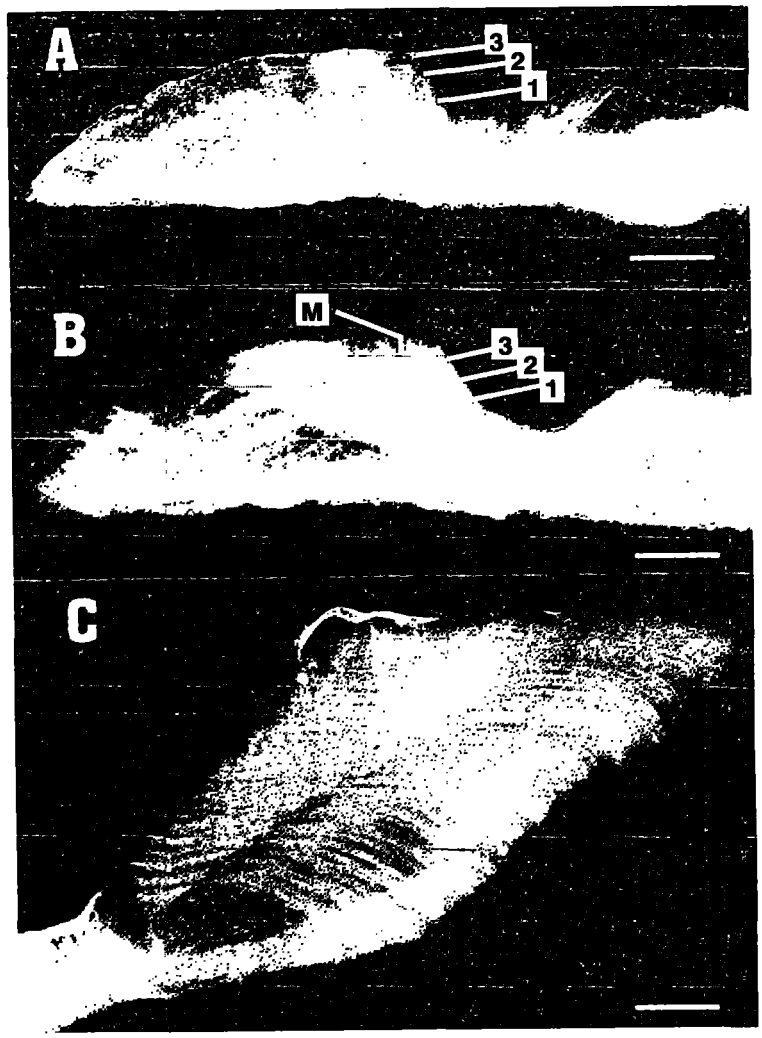


**Figure 3**

(**A**) Sectioned sagitta from a 3-year-old black grouper, *Mycteroperca bonaci* (508 mm TL), captured in May 1996. The third annulus is on the edge of the otolith. (**B**) Sectioned sagitta from a 3+ year-old black grouper (671 mm TL) captured in January 1996. Note the wide marginal increment (m) subsequent to the third annulus. (**C**) Sectioned sagitta from a 33-year-old male black grouper (1427 mm TL) captured in June 1996. Note the close spacing of annuli that caused difficulty in age estimation. Scale bars = 500 microns.

Marginal-increment analysis of otoliths from grouper 1–7 years old suggested that one annulus had been formed during April–June each year (Fig. 4). Median marginal increments had a consistent seasonal minimum during May–July and a maximum during December–March in both 1995 and 1996. Marginal increments during April–June tended to be either large (>75%) or small (<25%), suggesting that most individuals either had wide margins, as expected just prior to annulus formation, or had just formed an annulus and had either no marginal increment or a narrow margin. By June or July, individuals with wide margins were no longer present, suggesting that annulus formation was completed.

Of 1059 otoliths that we examined, 132 (12.5%) were rejected because of disagreements among readings. We had total agreement among annulus counts for 403 otoliths, but all of these otoliths were from grouper estimated to be less than 10 years old. The length-frequency distribution of fish whose otoliths were rejected because they were unsuitable for age estimation was not significantly different from that of fish whose otoliths were readable (Kolmogorov-Smirnov two-sample test, two-sided test statistic = 1.319, $P$=0.062), but the otolith weight distribution of fish whose otoliths were unreadable was significantly different from that of fish whose otoliths were readable (Kolmogorov-Smirnov two-sample test, two-sided test statistic=2.017, $P$<0.001). Otolith weight

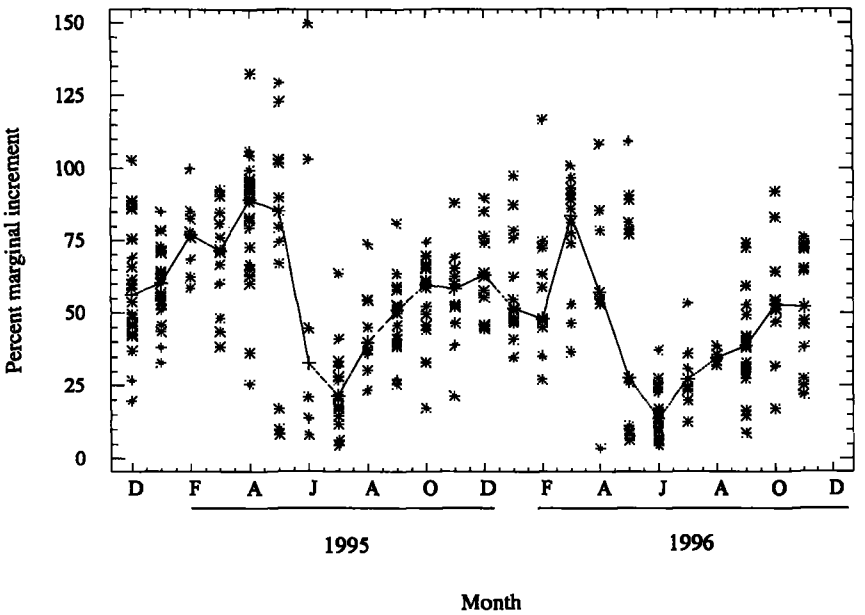


**Figure 4**

Percent marginal increments (*) and medians (+ and line) for black grouper, *Mycteroperca bonaci*, ages 1–7 captured from South Florida waters ($n$=330).

was closely related to fish age ($r^2$=0.952, Table 1, Fig. 5A), and the median weight (0.2437 g) of otoliths rejected as unreadable was significantly greater than that of otoliths that were readable (0.1571 g; Mann-Whitney $W$ test; $W$=12,492.0, $P$<0.001).

Black grouper growth was rapid until an age of about 10 years and then slowed considerably (Table 2, Fig. 5B). Most of the fish in our sample were from 2 to 10 years old, and the most abundant age classes were 2–6 years old (Fig. 6). The two oldest black grouper examined were a 33-year-old (1325-mm) fish that was not sexed and a 33-year-old (1427-mm) male (Table 2). The oldest female was a 1275-mm fish estimated to be 23 years old (Fig. 6); the largest female was 1310 mm long (Fig. 1) and was estimated to be 12 years old. Only three female black grouper were estimated to be over 20 years old. The smallest and youngest male was a 947-mm fish estimated to be 6 years old (Fig. 1 and 6). Black grouper landed in Pinellas County on Florida's Gulf coast by commercial fishermen were older overall than those landed in the Florida Keys, where only one fish older than 15 years was examined (Fig. 2). Estimates of von Bertalanffy growth model parameters are presented in Table 3.

## Sexual maturation and transition

Black grouper, like most epinepheline serranids, are protogynous hermaphrodites. Protogyny was suggested by the presence of peripheral sperm-collecting sinuses rather than the centrally located sinuses typical of gonochorists. Furthermore, a membrane-lined central lumen that was not used for sperm transport was present in testes and was a structural remnant of the ovarian lumen (Sadovy and Shapiro, 1987). Additional evidence of hermaphroditism was the presence of atretic vitellogenic oocytes in a transitional gonad containing proliferating testicular tissue (Fig. 7A). A second grouper that we would have considered transitional except for the presence of some mature sperm in peripheral sperm sinuses also contained degenerating vitellogenic oocytes (Fig. 7, B and C); this fish was considered to be a functional male. Transitional grouper also contained numerous PAS-positive melanomacrophage centers (Ravaglia and Maggese, 1995) referred to as "yellow-brown bodies" by Sadovy and Shapiro (1987). When stained with the PAS stain, these structures are brilliant purple. Melanomacrophage centers are thought to be active in degrading atretic oocytes, postovulatory follicles, and residual cells of the spermatogenic cycle (Chan et al., 1967; Ravaglia and Maggese, 1995). Many mature males contained scattered primary growth stage oocytes throughout the testis. We also noted that small amounts of testicular tissue were often present in functional ovaries that showed no evidence of undergoing transition. Finally, the differences in male and female length-frequency distri-

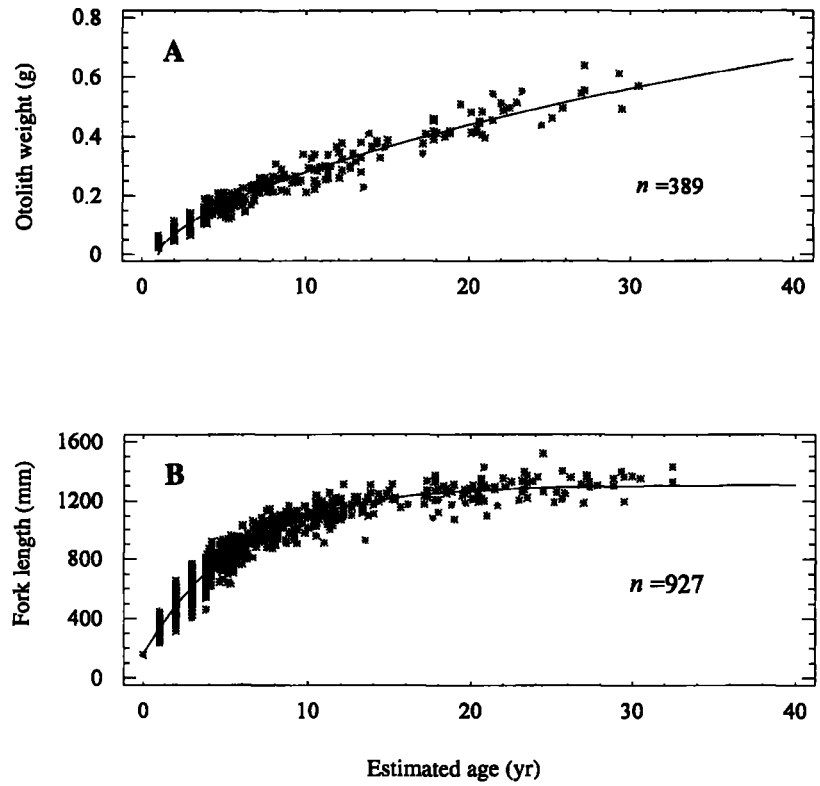


**Figure 5**

(**A**) The otolith weight–age relation for black grouper *Mycteroperca bonaci*, collected from South Florida waters. The equation for the relation is presented in Table 1. (**B**) Observed and predicted total lengths (mm) from the von Bertalanffy growth model for sexed and unsexed black grouper, *Mycteroperca bonaci*.

butions and the absence of small or young males are consistent with our hypothesis of protogynous hermaphroditism (Fig. 1).

We estimated that 50% of the females in the population reached sexual maturity by 826 mm and an age of 5.2 years (Table 1, Fig. 8). The smallest sexually mature female in our sample was 508 mm, and the youngest sexually mature female was 2 years old. All of the ovaries we examined contained primary growth stage oocytes. Cortical alveolar stage oocytes occurred only in ovaries from grouper larger than about 500 mm and older than 2 years, and they were common only among grouper larger than about 600 mm and older than 3 years (Fig. 9A). Vitellogenic oocytes were found only in ovaries from fish larger than about 600 mm and older than 2 years and were common only among grouper larger than 800 mm and older than 5 years (Fig. 9B). The length and age at which vitellogenic oocytes were commonly found agrees well with our estimate of the length and age at which 50% maturity was reached, suggesting that misclassification of regressed gonads did not greatly bias our estimates.

Transition from female to male was also partially a function of length and age. By a length of 1214 mm and an age of 15.5 years, 50% of the females in the population had transformed into males (Table 1, Fig. 8). We found only one transitional fish (1030 mm long; Fig. 7A) and a second grouper (947 mm long) that appeared to have recently completed transition (Fig. 7, B and C). We did not find any immature males (Moe's class 6) in our sample, suggesting that males become sexually active soon after transition. Most (91%) of the males we examined had ripe testes (Moe's class 9) that contained mature sperm.

Fin pigmentation differed between sexes in black grouper (Fig. 10). Ontogenetic color change independent of sex was ruled out because relatively small males (<1000 mm) displayed the male color phase, but the oldest and largest females (e.g., 1255 mm) did not. The pectoral fins, anal fin, and caudal fin were dark colored in females, but these fins were jet

black in males (Fig. 10, A–C). The jet black pigmentation of the pectoral fin was most apparent on the medial side. The dorsal interspinous membrane of females was yellow to dusky (Fig. 10D). In males, this membrane was usually dark black but was occasionally yellow or yellowish with black tips. Because this membrane can be yellow in both males and females, the coloration of this fin was the least reliable indicator of sex. The distal one-third of the soft dorsal fin was dark black in both sexes and was not useful in determining sex.

## Seasonality of gonad development

The frequencies of the four oocyte stages we counted in black grouper ovaries had a seasonal pattern that was repeated in both 1995 and 1996 (Fig. 11, A and B). Vitellogenic oocytes were present in greatest number in January–March in both 1995 and 1996 and were present in all months except September–November 1996. Cortical alveolar stage oocytes were also present in all months except September–November 1996 and were most abundant during December–April. Primary growth stage oocytes were present during all months and made up at least 55% of the total number of oocytes present. Oocytes in the final stages of maturation were not abundant, but they were most common during December–May (Fig. 11B). We examined six females with hydrated ovaries: one was caught during October, one in December, and four in March. The ovaries from these grouper contained a group of vitellogenic oocytes that ranged from 0.5 to 0.7 mm in diameter and a clutch of hydrated oocytes that ranged from 0.8 to 1.2 mm in diameter (Fig. 12). Most of the oocytes <0.2 mm in diameter, which we did not measure, were primary growth stage or cortical alveolar stage oocytes. Postovulatory follicles were not recognized in any female examined.

Females with the greatest GSIs (>5) were captured during February–March (Fig. 13). Male GSIs (range 0.086–0.399, $n$=43) were generally much less than female GSIs (range 0.032–10.108, $n$=201) and had no

**Table 2**

Average observed and predicted total lengths (mm) for sexed and unsexed black grouper, *Mycteroperca bonaci*, and average observed lengths for females and males. The average observed length at age includes some seasonal growth that occurred after the formation of the final annulus. Values in parentheses are standard error and sample size.

| | Sexed and unsexed | | Females | Males |
|---|---|---|---|---|
| Age (yr) | Average observed | Predicted | Average observed | Average observed |
| 0 | 155 (1) | 159 | 155 (1) | |
| 1 | 338 (8.7;41) | 337 | 339 (8.9; 39) | |
| 2 | 486 (5.7;113) | 487 | 486 (5.7;112) | |
| 3 | 606 (5.7;136) | 614 | 607 (5.7;134) | |
| 4 | 733 (5.5;155) | 722 | 734 (5.7;147) | |
| 5 | 814 (5.8;113) | 813 | 814 (6.1;97) | |
| 6 | 871 (7.7;70) | 889 | 857 (10.2;41) | 947 (1) |
| 7 | 972 (9.1;40) | 954 | 966 (13.6;20) | 1062 (1) |
| 8 | 1008 (11.6;39) | 1009 | 998 (20.5;15) | 1006 (46.0;2) |
| 9 | 1038 (12.3;31) | 1055 | 1024 (19.8;14) | 1058 (1) |
| 10 | 1074 (12.3;16) | 1094 | 1078 (14.6;5) | 1167 (1) |
| 11 | 1116 (13.1;33) | 1127 | 1147 (27.0;10) | 1130 (22.8;5) |
| 12 | 1138 (14.4;21) | 1155 | 1131 (29.0;9) | |
| 13 | 1164 (11.6;11) | 1178 | 1182 (16.0;6) | 1172 (1) |
| 14 | 1175 (30.6;11) | 1198 | 1192 (18.5;2) | 1222 (30.5;2) |
| 15 | 1239 (14.4;7) | 1215 | 1213 (1) | 1266 (26.0;3) |
| 16 | 1165 (10.5;2) | 1229 | | |
| 17 | 1244 (21.2;6) | 1241 | 1270 (1) | 1283 (47.5;2) |
| 18 | 1252 (30.3;10) | 1251 | | |
| 19 | 1226 (35.5;6) | 1260 | | 1285 (1) |
| 20 | 1248 (12.9;9) | 1267 | 1220 (1) | |
| 21 | 1264 (20.2;15) | 1273 | 1195 (1) | 1315 (38.7;4) |
| 22 | 1278 (29.6;5) | 1278 | | |
| 23 | 1298 (27.3;6) | 1283 | 1275 (1) | 1326 (68.5;2) |
| 24 | 1320 (26.6;5) | 1286 | | 1370 (1) |
| 25 | 1307 (72.2;4) | 1289 | | 1390 (128.0;2) |
| 26 | 1305 (44.5;4) | 1292 | | |
| 27 | 1309 (23.3;7) | 1294 | | 1291 (38.3;4) |
| 28 | 1300 (1) | 1296 | | |
| 29 | 1349 (28.3;3) | 1298 | | 1349 (28.3;3) |
| 30 | 1307 (55.9;3) | 1299 | | |
| 31 | 1350 (1) | 1300 | | 1350 (1) |
| 32 | 1301 | | | |
| 33 | 1376 (51.0;2) | 1302 | | 1427 (1) |

**Table 3**

Parameter estimates for the von Bertalanffy growth model for black grouper, *Mycteroperca bonaci*, collected from the waters of South Florida. Values in parentheses are standard errors.

| $n$ | $L_\infty$ (mm) | $K$ | $t_0$ | adjusted $r^2$ |
|---|---|---|---|---|
| 927 | 1306.2 (8.05) | 0.169 (0.0037) | –0.768 (0.0640) | 0.941 |

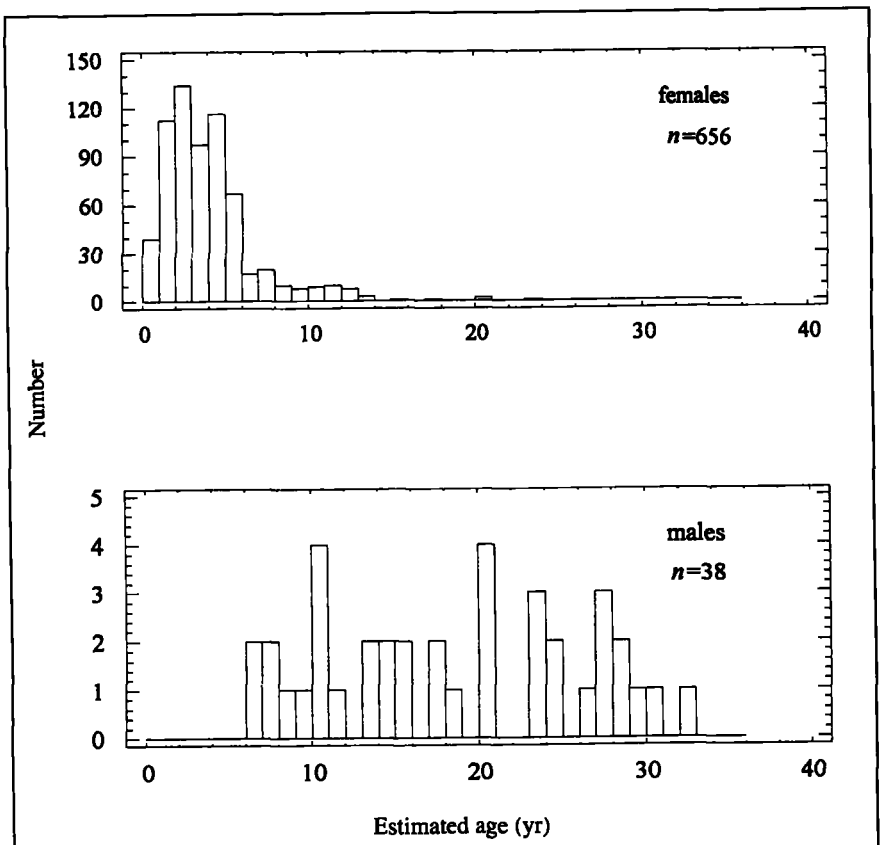


**Figure 6**

Age-frequency distributions for male and female black grouper, *Mycteroperca bonaci*, from South Florida waters.

seasonal trend (Fig. 13). Testes from sexually mature males ranged in weight from 14 to 197 g and were much smaller overall than ovaries from sexually mature females, which ranged in weight from 1 to 1354 g.

## Discussion

We obtained black grouper from a variety of fishery-dependent and fishery-independent sources, and it is difficult to assess the extent to which the length and age structure of our sample reflects that of the population or the degree to which different fishing gears biased the various samples. Although we sampled grouper that were landed in two geographically separate locations, the Florida Keys and in Pinellas County on Florida's Gulf coast, most of the grouper landed in both locations were caught in the waters off the Florida Keys. Most of the large (>1000 mm) fish and most of the males that we examined came from commercial fish houses on Florida's Gulf coast, and most of these grouper were caught on the Tortugas Banks west of the Florida Keys. Fish obtained from Keys headboats, fish houses, and spearfishermen were smaller and younger overall than grouper sampled from fish houses in Pinellas County (Fig. 2). Most black grouper landed in Pinellas County fish houses were caught with commercial longlines in depths greater than 37 m (20 fathoms); most of the fish landed in the Keys were captured by spear fishermen, principally in water 6–50 m deep. The greater depths fished and the greater distances traveled by Gulf-coast commercial fishermen to presumably more remote fishing areas probably account for the differences between the two samples.

### Age and growth

Black grouper appear, on the basis of marginal-increment validation for grouper 1–7 years old, to form a single annulus each year in late spring or early summer. We were unable to validate that annuli are annual marks in older grouper, and the accuracy of our age estimates for older fish is unknown. The annuli we counted on otolith sections from older grouper were similar in appearance to validated annuli;

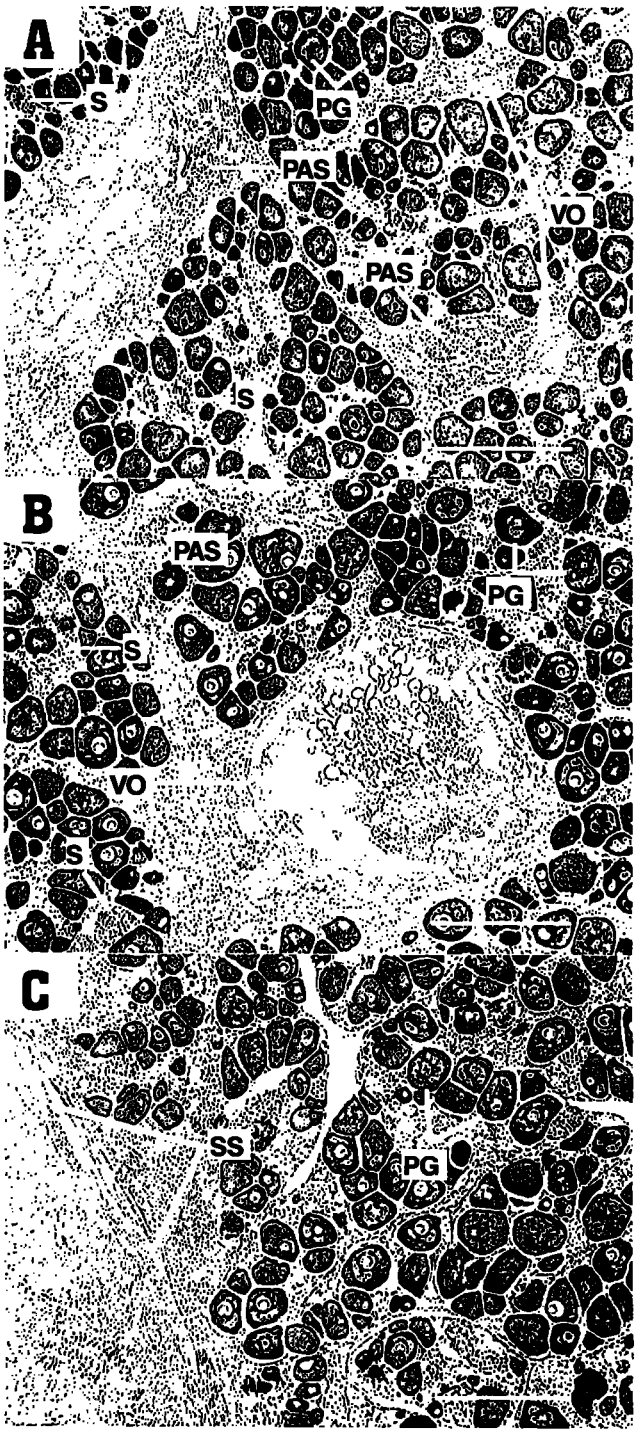


**Figure 7**

(**A**) A transitional gonad from a 1030-mm-TL black grouper, *Mycteroperca bonaci*, captured in September 1994 with proliferating spermatogenic tissue in sperm cysts (S), primary growth stage oocytes (PG), degenerating vitellogenic oocytes (VO), and PAS-positive melanomacrophage centers (PAS). (**B**) A 947-mm-TL black grouper captured in November 1995 with proliferating spermatogenic tissue in sperm cysts (S), primary growth stage oocytes (PG), degenerating vitellogenic oocytes (VO), and PAS-positive melanomacrophage centers (PAS). (**C**) The same ovary as in B showing the presence of mature sperm in peripheral sperm sinuses (SS). Scale bars = 200 microns.

however, as annuli became progressively more closely spaced, age estimation became more difficult. Additional work is needed to assess the accuracy of our age estimates for older grouper; consequently, our age estimates predicted lengths at age, and growth model parameters should be used with caution. From their analyses of marginal increments, Manooch and Mason (1987) also reported that black grouper from the Florida Keys form a single annulus each year. They found that annuli were usually formed during March–May, about a month earlier than we estimated. This difference is probably a result of differences in interpretation of the appearance of an annulus present on the otolith margin. Other congeners also form annuli during late spring and early summer. Collins et al. (1987) reported that gag, *M. microlepis,* off the southeastern U.S. coast form annuli during late spring to late summer, and Hood and Schlieder (1992) suggested that gag form annuli during summer in the eastern Gulf of Mexico. Bullock and Murphy (1994) reported that yellowmouth grouper, *M. interstitialis*, form opaque bands during late summer and early fall. Matheson et al. (1986) found that scamp, *M. phenax*, in North Carolina waters form an annual mark during April or May.

We rejected 12.5% of the otoliths we sectioned as unreadable, and this is a possible source of bias to our growth model parameters. Otolith weight is a useful predictor of age of black grouper ($r^2$=0.952), and the otoliths that we rejected were generally heavier and thus probably older than most of those that we considered readable. In addition, although the length-frequency distribution of fish whose otoliths were rejected was not significantly different from that of all fish whose otoliths were readable, the significance level of the test ($P$=0.062) was close enough to 0.05 to cause us to suspect that the distributions could have been different. If so, we may have rejected as unreadable more otoliths from large grouper than from small grouper. We may also have tended to exclude slower-growing older grouper from our sample of aged fish, and this could have biased our growth models. However, when we recalculated growth models and included all fish regardless of CV, the resulting growth-parameter estimates were all within one standard error of those in Table 3. Thus any bias to the growth model caused by our rejection of otoliths from older grouper appears to be negligible. Our choice of a threshold CV of 12% was arbitrary, but growth model parameters did not appear to be sensitive to the choice of CV thresh-

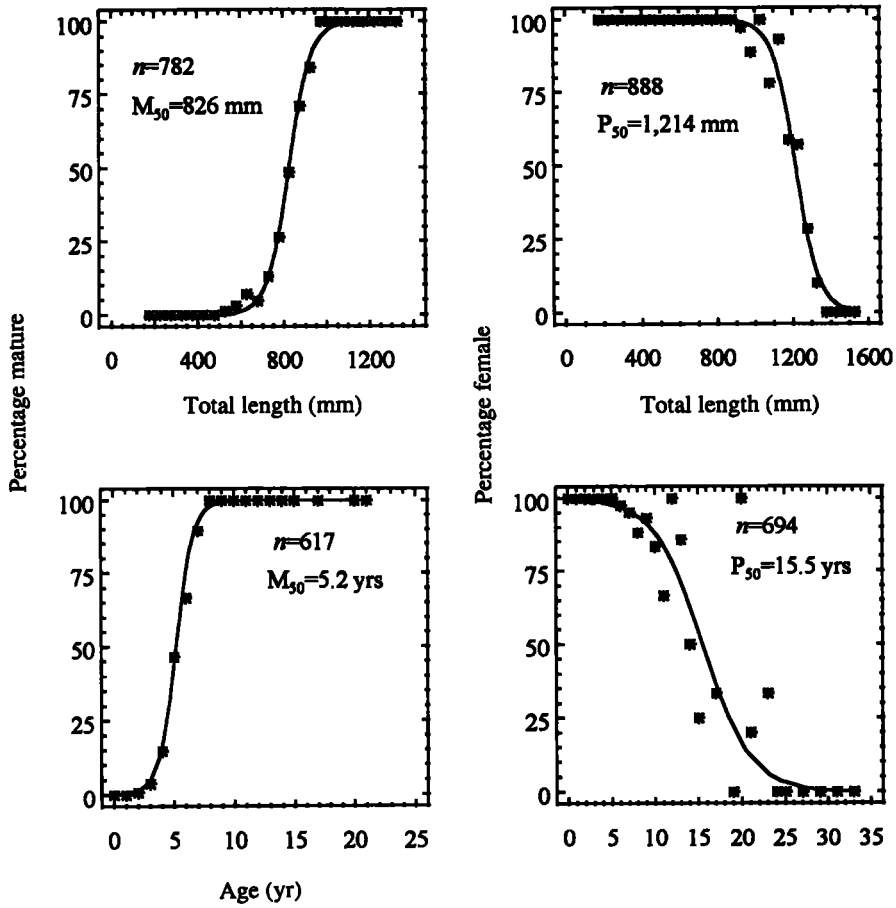


**Figure 8**

Logistic curves describing the percentage of female black grouper, *Mycteroperca bonaci*, collected from South Florida waters that were sexually mature and the percentage of our black grouper Sample that was made up by females as a function of both total length (mm) and age (years). $M_{50}$ is the length or age predicted by the logistic regression at which 50% of the female black grouper were sexually mature, and $P_{50}$ is the length or age predicted by the logistic regression at which 50% of the black grouper in our sample were females.

olds. When we recalculated growth models with CV thresholds of 10% and 5%, our estimates of $L_\infty$ and $K$ remained within two standard errors of the estimates at a CV of 12%, but the numbers of otoliths eliminated from our analysis increased substantially at lower CV thresholds.

The two oldest black grouper in our sample were both estimated to be 33 years old, considerably older than Manooch and Mason's (1987) oldest grouper (14 years). Manooch and Mason sampled hook-and-line-caught black grouper from Keys headboats during 1978–85 and speculated that the maximum age attained by black grouper was probably about 19 years. The presence of older fish in our sample is probably because our sample contained black grouper that were larger (largest 1518 mm) than those examined by Manooch and Mason (largest aged 1180 mm; largest measured 1259 mm). We measured 125 black grouper longer than 1200 mm and aged 94 of these. Of the 98 grouper that we estimated to be older than 14 years, 84% were longer than 1200 mm and were longer than any fish aged by Manooch and Mason. Most of the large black grouper in our sample were caught by commercial longliners and landed in Pinellas County; the lengths and ages of the grouper in our sample that were landed in the Keys were similar to those of Manooch and Mason (1987).

Our estimates of length at age are similar to those of Manooch and Mason (1987), and the predicted growth curves from both data sets are in general agreement (Fig. 14). In some cases, such as age classes 5–9, our estimates of mean length at age are

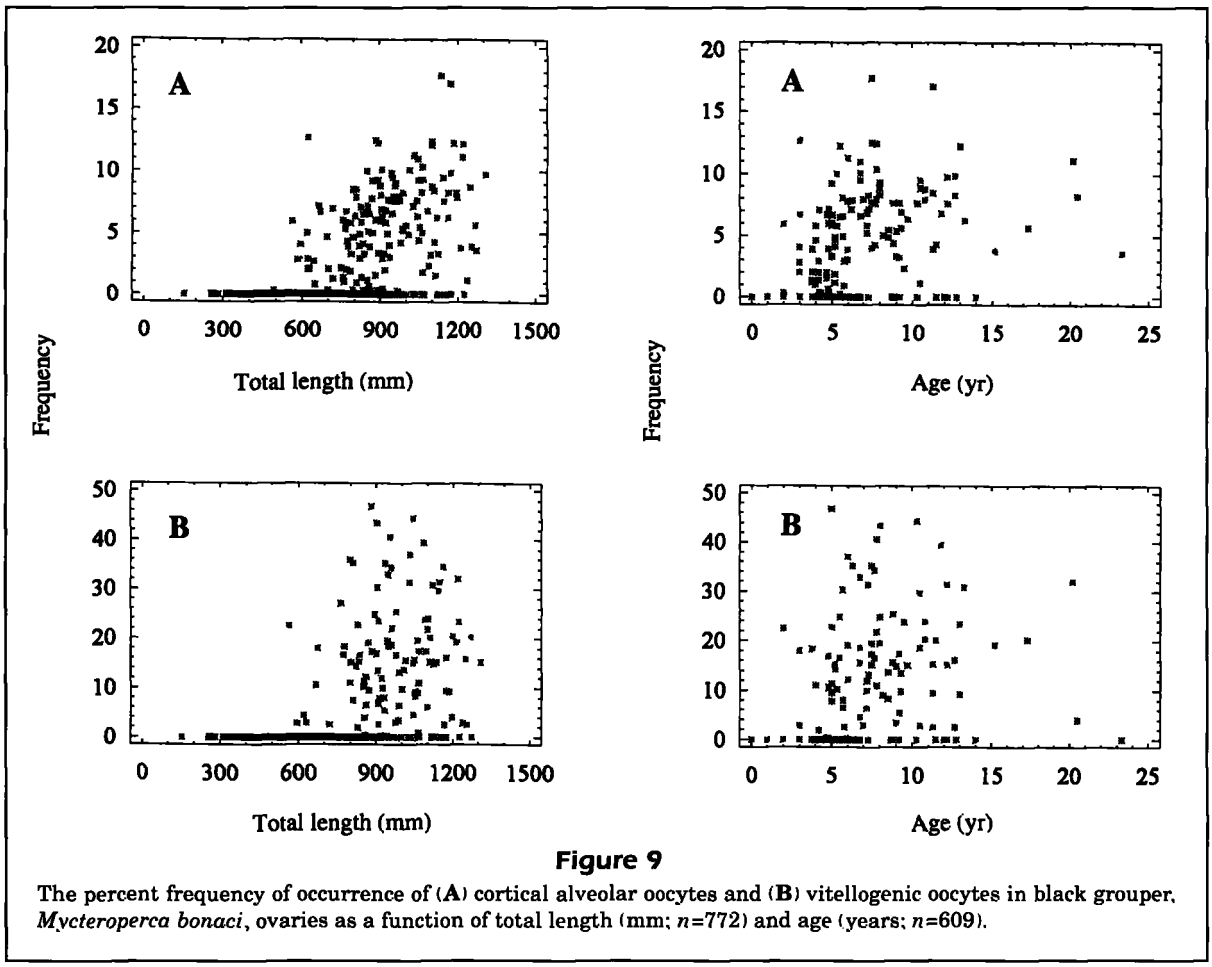


**Figure 9**

The percent frequency of occurrence of (**A**) cortical alveolar oocytes and (**B**) vitellogenic oocytes in black grouper, *Mycteroperca bonaci*, ovaries as a function of total length (mm; $n$=772) and age (years; $n$=609).

greater than those of Manooch and Mason, but their estimates for these age classes fall below not only our predicted lengths but also their predicted lengths. The von Bertalanffy growth model parameters estimated by Manooch and Mason were $L_\infty$ = 1,352 mm, greater than our estimate of $L_\infty$ = 1,306 mm, and $K$ = 0.1156, less than our estimate of $K$ = 0.169.

Black grouper, though not as large as jewfish or warsaw grouper, are among the largest species of grouper, and it is not surprising that they attain ages over 30 years. Estimates of the longevity of other grouper species are similar to our estimates for black grouper. Hood and Schlieder (1992) and Collins et al. (1987) estimated a maximum age of 21–22 years for gag, Bullock et al. (1992) estimated a maximum age of 37 years for jewfish (*E. itajara*), Bullock and Murphy (1994) estimated a maximum age of 28 years for yellowmouth grouper, Manooch and Mason (1987) reported that warsaw grouper (*E. nigritus*) reach 41 years, and Moe (1969) reported a red grouper (*E. morio*) 25 years old. The growth rate ($K$=0.169/year) of black grouper is similar to that estimated for gag ($K$=0.166/year, Hood and Schlieder, 1992), but is greater than the growth rates estimated for many other grouper species: jewfish $K$ = 0.126/year (Bullock et al., 1992), yellowmouth grouper $K$ = 0.08/year (Bullock and Murphy, 1994), and warsaw grouper $K$ = 0.054/year (Manooch and Mason, 1987).

## Sexual maturation and transition

Our histological analysis of black grouper gonads is consistent with the diagnostic criteria of Sadovy and Shapiro (1987) for a monandric protogynous hermaphrodite. Furthermore, the absence of small males and a sex ratio highly skewed towards females are consistent with our diagnosis of protogynous hermaphroditism. Although the length and age distributions of males and females overlapped, males occupied the largest and oldest length and age classes and were unrepresented in smaller and younger length and age classes (Figs. 1 and 6). This is an important difference between black grouper and Nassau grouper (*Epinephelus striatus*), which has recently been diagnosed as a gonochorist with potential for sex change (Sadovy and Colin, 1995). In

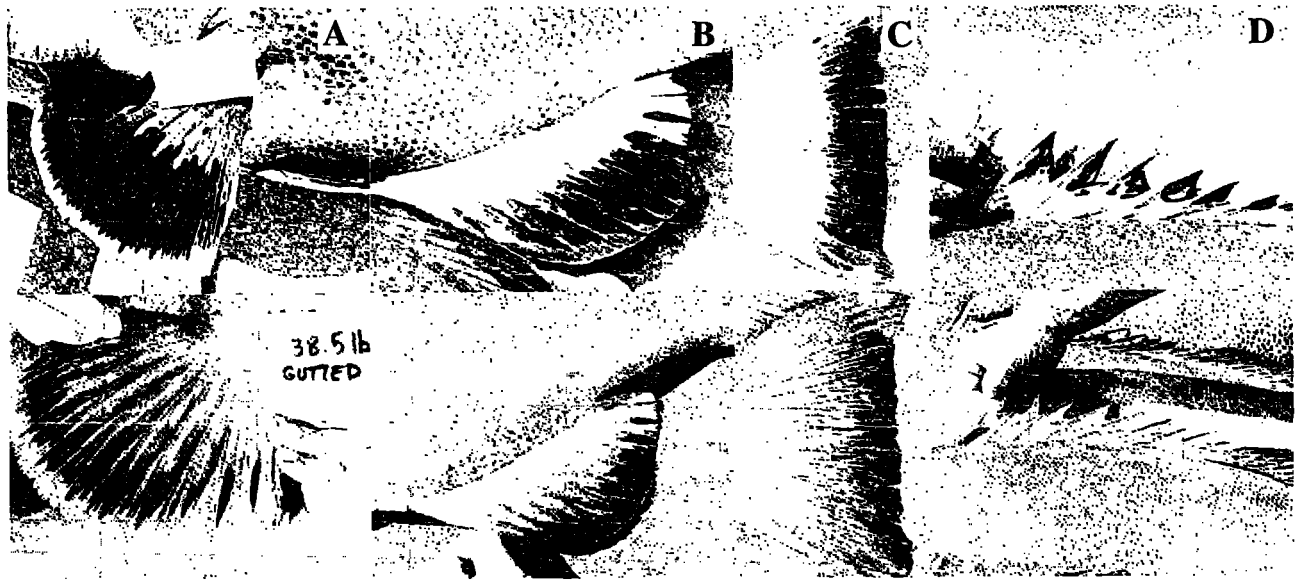


**Figure 10**

Differences in fin pigmentation in male (above) and female (below) black grouper, *Mycteroperca bonaci*. (**A**) Medial surface of pectoral fin, (**B**) anal fin, and (**C**) caudal fin jet black in males. (**D**) Dorsal interspinous membrane yellow or dusky in females, usually black in males.

Nassau grouper, both males and females can develop directly from juveniles and there is little difference in the lengths of males and females. Furthermore, there is little difference in the length at which sexual maturation occurs in both sexes, in contrast to black grouper. The scarcity of transitional black grouper and the absence of immature males in our samples suggest that transition occurs quickly and that testes become active soon after transition. The presence of large females in the population suggests that some females may not transform into males, but even the largest females we observed were considerably smaller and younger than the largest and oldest males (Figs. 1 and 6).

The current 20-inch (508-mm) minimum size limit is well below our estimate of the size at which 50% of females reach sexual maturity (826 mm and 5.2 years) and is not adequate to allow females to reproduce before recruiting to the fishery. Similar estimates of length at maturity were made by García-Cagide and García (1996) who reported that the smallest sexually mature female black grouper they examined from Cuban waters was 570 mm and that most mature females were 850–1100 mm. Huntsman et al. (1994) used an estimate of 5.04 years as the age at sexual maturity in yield per recruit and spawning stock per recruit models for black grouper. They did not present data to support this estimate, but it is within two standard errors of ours.

Female black grouper reached sexual maturity at a relatively large size compared to other grouper species. Female gag reach 50% sexual maturity at 600–650 mm and 3–4 years (Hood and Schlieder, 1992). Female yellowmouth grouper mature between 400 and 450 mm and 2–4 years (Bullock and Murphy, 1994). Yellowedge grouper, *E. flavolimbatus*, reach 50% maturity at 568 mm (Bullock et al., 1996). Larger grouper such as jewfish reach sexual maturity as females at even larger lengths of 1200–1350 mm and greater ages of 6–7 years than black grouper do (Bullock et al., 1992).

The length and age at which 50% of our sample consisted of females was 1215 mm and 15.5 years. García-Cagide and García (1996) reported that the smallest male black grouper from Cuban waters was 980 mm long and that most males were 1000 to 1100 mm long, similar to our findings even though their sample appeared to contain fewer large grouper than ours did. Our estimates of the length and age at transition for black grouper are both larger and older than estimates for other grouper species. Eastern Gulf of Mexico gag populations are 50% male at about 1050 mm and age 11 (Hood and Schlieder, 1992). Gag in the South Atlantic Bight undergo transition from female to male at 750–950 mm and age 5–11 (Collins et al., 1987). Transitional yellowmouth grouper examined by Bullock and Murphy (1994) were 505–643 mm and 5–14 years old. Yellowedge grouper popula-

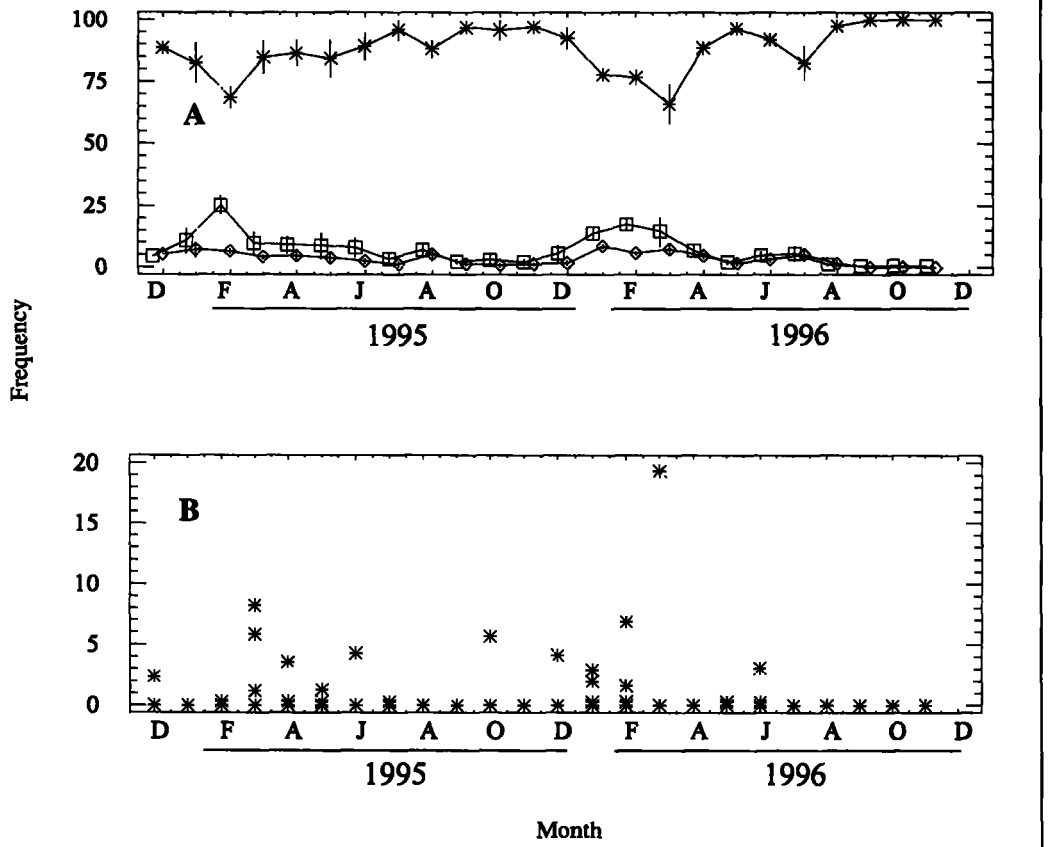


**Figure 11**

(**A**) Monthly mean percent frequency of occurrence and standard errors of oocyte stages in black grouper, *Mycteroperca bonaci*, ovaries ($n$=774) for 1995–96. * = primary growth stage oocytes, = cortical alveolar oocytes, and = vitellogenic oocytes. (**B**) The percent frequency of occurrence of oocytes in the final stages of maturation as a function of month in black grouper ovaries.

tions are 50% females at 817 mm (Bullock et al., 1996). Other large grouper such as warsaw grouper and jewfish have not been confirmed to be protogynous hermaphrodites.

The sex ratio of our sample (1:15.4, male:female) may not resemble that of the population because many black grouper that we examined, especially large fish, were eviscerated and could not be sexed. Most of these large fish were probably males, so we may have underestimated their numbers. We are not able to assess the extent of this bias. Furthermore, sex ratios appear to vary widely depending on the depth and location sampled. It is possible that fishing mortality has reduced the numbers of large males in the population, as has been reported for gag from the eastern Gulf of Mexico, where male:female sex ratios as extreme as 1:76.6 have been reported (Coleman et al., 1996). Unfortunately, there are no historical estimates of black grouper sex ratios with which to compare our estimates. García-Cagide and García (1996) reported a male:female sex ratio of 1:30.3 for black grouper from Cuban waters, more skewed towards females than our overall sex ratio but less skewed than the sex ratio of the black grouper we sampled that were landed in the Florida Keys (1:58.7).

Hydrated black grouper oocytes ranged from 0.8 to 1.2 mm in diameter and are similar in size to the hydrated oocytes reported for other groupers (Moe, 1969; Colin et al., 1987; Carter et al., 1994; Sadovy et al., 1994b). We usually did not know the time of day when fish were caught, so we could not estimate the time at which hydration began. Vitellogenic oocytes reached a diameter of about 0.6 mm before under going the final stages of maturation. A distinct group of vitellogenic oocytes with a mean diameter of about 0.6 mm, along with a clutch of larger hydrated oocytes, was present in most of the six grouper for which we measured oocytes. This is consistent with a group-synchronous mode of reproduction (Wallace and Selman, 1981).

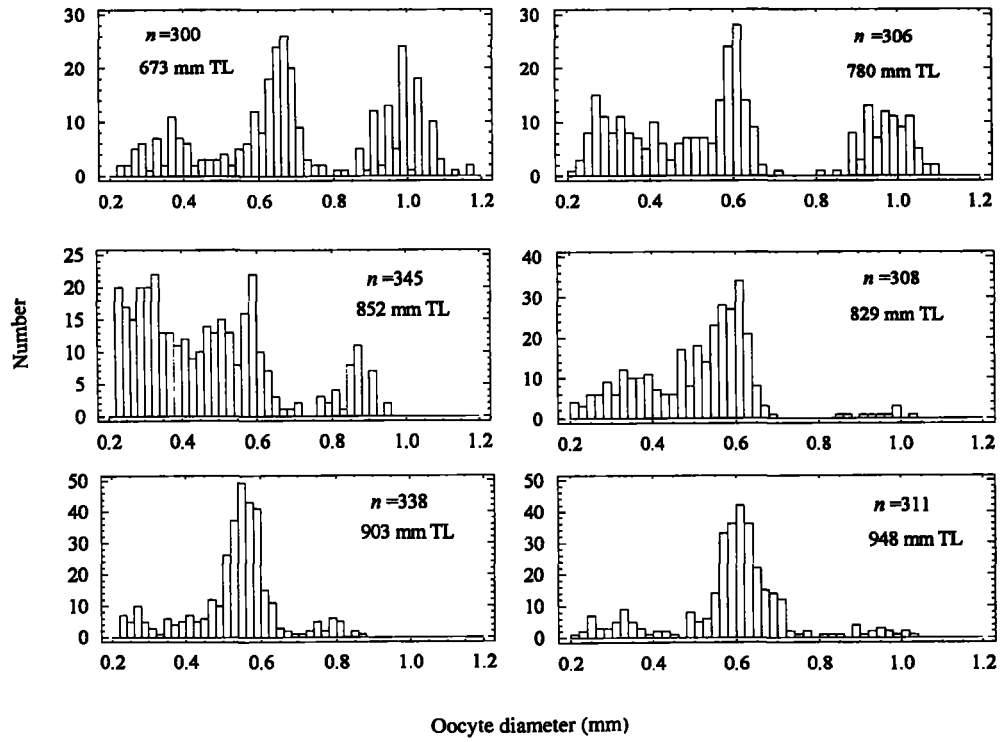


**Figure 12**

Oocyte diameter (mm) frequency distributions for six hydrated female black grouper, *Mycteroperca bonaci*, from South Florida waters. Hydrated oocytes were 0.8–1.2 mm in diameter. Only oocytes with diameters larger than 0.2 mm were measured. $n$ = the number of oocytes measured.

## Seasonality of gonad development

Reproduction in black grouper was seasonal, with peak gonad development during December–March, but females with vitellogenic oocytes were present during all months and females with elevated GSIs occurred in most months. In Cuban waters, García-Cagide and García (1996) also found that black grouper spawn during winter and spring. Other eastern Gulf of Mexico grouper species have similar seasonal patterns of gonad development, and in several species, the spawning season appears to be prolonged. In gag, gonad development occurs during December–May, and peak gonadal activity occurs during February and March (Hood and Schlieder, 1992). Yellowmouth grouper gonads are active throughout the year, and peak gonadal activity occurs during April–May (Bullock and Murphy, 1994). Jewfish have developed gonads from June–December, with peak activity during July–September (Bullock et al., 1992). Yellowedge grouper gonads are developed during January–October, with peak activity during May–September (Bullock et al., 1996).

Many grouper species are known to form seasonal spawning aggregations at specific times and locations each year (Sadovy, 1994). Aggregations of black grouper have been reported off Central America during January and February (Carter, 1989; Fine, 1990; Carter et al., 1994), the same time of year that we observed peak gonadal development and the greatest incidence of oocytes in the final stages of maturation. Among other species of *Mycteroperca*, aggregations of gag and scamp have been reported (Gilmore and Jones, 1992), and spawning by an aggregation of tiger grouper, *M. tigris*, was reported by Sadovy et al. (1994a). Spawning aggregations of black grouper have not been documented in Florida waters, but it is clear from the presence of oocytes in the final stages of maturation in our sample that spawning black grouper are landed in South Florida. Whether black grouper form spawning aggregations in Florida waters and the extent of these aggregations is unknown.

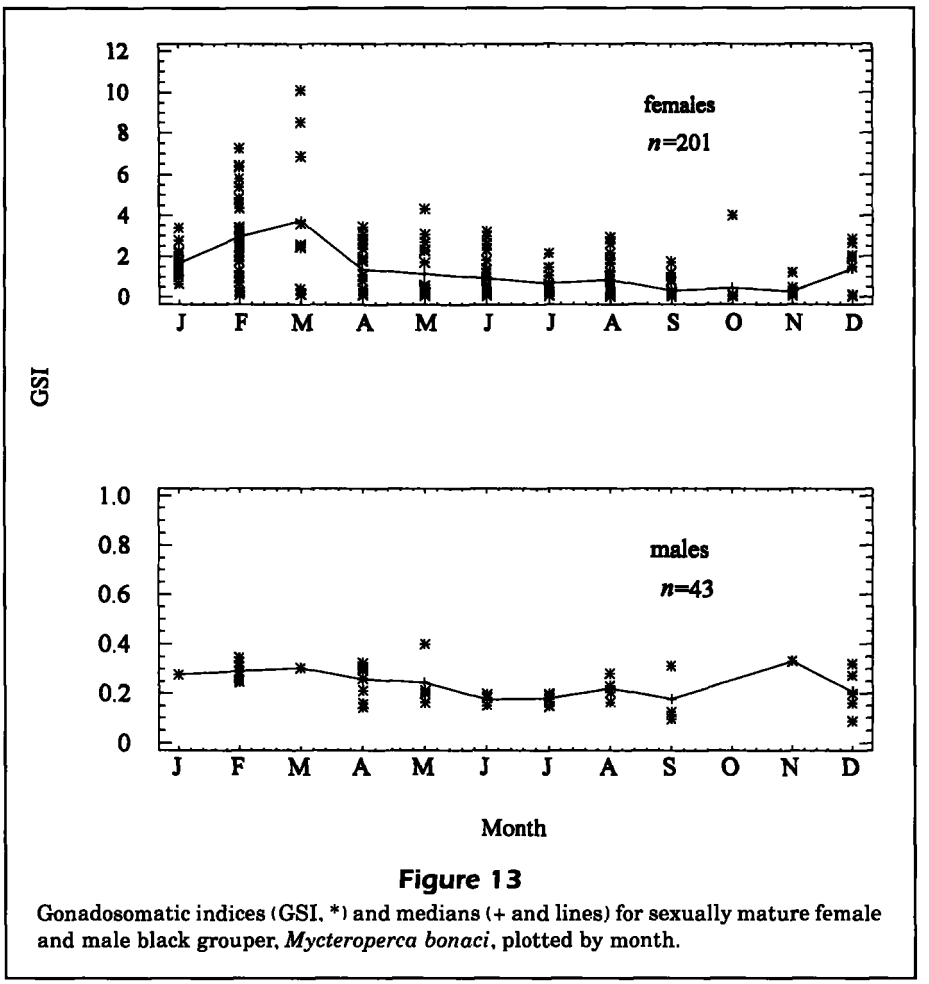


**Figure 13**

Gonadosomatic indices (GSI, *) and medians (+ and lines) for sexually mature female and male black grouper, *Mycteroperca bonaci*, plotted by month.

## Conclusions

The status of black grouper stocks is unclear. Our sample contained many old and large grouper, most of which came from the commercial longline fishery. Large grouper are apparently still abundant in some areas, and their continuing presence in the commercial fishery could reflect the expansion of fishing effort into deeper and more remote areas. In the shallow waters adjacent to the Florida Keys, large and old black grouper were rare, probably a consequence of fishing mortality. The current minimum size does not protect sexually mature females, and the fishery could substantially reduce spawning success in black grouper. In addition, size-selective fishing mortality may selectively remove males from the population. Sex ratios are currently skewed towards females, and it is unknown if populations can compensate by reducing the size of transition as males are selectively removed. Finally, additional research is needed to document the existence of black grouper spawning aggregations in the eastern Gulf of Mexico and in the waters off the Florida Keys and to evaluate the extent to which these aggregations have been affected by fishing mortality.

## Acknowledgments

We thank D. DeMaria and K. DeMaria for collecting black grouper from the Florida Keys. We also thank C. Boniface and M. Puig for their assistance in sampling in the Keys. Many commercial fishermen cooperated by providing ungutted black grouper, and Dick's Seafood, Madeira Beach Seafood, and Captain's Finest Seafood allowed sampling of grouper during their busy schedules. Captains C. Sullivan, B. Banks, and G. Haring deserve special thanks for saving gonads with their catch. We acknowledge the following FMRI personnel for their assistance: M. Cladas, L. French, G. Gerdeman, D. Harshany, M. Norris, D. Merryman, H. Patterson, T. Sminkey, F. Stengard, and C. Stevens. A. Collins, NMFS, Panama City, FL, provided samples from the

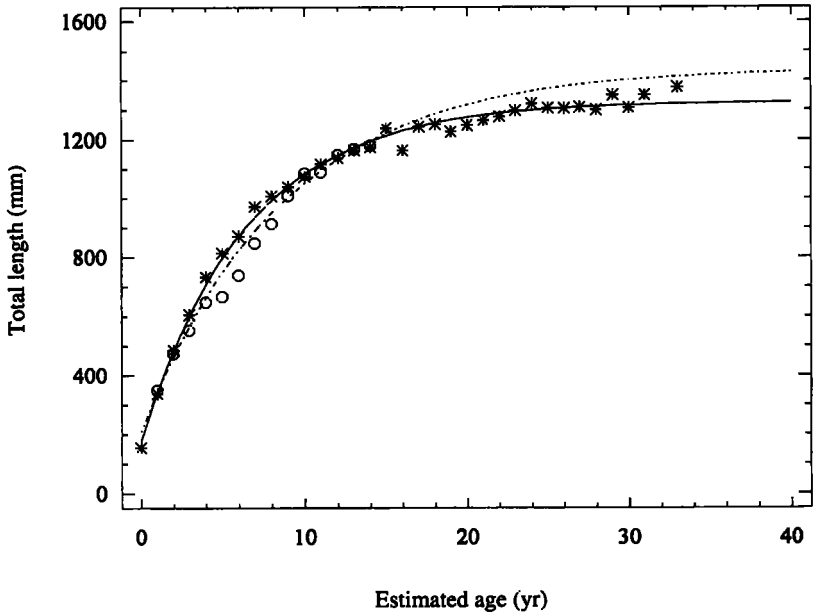


**Figure 14**

Mean length at age and von Bertalanffy growth curves for black grouper, *Mycteroperca bonaci*, based on data from our study (* and solid line) and from Manooch and Mason (1987; ⁻ and broken line).

Florida Panhandle. J. Leiby, R. McBride, M. Murphy, J. Quinn, and D. Winkelman made helpful comments that improved the manuscript. Lastly, we thank C. Manooch and M. Burton for providing us with the data described in Manooch and Mason (1987). This project was funded by a grant from the National Marine Fisheries Service, U.S. Department of Commerce, Award NA57FF0060, L.H. Bullock and R.E. Crabtree, principal investigators.

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# Feeding habits of bonefish, *Albula vulpes*, from the waters of the Florida Keys

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**Abstract**—We examined stomach contents of 385 bonefish that ranged in length from 228 to 702 mm FL. Relatively few prey species made up most of the diet by weight—xanthid crabs (29.9%), gulf toadfish, *Opsanus beta* (17.2%), portunid crabs (10.9%), alpheid shrimp (9.2%), and penaeid shrimp (7.7%) together made up 74.9%. A variety of gastropods (17 families and 24 species) and bivalves (9 families and 16 species) were eaten, but gastropods made up only 2.7% of the diet by weight and bivalves made up only 2.5%. Polychaetes, represented by at least seven families, were important in the diet numerically (37.1%) but made up little of the diet by weight (1.4%). Cluster analysis and ordination of stomach contents permitted bonefish to be grouped according to length. Large bonefish (>439 mm FL) ate more xanthid crabs, alpheid shrimp, *Callinectes* spp., and *O. beta* than did small bonefish; penaeid shrimp were more important in the diet of small bonefish (<440 mm FL). The stomach contents of bonefish caught in Florida Bay were significantly different from those of bonefish caught on the ocean (Florida Straits) side of the Florida Keys, but the differences were slight and the same prey taxa dominated the diet in both areas. Xanthid crabs, alpheid shrimp, *O. beta*, penaeid shrimp, and *Callinectes* spp. together made up over 50% of the dissimilarity in diet of bonefish between the two areas. Some seasonal effects on diet were found, but variable sample sizes among seasons in the respective sampling areas made it difficult to detect seasonal trends. Bonefish fed selectively on some prey groups, but other common prey groups were not selected and were less common in stomachs than in the prey environment. The suite of epibenthic crustaceans and fishes found in bonefish stomachs was significantly different from that available as prey in the environment. Our results suggest that teleosts, mainly *O. beta*, are more important in the diet of bonefish than reported in previous studies.

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Bonefish, *Albula vulpes*, are the basis of an economically important recreational fishery in the Florida Keys and many parts of the Caribbean. In the Florida Keys, fishing for bonefish is a year-round activity and provides an important source of income to professional fishing guides. Most bonefish are caught in relatively shallow (<2 m) water over either seagrass or sandy bottom, and it is common for bonefish to forage in water less than 0.3 m deep, where their tails and dorsal fins can often be seen extending from the water as they feed on benthic and epibenthic prey. Bonefish are known for their wariness when approached in shallow water and for their strong fighting abilities when hooked. In Florida, the commercial sale of bonefish is prohibited, and regulations on the recreational fishery include a bag limit of one fish per angler per day and a minimum total length of 457 mm (390 mm fork length). Bonefish are not considered a food fish in Florida, and therefore most bonefish caught are released.

Crabtree et al. (1996, 1997) recently described the age, growth, and reproduction of bonefish from South Florida waters and found that bonefish can attain ages of 19 years. In the Florida Keys, 50% of male bonefish reach sexual maturity at 418 mm and an age of 3.6 years, and 50% of female bonefish reach sexual maturity at 488 mm FL and an age of 4.2 years. Bonefish gonadal activity in the Florida Keys is seasonal and spawning occurs during November–May.

Feeding habits of bonefish have been studied by Warmke and Erdman (1963) in Puerto Rico, by Bruger (1974) in the Florida Keys, and by Colton and Alevizon (1983) in the Bahamas; however, none of these studies have adequately described the diet of bonefish. Warmke and Erdman (1963) identified only mollusks, Bruger (1974) presented frequency of occurrence data for crustaceans but did not quantify noncrustacean prey, and Colton and Alevizon (1983) sorted prey into 10 broad taxonomic categories but did not quantify the abundance of each prey species. Consequently, the relative importance of each prey species in the diet of bonefish is unknown. This information is needed to evaluate the effects of habitat changes on Keys bonefish populations and is particularly important considering the recent seagrass die-offs that have been documented in Florida Bay (Robblee et al., 1991; Carlson et al., 1994; Durako, 1994; Butler et al., 1995; Matheson et al.[1]). If changes in the benthic epifauna and infauna

have resulted from the seagrass die-off, these changes could potentially affect both feeding and occurrence of bonefish in Florida Bay. In this article, we describe the feeding habits of bonefish from waters off the Florida Keys. We consider both length-related and seasonal changes in bonefish diet. In addition, we compare the diets of bonefish collected from two important Keys areas: Florida Bay (including parts of Everglades National Park and adjacent waters) and ocean-side (Florida Straits) fishing areas off the Florida Keys.

## Methods

### Collections

We examined stomach contents of 385 bonefish collected from South Florida waters from December 1991 to April 1995. Most of these bonefish were caught with hook-and-line gear in waters off the Florida Keys, Florida Bay, and Biscayne Bay during daylight hours either by biologists or by a single professional bonefish guide and his anglers. Supplemental collections of small bonefish (<425 mm FL, $n$=22) were made with seines and gill nets of various sizes in waters off the Florida Keys. Bonefish were placed on ice immediately after capture. Fork length (FL) was later measured to the nearest millimeter (mm), stomachs were removed, and the contents preserved in 10% buffered formalin. Contents of individual stomachs were sorted and identified to the lowest possible taxon. Fragments of prey organisms were counted as one, unless countable parts such as eye lenses were found. Weights of prey organisms were measured by blotting prey items on filter paper and weighing them on an analytical balance. The number of individuals of each food type as a percentage of the total number of identifiable prey items (percent numerical abundance, $N$), the percentage of stomachs containing prey in which a particular prey taxa occurred (frequency of occurrence, $F$), and wet weight as a percentage of the total weight of all prey items (percent weight, $W$) were determined. For the larger and more abundant prey taxa (alpheid shrimp, penaeid shrimp, portunid crabs, xanthid crabs, and *Opsanus beta*), we measured prey size to examine the relation between predator and prey size. We measured total length (TL, tip of the rostrum to tip of the uropod) of shrimp, carapace width of crabs, and standard length (SL) of *O. beta*.

We compared the abundance of prey found in bonefish stomachs with the abundance of benthic and epibenthic crustaceans and fishes from typical Florida Keys bonefish habitat. Information on the abundance of potential prey in Florida Bay is based on meter-square throw-trap collections by Matheson et al.[1] during 1994–96. We used data for Buchanan Bank ($n$=30 collections) in the Atlantic subenvironment as described by Zieman et al. (1989) and followed by Matheson et al.[1] The Atlantic subenvironment, and specifically the Buchanan Bank area sampled by Matheson et al.,[1] is an area where many of our Florida Bay bonefish were caught. Data on prey abundance from ocean-side (Florida Straits) areas of the Florida Keys are from 54 samples that we collected following the methods of Sogard et al. (1987) and Matheson et al.[1] with meter-square throw traps. Ocean-side samples were taken during September 1996 ($n$=14) and January 1997 ($n$=40) at various locations from the middle Keys north to Elliot Key. We sampled areas where we had previously caught bonefish and that appeared to be representative of typical ocean-side bonefish flats. Throw-trap samples were collected over a different time period (1994–97) than that for our bonefish specimens (1991–95), and we assumed for our comparisons that prey availability did not change over this time. If prey abundance changed during 1991–97, this change could have biased our comparisons.

### Data analysis

Nonparametric multivariate techniques were used to analyze feeding data. Similarity matrices were constructed with pairwise Bray-Curtis similarity coefficients (Bray and Curtis, 1957). Square-root-transformed, percent-standardized prey-weight data were used to generate similarities. Prey weight was used for all comparisons except feeding selectivity comparisons, because this measure more closely reflects the energetic importance of a prey species in the diet than does either frequency of occurrence or percent numerical abundance. Percent numerical abundance was used in feeding selectivity comparisons because we were interested in the relative abundance of prey in stomachs and in the environment. Hierarchical agglomerative cluster analysis that incorporated a group-average linking method was used to search for groups among bonefish stomach contents. A nonparametric ordination technique, nonmetric multidimensional scaling (MDS), was used to ordinate sites on the basis of the similarity matrix. The contribution of the various prey categories to the percentage similarity within groups and the differences among groups were estimated with a simi-

[1] Matheson, R. E., D. A. Camp, S. M. Sogard, and K. A. Bjorgo. 1998. Changes in seagrass-associated fish and crustacean communities on Florida Bay mud banks: the effects of recent ecosystem changes? Manuscript in review.

larities percentage (SIMPER) procedure (Clarke, 1993; Clarke and Warwick, 1994). All multivariate analyses were performed with Plymouth Routines in Marine Environmental Research (PRIMER) programs (copyright M. R. Carr and K. R. Clarke, Marine Biological Laboratory, Plymouth, UK; Clarke and Warwick, 1994).

Separate analyses were performed to compare stomach contents between various length groups of bonefish, between seasons, and between areas (Table 1). To detect length-related differences in feeding, we pooled bonefish into 20-mm length intervals and used cluster and MDS analyses to compare stomach contents. Stomach contents of all 20-mm length groups within the 480- to 699-mm length range had a level of similarity >55%, so we restricted all other comparisons to this length group in order to minimize length-related dietary shifts that could have confounded comparisons of areas and seasons. We compared stomach contents of bonefish from two areas, Florida Bay and the ocean (Florida Straits) side of the Keys, using the analysis of similarity (ANOSIM) permutation test (Clarke, 1993; Clarke and Warwick, 1994). We did not include the lower Keys or Biscayne Bay in our area comparisons because we examined relatively few bonefish stomachs from these two areas. Bonefish move seasonally between Florida Bay and ocean-side areas; thus for any given month sample sizes were rarely the same for the two areas. To reduce confounding from seasonal effects that could result from unequal seasonal representation of the two areas, we eliminated some stomachs from our analysis to achieve equal monthly sample sizes for the two areas for each month. We pooled samples from all years, totaled the number of samples by month for each area, and then randomly eliminated stomachs for each month from the area with the greatest sample size so that, for any given month, both areas had equal sample sizes. The resulting sample of 50 stomachs from each area contained equal sample sizes from both areas for each month, but the total sample size varied from month to month (Table 1). To detect seasonal dietary shifts, collections were pooled into four seasonal groupings: January–March, April–June, July–September, and October–December. We used ANOSIM to make seasonal comparisons of the diets of bonefish separately for the two principal sampling areas. Six pairwise comparisons were made among seasons for each area. No adjustment of significance levels exists for ANOSIM to account for the increased possibility of type-1 error associated with multiple comparisons (Clarke and Warwick, 1994).

To determine feeding selectivity, we used ANOSIM to compare the species of crustaceans and fishes found in the stomachs of bonefish 480–699 mm long to those found in samples collected in the potential-prey environment. We included only bonefish collected during the same seasons as those when the throw-trap collections were made. For Florida Bay comparisons, bonefish collected during March, May, June, and September were included; for ocean-side comparisons, bonefish collected during January, February, August, September, and October were included (Table 1). Significant differences in the suite of crustaceans and fishes found in bonefish stomachs and the potential prey available in the environment would imply selective feeding. We used SIMPER to indicate the percentage of dissimilarity contributed by each prey species and thus show which prey were selected or not selected. Taxa that were not selected

**Table 1**

Sample sizes, and collection months and years for data included in ANOSIM comparisons. Numbers in parentheses are the number of samples collected during a particular month. Bonefish, *Albula vulpes*, fork lengths for all comparisons ranged from 480 to 699 mm.

| Comparison | *n* | Months | Years |
|---|---|---|---|
| Area | | | |
| Florida Bay | 50 | Jan (5), Feb (3), Mar (2), Apr (5), May (7), Jun (1), Jul (4), Aug (4), Sep (3), Oct (6), Nov (7), Dec (3) | 1991–1995 |
| Ocean side | 50 | same monthly sample sizes as Florida Bay | 1991–1995 |
| Season | | | |
| Ocean side | | | |
| Jan–Mar | 39 | | 1991–1995 |
| Apr–Jun | 43 | | |
| Jul–Sep | 6 | | |
| Oct–Dec | 33 | | |
| Florida Bay | | | 1991–1995 |
| Jan–Mar | 8 | | |
| Apr–Jun | 25 | | |
| Jul–Sep | 70 | | |
| Oct–Dec | 18 | | |
| Stomach throw trap | | | |
| Ocean side | | | |
| Stomachs | 39 | Jan. (7), Feb (13), Aug (4), Sept (3), Oct (12) | 1991–1995 |
| Throw traps | 54 | Jan (40), Sep (14) | 1996–1997 |
| Florida Bay | | | |
| Stomachs | 45 | Mar (2), May (9), Jun (10), Sep (24) | 1991–1995 |
| Throw traps | 30 | Mar (6), May (6), Jun (6), Sep (12) | 1994–1996 |

could have been avoided, not preferred, or only incidentally ingested by bonefish. Alternatively, taxa that were not selected could have been preferred, but were able to evade capture.

## Results

Stomachs of 385 bonefish that ranged in length from 228 to 702 mm contained prey (Fig. 1) consisting mostly of small benthic and epibenthic organisms (Table 2). Stomachs of 67 of the bonefish we examined were empty. Decapods and teleosts dominated the diet by weight, but gastropods and bivalves were among the most speciose prey categories. Relatively few prey species made up most of the diet by weight; xanthid crabs ($W$=29.9%), the gulf toadfish, *Opsanus beta* ($W$=17.2%), portunid crabs ($W$=10.9%), alpheid shrimp ($W$=9.2%), and penaeid shrimp ($W$=7.7%) together made up 74.9% of the diet. At least 17 families and 24 species of gastropods and 9 families and 16 species of bivalves were recognized, but gastropods made up only 2.7% of the diet by weight and bivalves made up only 2.5%. Polychaetes, represented by at least seven families, were important numerically ($N$=37.1%) but made up only 1.4% of the diet by weight.

Both the cluster analysis and the MDS ordination grouped bonefish stomach contents according to fish length (Fig. 2). Cluster analysis organized the 23 length groups into two principal clusters that were linked at a level of similarity greater than 20% and one outlying group of bonefish 280–299 mm long (group 2) that was linked to the other clusters at a level of similarity less than 10%. One principal cluster contained bonefish 260 to 439 mm long, and a second principal cluster contained mostly larger fish 400 to 702 mm long. Bonefish in the 400–419 mm length interval (group 8) were classified with larger fish, and bonefish in the 420–439 mm length interval (group 9) were classified with smaller bonefish. In Table 3, stomach contents are summarized separately for small bonefish (<440 mm) and large bonefish (>439 mm) on the basis of cluster analysis, but we reassigned bonefish stomachs in the 400–419 mm length interval (group 8) into the <440 mm group to avoid any overlap in the table between lengths of small (<440 mm) and large (>439 mm) bonefish. In the SIMPER analysis (Table 4), bonefish stomachs were grouped according to the cluster analysis shown in Figure 2, and no groups were reassigned. Levels of similarity among stomach contents of the 20-mm length groups within the 260–439 mm cluster were less overall than the levels of similarity of stomach contents of the 20-mm length groups of bonefish in the 400–699 mm cluster. Stomach contents of bonefish length groups ranging from 480 to 699 mm had a high level of similarity (>55%) and were tightly grouped in the MDS; we chose this length group as the basis for all other statistical comparisons.

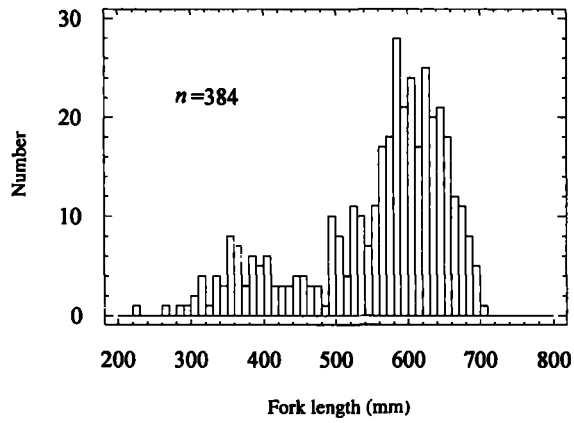


**Figure 1**

Length-frequency distribution of 384 bonefish, *Albula vulpes*, whose stomachs contained recognizable prey. The tail of one of the 385 bonefish whose stomach contents were examined was eaten by a shark during capture, so that fish was not measured.

SIMPER analysis suggested that much of the dissimilarity between the two principal length clusters was due to xanthid crabs, penaeid shrimp, alpheid shrimp, and *O. beta* (Table 4). The large values of the ratios ($\delta_i$/SD($\delta_i$)) between the mean contribution ($\delta_i$) to the overall level of dissimilarity and the standard deviation (SD) of the $\delta_i$ values across all stomachs suggest that these taxa consistently contributed to the level of dissimilarity, and so they are probably reliable discriminating prey taxa characteristic of one or the other length clusters. Bonefish longer than 439 mm consumed more decapods (alpheid shrimp, xanthid crabs, and *Callinectes* spp.) and teleosts than smaller bonefish (Tables 3 and 4). The most striking difference was in the consumption of teleosts, principally *O. beta*, which was not eaten by bonefish shorter than 440 mm but made up 17.8% of the diet of bonefish longer than 439 mm. Penaeid shrimp made up a larger proportion of the diet of small bonefish ($W$=40.5) than large bonefish ($W$=6.7), but they were eaten by bonefish of all sizes. Portunid crabs were eaten in nearly equal amounts by both length groups of bonefish, but this finding is misleading because all the *Portunus* spp. eaten by small bonefish were eaten by a single individual collected in Florida Bay; thus the importance of portunid crabs in the diet of small bonefish is probably less than what is suggested in Table 3. No crabs of the genus *Callinectes* were eaten by small bonefish.

## Table 2

Food items found in stomachs of bonefish, *Albula vulpes*, caught in the waters of the Florida Keys ($n$=385). $W$ = percent weight, $F$ = percent frequency of occurrence, $N$ = percent numerical abundance.

| Taxon and prey item | $W$ | $F$ | $N$ |
|---|---|---|---|
| Plant material | 0.6 | 34.5 | — |
| Algae | <0.1 | 0.5 | — |
| *Halimeda* | <0.1 | 8.1 | — |
| Unidentifiable seagrass | 0.1 | 8.1 | — |
| *Halodule* | <0.1 | 7.0 | — |
| *Syringodium* | <0.1 | 1.6 | — |
| *Thalassia* | 0.3 | 19.2 | — |
| Annelida | | | |
| Total Polychaeta | 1.4 | 39.5 | 37.1 |
| Unidentified Polychaeta | 0.2 | 6.8 | 1.7 |
| Amphinomidae | 0.3 | 1.3 | <0.1 |
| Lumbrinereidae | | | |
| *Lumbrinereis* spp. | <0.1 | 0.8 | 0.7 |
| Opheliidae | 0.7 | 30.1 | 33.0 |
| Spionidae | <0.1 | 0.8 | 0.4 |
| Orbiniidae | <0.1 | 1.3 | 0.9 |
| Capitellidae | | | |
| Unidentified Capitellidae | <0.1 | 1.6 | 0.1 |
| *Dasybranchus* spp. | <0.1 | 0.5 | <0.1 |
| Sabellidae | <0.1 | 1.0 | 0.1 |
| Mollusca | | | |
| Unidentified Mollusca | 1.6 | 15.6 | 0.8 |
| Total Gastropoda | 2.7 | 31.2 | 5.9 |
| Unidentified Gastropoda | 0.3 | 8.6 | 0.6 |
| Acmaeidae | | | |
| Unidentified Acmaeidae | <0.1 | 0.3 | <0.1 |
| *Patelloida pustulata* | <0.1 | 0.3 | <0.1 |
| Trochidae | | | |
| *Tegula fasciata* | <0.1 | 0.3 | <0.1 |
| Turbinidae | | | |
| *Turbo castanea* | <0.1 | 0.3 | <0.1 |
| *Eulithidium affine* | <0.1 | 1.3 | 0.5 |
| Turritellidae | | | |
| *Torcula acropora* | <0.1 | 0.3 | <0.1 |
| Modulidae | | | |
| *Modulus modulus* | <0.1 | 1.8 | 0.1 |
| Cerithiidae | | | |
| Unidentified Cerithiidae | <0.1 | 1.0 | <0.1 |
| *Cerithium eburneum* | <0.1 | 0.8 | <0.1 |
| *Cerithium muscarum* | <0.1 | 0.5 | <0.1 |
| Triviidae | | | |
| *Trivia quadripunctata* | <0.1 | 0.5 | <0.1 |
| Naticidae | | | |
| *Natica canrena* | <0.1 | 0.8 | <0.1 |
| Columbellidae | | | |
| Unidentified Columbellidae | <0.1 | 0.3 | <0.1 |
| *Anachis avara* | <0.1 | 1.0 | <0.1 |
| *Columbella rusticoides* | <0.1 | 0.3 | <0.1 |
| *Zafrona taylorae* | <0.1 | 0.5 | <0.1 |
| Nassariidae | | | |
| *Nassarius* sp. | <0.1 | 0.3 | <0.1 |
| Fasciolariidae | | | |
| *Leucozonia nassa* | <0.1 | 0.3 | <0.1 |
| *Fasciolaria tulipa* | 1.5 | 6.8 | 0.6 |
| *Fasciolaria* spp. | <0.1 | 0.5 | <0.1 |
| Olividae | | | |
| Unidentified Olividae | <0.1 | 0.8 | <0.1 |
| *Jaspidella jaspidea* | 0.2 | 8.3 | 0.7 |
| Marginellidae | | | |
| Unidentified Marginellidae | <0.1 | 1.3 | <0.1 |
| *Prunum apicinum* | 0.3 | 8.1 | 1.7 |
| *Prunum* sp. | <0.1 | 1.3 | <0.1 |
| *Volvarina avena* | <0.1 | 1.6 | 0.1 |
| Cystiscidae | | | |
| *Persicula catenata* | <0.1 | 1.6 | <0.1 |
| *Persicula pulcherrima* | <0.1 | 0.3 | <0.1 |
| Conidae | | | |
| *Conus stearnsi* | <0.1 | 0.3 | <0.1 |
| Bullidae | | | |
| *Bulla striata* | <0.1 | 2.3 | 0.7 |
| Nudibranchia | <0.1 | 0.3 | <0.1 |
| Total Bivalvia | 2.5 | 24.9 | 2.9 |
| Unidentified Bivalvia | 0.5 | 5.2 | 0.4 |
| Mytilidae | | | |
| *Brachidontes modiolus* | <0.1 | 0.5 | 0.3 |
| Pteriidae | | | |
| *Pinctada imbricata* | <0.1 | 0.5 | <0.1 |
| Limidae | | | |
| *Limaria pellucida* | 0.1 | 3.9 | 0.6 |
| Pectinidae | | | |
| Unidentified Pectinidae | <0.1 | 0.8 | <0.1 |
| *Argopecten irradians* | 0.5 | 2.1 | 0.1 |
| *Argopecten* spp. | <0.1 | 0.8 | <0.1 |
| Lucinidae | | | |
| Unidentified Lucinidae | 0.2 | 1.6 | 0.1 |
| *Codakia orbicularis* | <0.1 | 0.3 | <0.1 |
| *Codakia orbiculata* | <0.1 | 0.3 | <0.1 |
| Carditidae | | | |
| *Carditamera floridana* | <0.1 | 1.3 | <0.1 |
| Cardiidae | | | |
| Unidentified Cardiidae | <0.1 | 0.5 | <0.1 |
| *Americardia media* | <0.1 | 0.3 | <0.1 |
| *Laevicardium mortoni* | <0.1 | 0.3 | <0.1 |
| *Trachycardium muricatum* | <0.1 | 0.3 | <0.1 |
| Tellinidae | | | |
| Unidentified Tellinidae | <0.1 | 1.0 | <0.1 |
| *Strigilla carnaria* | <0.1 | 0.3 | <0.1 |
| *Tellina fausta* | <0.1 | 0.3 | 0.1 |
| *Tellina similis* | <0.1 | 3.9 | 0.3 |
| *Tellina tampaensis* | <0.1 | 0.5 | 0.1 |
| *Tellina* spp. | <0.1 | 1.3 | <0.1 |
| Veneridae | | | |
| *Chione cancellata* | 0.6 | 6.5 | 0.4 |
| *Transennella conradina* | <0.1 | 0.3 | <0.1 |
| Crustacea | | | |
| Unidentified Crustacea | <0.1 | 1.6 | <0.1 |
| Copepoda | <0.1 | 0.3 | <0.1 |
| Total Stomatopoda | 2.0 | 10.9 | 1.0 |
| Unidentified Stomatopoda | 1.0 | 5.7 | 0.6 |
| *Pseudosquilla ciliata* | 1.0 | 5.2 | 0.3 |

continued

There was a significant positive correlation between prey size and bonefish length for xanthid crabs ($n$=286, $r$=0.262, $P$<0.001) and portunid crabs ($n$=58, $r$=0.465, $P$<0.001), but not for alpheid shrimp ($P$=0.630), penaeid shrimp ($P$=0.063), or *O. beta* ($P$=0.782). The largest prey consumed were *O. beta* (largest 113 mm SL), the portunid crab *Callinectes sapidus* (largest 106 mm carapace width), and penaeid shrimp (largest 100 mm TL; Fig. 3). Most of these relatively large animals were consumed only as juveniles by bonefish.

The stomach contents of bonefish caught in Florida Bay were significantly different from those of bonefish caught on the ocean side of the Keys (ANOSIM, $R$=0.034; $P$=0.013). The statistic $R$ can range from −1 to 1 with a value of 1 indicating that all replicates within a sample are more similar to each other than to any replicates from the other samples and with a value of 0 indicating that the similarities between and within samples are on average equal (Clarke and Warwick, 1994). Although the $R$ value of 0.034 was

**Table 2 (continued)**

| Taxon and prey item | W | F | N |
|---|---|---|---|
| Total Decapoda | 67.8 | 88.6 | 42.1 |
| Unidentified Dendrobranchiata | 0.2 | 8.3 | 0.9 |
| Penaeidae | | | |
| Unidentified Penaeidae | 0.9 | 4.9 | 1.2 |
| *Penaeus* spp. | 3.8 | 17.9 | 2.9 |
| *Penaeus duorarum* | 3.0 | 5.5 | 1.1 |
| Palaemonidae | | | |
| Unidentified Palaemonidae | <0.1 | 8.6 | 1.1 |
| *Brachycarpus biunguiculatus* | <0.1 | 0.8 | <0.1 |
| Alpheidae | | | |
| Unidentified Alpheidae | 0.9 | 9.4 | 1.8 |
| *Alpheus floridanus* | <0.1 | 1.0 | <0.1 |
| *Alpheus normanni* | 7.6 | 35.3 | 13.2 |
| *Alpheus* spp. | 0.6 | 6.8 | 0.9 |
| Hippolytidae | | | |
| Unidentified Hippolytidae | 0.1 | 4.7 | 1.2 |
| *Thor* spp. | 0.3 | 19.7 | 5.6 |
| *Tozeuma* spp. | <0.1 | 0.5 | <0.1 |
| Palinuridae | | | |
| *Panulirus argus* | 0.6 | 0.5 | <0.1 |
| Unidentified Brachyura | 3.8 | 17.7 | 1.0 |
| Majidae | | | |
| Unidentified Majidae | 3.0 | 6.2 | 0.6 |
| *Pitho mirabilis* | 0.2 | 0.3 | <0.1 |
| *Pitho* spp. | 0.7 | 2.3 | 0.2 |
| Portunidae | | | |
| Unidentified Portunidae | 2.9 | 8.1 | 0.6 |
| *Callinectes ornatus* | 1.3 | 1.0 | 0.2 |
| *Callinectes sapidus* | 2.5 | 1.8 | 0.2 |
| *Callinectes* spp. | 3.1 | 7.0 | 0.5 |
| *Portunus* spp. | 1.1 | 1.0 | 0.5 |
| Xanthidae | | | |
| Unidentified Xanthidae | 29.9 | 49.6 | 8.2 |
| *Neopanope* sp. | <0.1 | 0.3 | <0.1 |
| *Panopeus* spp. | 0.1 | 0.8 | 0.1 |
| Grapsidae | | | |
| Unidentified Grapsidae | <0.1 | 1.0 | 0.1 |
| *Sesarma sp.* | <0.1 | 0.3 | <0.1 |
| Palicidae | | | |
| Unidentified Palicidae | <0.1 | 0.3 | <0.1 |
| Mysidae | <0.1 | 0.5 | <0.1 |
| Tanaidacea | <0.1 | 2.9 | 4.0 |
| Isopoda | <0.1 | 0.3 | <0.1 |
| Echinodermata | | | |
| Ophiuroidea | 0.5 | 1.8 | 1.0 |
| Holothuroidea | 0.5 | 2.9 | 0.2 |
| Ascidiacea | <0.1 | 0.3 | <0.1 |
| Chordata | | | |
| Total Teleostei | 20.5 | 44.9 | 4.9 |
| Unidentified teleostei | 0.5 | 10.1 | 0.6 |
| Ophicthidae | | | |
| Unidentified Ophicthidae | 0.2 | 1.3 | 0.1 |
| *Ahlia egmontis* | 0.7 | 2.9 | 0.2 |
| *Myrophis punctatus* | 0.7 | 2.6 | 0.1 |
| Engraulidae | | | |
| Unidentified Engraulidae | <0.1 | 0.3 | <0.1 |
| *Anchoa* sp. | <0.1 | 0.3 | <0.1 |
| Batrachoididae | | | |
| *Opsanus beta* | 17.2 | 29.1 | 3.1 |
| Bythitidae | | | |
| *Ogilbia cayorum* | <0.1 | 0.8 | <0.1 |
| Cyprinodontidae | | | |
| *Floridichthys carpio* | <0.1 | 0.3 | <0.1 |
| *Lucania parva* | <0.1 | 1.0 | <0.1 |
| Syngnathidae | | | |
| Unidentified Syngnathidae | <0.1 | 1.6 | <0.1 |
| *Hippocampus zosterae* | <0.1 | 0.3 | <0.1 |
| *Hippocampus* sp. | <0.1 | 0.3 | <0.1 |
| *Syngnathus floridae* | <0.1 | 0.5 | <0.1 |
| *Syngnathus scovelli* | <0.1 | 0.3 | <0.1 |
| *Syngnathus* spp. | 0.1 | 1.6 | 0.1 |
| Lutjanidae | | | |
| *Lutjanus griseus* | 0.1 | 0.3 | <0.1 |
| Scaridae | 0.2 | 0.8 | <0.11 |
| Gobiidae | | | |
| Unidentified Gobiidae | <0.1 | 1.3 | <0.1 |
| *Gobiosoma robustum* | <0.1 | 0.3 | <0.1 |
| Balistidae | | | |
| *Monacanthus ciliatus* | <0.1 | 0.3 | <0.1 |
| *Monacanthus hispidus* | 0.2 | 0.8 | <0.1 |
| Ostraciidae | | | |
| *Lactophrys* sp. | 0.1 | 0.3 | <0.1 |
| Miscellaneous material | — | 28.1 | — |
| Nonfood material | | | |
| sandy debris | — | 1.8 | — |
| coral rock | — | 0.3 | — |

significantly different from zero, the difference was small and thus the differences between the stomach contents of Florida Bay and ocean-side bonefish were probably slight. Xanthid crabs, alpheid shrimp, *O. beta*, penaeid shrimp, and *Callinectes* spp. together made up over 50% of the dissimilarity between the two areas (Table 5). Although these taxa contributed to the overall level of dissimilarity, the ratios ($\delta_i$/SD($\delta_i$)) between the mean contribution ($\delta_i$) to the overall level of dissimilarity and the standard deviation of the $\delta$ values across all stomachs were low for each prey taxa. Thus, these taxa did not consistently contribute to the level of dissimilarity, and are probably not reliable discriminating prey taxa characteristic of either area. In both areas, the same prey taxa dominated the diet (Table 6).

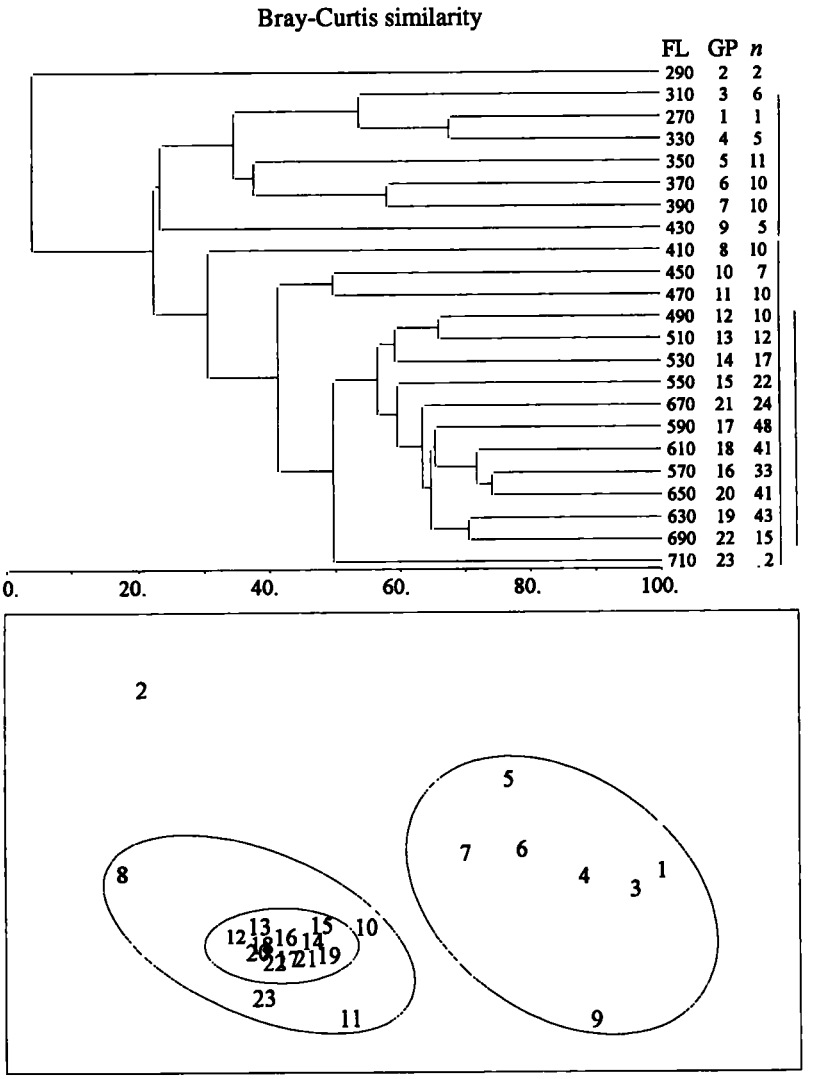


**Figure 2**

Dendrogram and multidimensional scaling (MDS) ordination showing similarities in diet among bonefish, *Albula vulpes*, grouped into 20-mm length intervals. Stress for the MDS plot = 0.13. FL = median fork length of the 20-mm length intervals, GP = group number used on the MDS ordination, and $n$ = the number of bonefish in each 20-mm length interval. The vertical bars to the right of the cluster show the two principal length groupings referred to in the text and the 480–699 mm length grouping used for all statistical comparisons. The circled groups in the MDS ordination correspond to the principal groupings shown on the cluster dendrogram and referred to in the text.

A seasonal effect on feeding was found for ocean-side bonefish (ANOSIM, $R$=0.069; $P$=0.002) but not for bonefish collected from Florida Bay (ANOSIM, $R$=0.066; $P$=0.080). For both tests, the $R$ values were close enough to zero to suggest that any seasonal differences in diet were slight. On the ocean side of the Keys, pairwise tests between bonefish caught during January–March and those caught during all other seasons were significant at $P<0.05$; no other pairwise seasonal comparisons were significant. Xanthid crabs, alpheid shrimp, brachyuran crabs (excluding xanthids, portunids, and majids), *O. beta*, penaeid shrimp, and stomatopods accounted for most of the dissimilarity between stomach contents of bonefish collected during January–March and those of bonefish collected during other seasons (Table 7). The ratios ($\delta_i$/SD($\delta_i$)) between the mean contribution ($\delta_i$) to the overall level of dissimilarity and the standard deviation of the values across all stomachs were low for each prey taxa. No taxa consistently contributed to the level of dissimilarity, and there were no reliable discriminating prey taxa characteristic of any particular season. Variable sample sizes between seasons in both areas reduced the power of our seasonal comparisons; most ocean-side bonefish were caught during January–May, and most Florida Bay bonefish were caught during June–December. Only six stomachs were examined from ocean-side bonefish captured during July–September. Although the stomach contents of these six bone-

**Table 3**

Food items found in stomachs of bonefish, *Albula vulpes*, caught in the waters of the Florida Keys ($n$=384) by bonefish length interval. $W$ = percent weight, $F$ = percent frequency of occurrence, $N$ = percent numerical abundance.

| Taxon and prey item | <440 mm FL ($n$=611) | | | >439 mm FL ($n$=323) | | |
|---|---|---|---|---|---|---|
| | *W* | *F* | *N* | *W* | *F* | *N* |
| Annelida | | | | | | |
| Polychaeta | 3.06 | 19.67 | 9.54 | 1.34 | 43.34 | 40.08 |
| Mollusca | | | | | | |
| Unidentified Mollusca | 2.29 | 19.67 | 1.82 | 1.56 | 14.24 | 0.67 |
| Gastropoda | 4.99 | 21.31 | 13.18 | 2.53 | 32.82 | 5.07 |
| Bivalvia | 4.64 | 22.95 | 3.51 | 2.39 | 25.70 | 2.81 |
| Crustacea | | | | | | |
| Stomatopoda | 2.26 | 3.28 | 2.52 | 2.03 | 12.38 | 0.79 |
| Decapoda | | | | | | |
| Penaeidae | 40.45 | 36.07 | 11.50 | 6.68 | 26.01 | 4.37 |
| Alpheidae | 0.35 | 8.20 | 1.12 | 9.36 | 51.70 | 17.52 |
| Hippolytidae | 1.87 | 11.48 | 7.99 | 0.33 | 26.01 | 6.76 |
| Majidae | 3.28 | 8.20 | 0.70 | 3.92 | 8.98 | 0.89 |
| Portunidae | 15.64 | 8.20 | 3.37 | 10.91 | 19.50 | 1.83 |
| Xanthidae | 7.43 | 13.11 | 1.68 | 31.49 | 56.97 | 8.94 |
| Chordata | | | | | | |
| Teleostei | 3.90 | 19.67 | 3.09 | 21.10 | 49.54 | 5.07 |
| Batrachoididae | | | | | | |
| *Opsanus beta* | 0.00 | 0.00 | 0.00 | 17.83 | 34.67 | 3.43 |

fish were significantly different from those of bonefish collected in January–March (ANOSIM, $R$=0.284, $P$=0.018), we have little confidence in this test because of the small sample size, and these results are not included in Table 7.

Bonefish fed selectively on some prey groups but did not select others. The suite of epibenthic crustaceans and fishes found in bonefish stomachs was significantly different from that collected with throw traps both on the ocean side of the Florida Keys (ANOSIM, $R$=0.261, $P$<0.001) and in Florida Bay (ANOSIM, $R$=0.419, $P$<0.001). Bonefish on the ocean side of the Florida Keys fed selectively on alpheid shrimp, xanthid crabs, *P. duorarum*, and *O. beta*, whereas they did not select the small but abundant crustaceans *Thor* spp. and *Periclimenes americanus* (Table 8). Similarly, Florida Bay bonefish fed selectively on xanthid crabs, alpheid shrimp, *O. beta*, *P. duorarum*, and *Callinectes* spp. but did not select the abundant but small crustaceans *Thor* spp., *Hippolyte zostericola*, and *P. americanus*, as well as the abundant goby *Gobiosoma robustum* (Table 9).

## Discussion

A variety of factors could have biased our description of the diet of bonefish. Some prey, particularly soft-bodied prey, may have been digested more rapidly than others with bony or chitinous skeletons. Consequently, we may have underestimated the importance of soft-bodied organisms such as polychaetes. Furthermore, bonefish have massive pharyngeal tooth plates capable of crushing shells and other hard structures. If bonefish are able to expel the crushed shells of mollusks and swallow only the soft-bodied organism, then we could have underestimated the importance of mollusks. This might explain why mollusks were relatively unimportant in our samples. Our sample consisted principally of bonefish caught with hook-and-line gear; therefore most of the fish we examined were probably actively foraging or they would not have consumed the bait presented by anglers. We do not believe that the number of fish with empty guts in our sample reflects the number of fish in the area that were not feeding, therefore we did not attempt to evaluate temporal feeding patterns. We cannot eliminate the possibility that some bonefish regurgitated prey during capture trauma; if some prey taxa were more likely to be regurgitated than others, this could have biased our results. Most of the bonefish in our sample came from relatively shallow (<2 m) grass, sand, or hard-bottom flats, but because the fish were caught by anglers, we did not have corresponding data on bottom type for each fish. Colton and Alevizon (1983) found differences in the

**Table 4**

Breakdown into the most important prey groups of the mean dissimilarity between stomach contents (percent weight) of bonefish, *Albula vulpes*, from the two principal clusters shown in Figure 2. Small bonefish ranged from 260 to 439 mm FL and large bonefish ranged from 400 to 699 mm FL. Prey groups are listed in order of decreasing contribution to the overall dissimilarity between the two bonefish length groups. $\delta_i$ is the mean contribution of the *i*th species to the dissimilarity between the two groups, $\delta_i / SD(\delta_i)$ is the ratio between the mean contribution of the *i*th species ($\delta_i$) and the standard deviation of the values for that species [$SD(\delta_i)$], $\delta_i$ % is the contribution to the total dissimilarity scaled as a percentage, and Cum $\delta_i$ % is the cumulative contribution to the total dissimilarity scaled as a percentage. Taxa that are likely to be reliable discriminators of the two length groups are indicated by ** in the $\delta_i / SD(\delta_i)$ column. Taxa proportionally more important in the diet of large bonefish than small bonefish are shown in bold type.

| Species | $\delta_i$ | $\delta_i/SD(\delta_i)$ | $\delta_i$ % | Cum $\delta_i$ % |
|---|---|---|---|---|
| Penaeidae | 8.13 | 1.94** | 10.47 | 10.47 |
| **Xanthidae** | 7.97 | 2.48** | 10.26 | 20.73 |
| **Alpheidae** | 5.29 | 1.84** | 6.81 | 27.54 |
| ***O. beta*** | 5.28 | 1.84** | 6.80 | 34.34 |
| **Portunidae (unidentified)** | 4.62 | 1.26 | 5.95 | 40.29 |
| Brachyura[1] | 3.68 | 1.37 | 4.73 | 45.02 |
| Majidae | 3.25 | 1.05 | 4.19 | 49.21 |
| *Portunus* spp. | 2.80 | 0.45 | 3.60 | 52.81 |
| Stomatopoda | 2.51 | 1.16 | 3.23 | 56.03 |
| ***Callinectes* spp.** | 2.50 | 0.97 | 3.23 | 59.26 |

[1] Excluding xanthids, portunids, and majids.

**Table 5**

Breakdown into the most important prey groups of the mean dissimilarity between stomach contents (percent weight) of bonefish, *Albula vulpes* (480–699 mm FL), caught on the ocean side of the Florida Keys ($n$=50) and in Florida Bay ($n$=50). Prey groups are listed in order of decreasing contribution to the overall dissimilarity between the two study areas. Taxa proportionally more important in the diet of ocean-side bonefish than Florida Bay bonefish are shown in bold type. The low values of $\delta_i / SD(\delta_i)$ suggest that the data were variable and that no taxa were reliable discriminators of either area. Symbols are explained in the legend of Table 4.

| Species | $\delta_i$ | $\delta_i/SD(\delta_i)$ | $\delta_i$ % | Cum $\delta_i$ % |
|---|---|---|---|---|
| **Xanthidae** | 13.47 | 1.15 | 17.17 | 17.17 |
| **Alpheidae** | 8.56 | 1.06 | 10.91 | 28.08 |
| ***O. beta*** | 8.04 | 0.82 | 10.24 | 38.32 |
| Penaeidae | 7.49 | 0.82 | 9.55 | 47.87 |
| *Callinectes* spp. | 4.53 | 0.46 | 5.78 | 53.65 |

stomach contents of Bahamian bonefish collected over different bottom types, and this variation probably also occurs in the Florida Keys. There was also no evidence that bonefish do not feed in deeper waters than those traditionally fished by anglers; prey availability and bonefish feeding may be quite different at greater depths than in the shallow waters we sampled.

Most (77%) of the fish in our sample were longer than 500 mm (Fig. 1); consequently, the diet of large bonefish is better described by our data than that of small bonefish. The inadequacy of our description of the diet of small bonefish is reflected in the low levels of similarity among 20-mm length intervals of bonefish smaller than 480 mm (Fig. 2). Many of the length intervals smaller than 500 mm contained few fish and resulted in greater variation in diet among length intervals and probably caused the lower levels of similarity among 20-mm length groups of small bonefish than among large fish.

The changes in diet as length of bonefish increased in general reflect the expansion of the diet to include larger prey such as *O. beta* and crabs of the genus *Callinectes*. In some cases, for example xanthid and portunid crabs, prey size was positively correlated with predator length. In other cases, for example *O. beta*, prey were not eaten at all by small bonefish, and there was no correlation between prey size and predator length among large bonefish. Small but abundant crustaceans such as *Thor* spp., *H. zostericola*, and *P. americanus* were not important in the diet of the bonefish we examined. These small crustaceans may be eaten by smaller bonefish (<228 mm), but they are apparently outside of the size range of prey typically consumed by the size of bonefish we considered.

Bruger (1974) examined the stomachs of 129 bonefish ranging from 221 to 679 mm FL (reported as 210 to 656 mm SL) collected from the waters off the Keys and reported the frequency of occurrence of crustaceans in the diet. Of these 129 stomachs, 19 were empty. We recalculated his frequency of occurrences on the basis of only the number of stomachs with prey ($n$=110) to compare with our frequency data: the recalculated results were 85% crustaceans, 33% mollusks, and 17% teleosts. These results are in general agreement with our findings of 89% crustaceans, 51% mollusks, and 45% teleosts, except that our samples contained more teleosts than Bruger's. Among crustacean prey, Bruger's results resemble ours; penaeid shrimp, alpheid shrimp, portunid crabs, and xanthid crabs were the most frequently occurring crustacean prey. Although Bruger did not quantify by species the fishes found in stomachs, he did not include *O. beta* in his list of teleosts eaten by

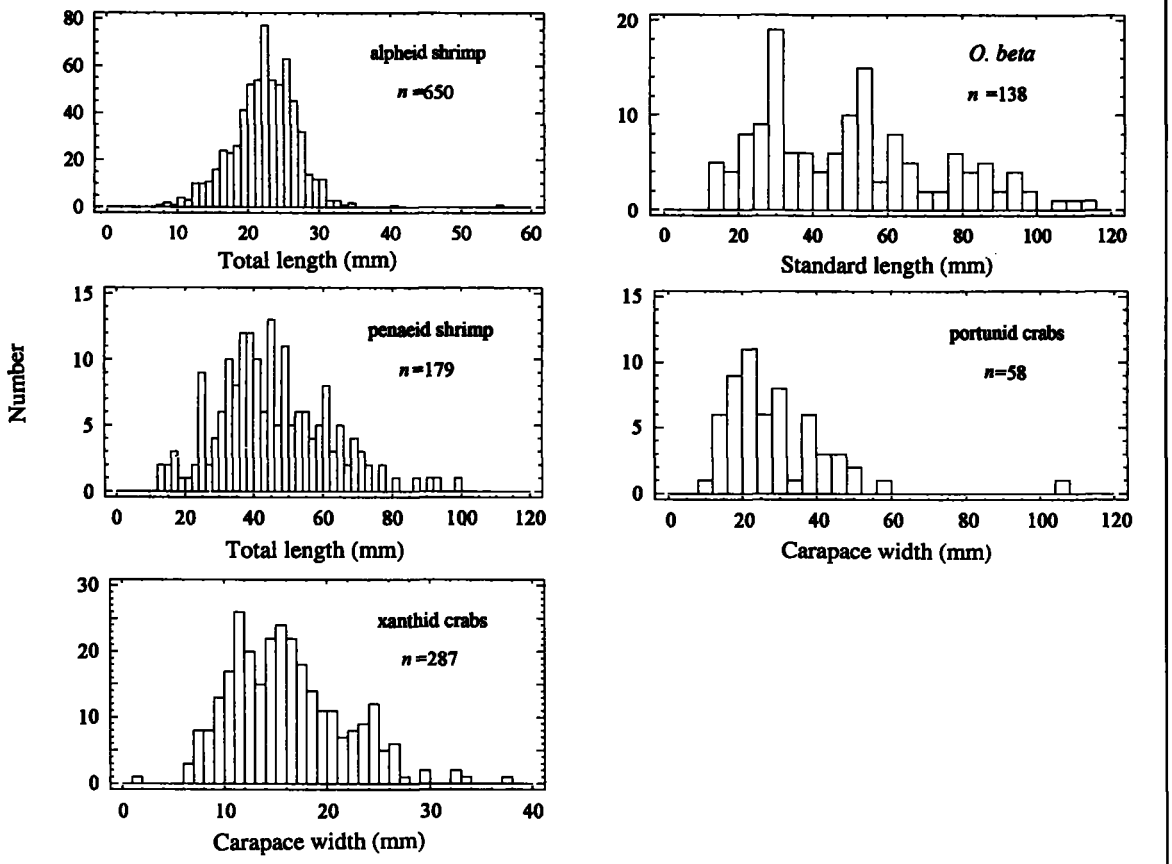


**Figure 3**

Size-frequency distributions of some prey important in the diet of bonefish, *Albula vulpes*.

bonefish. In contrast, *O. beta* was the teleost most frequently eaten by the bonefish we examined (*F*=29.1%). Most of Bruger's bonefish were collected in the lower Keys between Marathon and Key West, but most of our bonefish were captured in the upper Keys from Marathon north to Key Biscayne and including Florida Bay. Although we have no data on prey availability in the lower Keys, habitat differences between the two study areas could account for some of the differences between our results and Bruger's.

Colton and Alevizon (1983) examined the stomach contents of 365 Bahamian bonefish ranging from 268 to 652 mm FL (reported as 256 to 630 mm SL). Bivalves made up 39.2% of the diet of Bahamian bonefish by dry weight, but they made up only 2.5% of the diet of Keys bonefish by weight. Bivalves were the most important prey of Bahamian bonefish both in terms of dry weight (39.2%) and frequency of occurrence (66.3%); portunid (*W*=20.1%; *F*=40.5%) and xanthid crabs (*W*=15.0%; *F*=24.8%) were also important. Teleosts (*O. beta* and *Bathygobius soporator*; pooled *W*=4.9%), alpheid shrimp (*W*=4.6%), *Pseudosquilla ciliata* (*W*=3.2%), polychaetes (*W*=3.2%), gastropods (*W*=2.4%), and *Penaeus duorarum* (*W*=1.6%) occurred in 15–25% of the guts that Colton and Alevizon examined but made up little of the diet in terms of dry weight. The most notable difference between Keys and Bahamian bonefish diets was the greater importance of *O. beta* in the diet of Keys bonefish (*W*=17.2%).

Colton and Alevizon (1983) reported length-related changes in the diet of Bahamian bonefish that were similar to those that we observed in the Florida Keys. They found that bonefish larger than 416 mm FL (400 mm SL) ate more xanthid and majid crabs, alpheid shrimp, and teleosts than smaller bonefish did. Teleosts (gobiids, batrachoidids, ophichthids, and small lutjanids) were found principally in stomachs from bonefish larger than 575 mm FL (555 mm SL). In contrast to our conclusions, Colton and Alevizon (1983) found that small bonefish (<416 mm) ate more portunid crabs (*Callinectes ornatus*) than large bonefish did; we found no *Callinectes* spp. in any bone-

**Table 6**

Food items found in stomachs of bonefish, *Albula vulpes*, caught in Florida Bay ($n$=130) and on the ocean side ($n$=144) of the Florida Keys. Stomachs from all bonefish 480 to 699 mm FL collected during all months are included. $W$ = percent weight; $F$ = percent frequency of occurrence; $N$ = percent numerical abundance.

| Taxon and prey item | Florida Bay | | | Ocean side | | |
|---|---|---|---|---|---|---|
| | *W* | *F* | *N* | *W* | *F* | *N* |
| Annelida | | | | | | |
| Polychaeta | 0.62 | 34.62 | 34.22 | 1.63 | 52.08 | 32.72 |
| Mollusca | | | | | | |
| Gastropoda | 1.86 | 33.85 | 4.94 | 2.83 | 32.64 | 3.52 |
| Bivalvia | 2.68 | 28.46 | 3.00 | 2.02 | 24.13 | 1.85 |
| Crustacea | | | | | | |
| Stomatopoda | 0.35 | 3.85 | 0.24 | 3.85 | 19.44 | 0.73 |
| Decapoda | | | | | | |
| Penaeidae | 8.30 | 35.38 | 6.72 | 4.30 | 15.97 | 1.35 |
| Alpheidae | 5.13 | 40.77 | 11.93 | 14.12 | 60.42 | 13.16 |
| Hippolytidae | 0.38 | 32.31 | 11.38 | 0.33 | 23.61 | 2.81 |
| Majidae | 1.97 | 4.62 | 0.28 | 4.45 | 9.72 | 0.67 |
| Portunidae | 17.06 | 23.85 | 2.96 | 5.00 | 14.58 | 0.60 |
| Xanthidae | 33.53 | 63.08 | 10.94 | 27.78 | 52.78 | 4.64 |
| Chordata | | | | | | |
| Teleostei | 21.25 | 56.92 | 7.43 | 24.87 | 43.75 | 2.31 |
| Batrachoididae | | | | | | |
| *Opsanus beta* | 18.94 | 48.46 | 5.85 | 19.87 | 25.00 | 1.19 |

**Table 7**

Breakdown into the most important prey groups of the mean dissimilarity between stomach contents (percent weight) of bonefish, *Albula vulpes* (480–699 mm FL), collected on the ocean side of the Florida Keys during January–March ($n$=39), April–June ($n$=43), and October–December ($n$=33). Prey groups are listed in order of decreasing contribution to the overall dissimilarity between the seasonal samples. Taxa proportionally more important in the diet of bonefish collected during January–March than during other seasons are shown with bold type. The low values of $\delta_i/SD(\delta_i)$ suggest that the data were variable and that no taxa were reliable discriminators of any particular season. Symbols are explained in the legend of Table 4.

| Species | $\delta_i$ | $\delta_i/SD(\delta_i)$ | $\delta_i$ % | Cum $\delta_i$ % |
|---|---|---|---|---|
| Jan–Mar vs. Apr–Jun | | | | |
| Xanthidae | 12.44 | 1.16 | 16.02 | 16.02 |
| **Alpheidae** | 11.77 | 1.28 | 15.16 | 31.18 |
| **Brachyura**[1] | 6.71 | 0.69 | 8.64 | 39.81 |
| *O. beta* | 5.41 | 0.62 | 6.97 | 46.78 |
| Stomatopoda | 5.18 | 0.64 | 6.67 | 53.45 |
| Jan–Mar vs. Oct–Dec | | | | |
| **Alpheidae** | 11.52 | 1.27 | 14.52 | 14.52 |
| Xanthidae | 10.99 | 0.99 | 13.86 | 28.38 |
| **Brachyura**[1] | 7.26 | 0.75 | 9.16 | 37.54 |
| Penaeidae | 4.97 | 0.76 | 6.27 | 43.81 |
| *O. beta* | 4.90 | 0.56 | 6.18 | 50.00 |

[1] Excluding xanthids, portunids, and majids.

fish smaller than 440 mm, although crabs of the genus *Portunus* were eaten in large numbers by one 435-mm bonefish.

There was evidence of a seasonal effect on diet, but small sample sizes during some seasons in each of the respective sampling areas reduced our ability to detect significant differences. Colton and Alevizon (1983) also found seasonal differences in feeding in Bahamian bonefish. Bivalves were eaten more during the summer by bonefish of all lengths, whereas small bonefish (<416 mm) ate more portunid crabs during the winter. They also noted habitat-related differences in bonefish feeding. Penaeid shrimp were eaten almost exclusively by bonefish caught over grassy bottom and not by those caught over sandy bottom. Bonefish caught over sandy bottom ate relatively more crabs and bivalves than did bonefish caught over grassy areas.

Warmke and Erdman (1963) examined the stomach contents of 56 bonefish ranging from 292 to 663 mm FL (reported as 0.75 to 10.25 pounds) from Puerto Rican waters and, like Colton and Alevizon (1983), found that mollusks were the most important prey. Stomachs of Puerto Rican bonefish contained 56% mollusks, 42% crustaceans, and 2% other prey types by volume. In contrast, we found that mollusks accounted for only about 7% of the diet of Keys bonefish by weight and that crustaceans accounted for about 70% of the diet. Teleosts were part of Warmke and Erdman's "other" classification and made up less than 2% of the diet in their study; in the Keys, teleosts made up over 20% of the diet by weight. Warmke and Erdman identified only mollusks to species. The most important mollusk they found was the bivalve *Codakia costata*, which occurred in 62% of the stomachs they examined. *Codakia orbicularis* and *C. orbiculata* occurred in stomachs from Keys bonefish but made up less than 1% of the diet by numbers or weight. *Codakia costata* was not found in Keys bonefish stomachs and was not reported to occur in Florida Bay by Turney and Perkins (1972).

There were slight but significant differences between the diets of bonefish from Florida Bay and those from the ocean side of the Keys. These differences may reflect differences in prey availability in the two areas, but overall the dominant prey eaten by bonefish was the same in the two areas. The fauna of Florida Bay has been characterized as Gulf-Carolinian in nature, whereas that of the Keys ocean side is Antillean (Sogard et al., 1987; Holmquist et al.,

**Table 8**

Breakdown into the most important prey groups of the mean dissimilarity between stomach contents (percent number) of bonefish, *Albula vulpes* (480–699 mm FL), caught on the ocean side of the Florida Keys ($n$=39) and throw-trap samples ($n$=54) from the ocean side of the Florida Keys. Prey groups are listed in order of decreasing contribution to the overall dissimilarity between the two samples. Taxa proportionally more important in the diet of bonefish than suggested by their proportional abundance in throw-trap samples are shown with bold type. The low values of $\delta_i/SD(\delta_i)$ suggest that the data were variable and that no taxa were reliable discriminators of either sample source. Symbols are explained in the legend of Table 4.

| Species | $\delta_i$ | $\delta_i/SD(\delta_i)$ | $\delta_i$ % | Cum $\delta_i$ % |
|---|---|---|---|---|
| **Alpheidae** | 10.58 | 1.31 | 13.87 | 13.87 |
| **Xanthidae** | 7.89 | 1.13 | 10.35 | 24.23 |
| *Periclimenes americanus* | 6.83 | 0.93 | 8.96 | 33.19 |
| *Thor* spp. | 6.11 | 0.97 | 8.02 | 41.20 |
| ***P. duorarum*** | 5.95 | 0.88 | 7.81 | 49.01 |
| ***O. beta*** | 4.61 | 0.80 | 6.05 | 55.06 |

**Table 9**

Breakdown into the most important prey groups of the mean dissimilarity between stomach contents (percent number) of bonefish, *Albula vulpes* (480-699 mm FL), caught in Florida Bay ($n$=45) and throw-trap samples ($n$=30) from Florida Bay (Matheson et al.[1]). Prey groups are listed in order of decreasing contribution to the overall dissimilarity between the two samples. Taxa that are likely to be reliable discriminators of the two samples are indicated by ** in the $\delta_i/SD(\delta_i)$ column. Taxa proportionally more important in the diet of bonefish than suggested by their proportional abundance in throw-trap samples are shown with bold type. Symbols are explained in the legend of Table 4.

| Species | $\delta_i$ | $\delta_i/SD(\delta_i)$ | $\delta_i$ % | Cum $\delta_i$ % |
|---|---|---|---|---|
| *Thor* spp. | 18.13 | 1.97** | 23.03 | 23.03 |
| **Xanthidae** | 9.63 | 1.17 | 12.24 | 35.27 |
| **Alpheidae** | 7.61 | 1.23 | 9.67 | 44.94 |
| ***O. beta*** | 7.51 | 1.15 | 9.55 | 54.49 |
| ***P. duorarum*** | 5.17 | 0.81 | 6.57 | 61.06 |
| *Hippolyte zostericola* | 5.00 | 1.65** | 6.36 | 67.42 |
| *Periclimenes americanus* | 4.55 | 1.85** | 5.78 | 73.20 |
| ***Callinectes* spp.** | 3.23 | 0.48 | 4.10 | 77.30 |
| *Gobiosoma robustum* | 3.03 | 1.98** | 3.85 | 81.15 |

1989a, 1989b). Our sampling effort was over a large and diverse area, and this limited our ability to resolve area-specific differences in bonefish diet. Some Florida Bay areas that we sampled were near passes leading to ocean-side flats and may have more closely resembled ocean-side areas than some of the more remote areas in Florida Bay where we occassionally caught bonefish. Larger sample sizes, more intensive sampling of specific areas along with site-specific descriptions of habitat types, and sampling of prey availability concurrent with bonefish collections are needed to better describe spatial variation in the diet of Keys bonefish.

Comparisons of the stomach contents of bonefish collected in Florida Bay and ocean-side areas as well as seasonal comparisons were complicated by the variable monthly sample sizes from the two areas. We excluded over half of the bonefish in our sample from our area comparisons because seasonal sample sizes from the two areas were greatly unequal. The variable sample sizes from the two areas reflect general seasonal trends in bonefish availability in the two areas. Bonefish are typically most abundant in Florida Bay during summer and fall. Winter cold fronts tend to reduce Florida Bay temperatures more than ocean-side temperatures (Hudson et al., 1976; Roberts et al., 1982; Chiappone, 1996), and many productive summer–fall fishing areas in Florida Bay rarely hold bonefish during winter and spring because bonefish move to ocean-side areas with more moderate temperatures and closer proximity to deep water. Thus, most of our Florida Bay bonefish were captured during summer and fall, and most ocean-side bonefish were caught during winter and spring.

Seagrass die-offs have recently been documented in Florida Bay (Robblee et al., 1991; Carlson et al., 1994; Durako, 1994; Butler et al., 1995). Anecdotal evidence suggests that changes in the Everglades ecosystem have caused a decline in the quality of fishing in Florida Bay and the waters of the Florida Keys (Chiappone and Sulka, 1996). If changes in the benthic epifauna and infauna have resulted from the seagrass die-off, these changes could potentially affect feeding and occurrence of bonefish in Florida Bay. Data on the species composition and abundance of epifaunal crustaceans and fishes collected subsequent to the sea grass die-off and the studies of Sogard et al. (1987, 1989) and Holmquist et al. (1989a, 1989b) prior to the seagrass die-off suggest little evidence of declines in populations of important bonefish prey species (Matheson et al.[1]). One significant change reported by Matheson et al.[1] was an increase in the abundance of *O. beta* in some areas of Florida Bay since the 1980s. Whether the increased abundance of *O. beta* compared to that found in previous studies accounts for its greater prominence in stomachs of the bonefish we sampled is unknown.

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# Population structure in greater amberjack, *Seriola dumerili*, from the Gulf of Mexico and the western Atlantic Ocean*

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**Abstract**—Variation in restriction sites of mitochondrial (mt)DNA was examined from 444 greater amberjack (*Seriola dumerili*) sampled from 11 offshore localities in the northern Gulf of Mexico (Gulf) and along the U.S. southeast Atlantic coast (Atlantic). A total of 49 mtDNA haplotypes (genotypes) were detected. Percent nucleotide sequence divergence among the haplotypes ranged from 0.156 to 2.623 (mean ±SE=0.980 ±0.015). Nucleon diversity within samples ranged from 0.845 to 0.906, and intrapopulational mtDNA diversities ranged (mean ±SD) from 0.483 ±0.370 to 0.619 ±0.419. The latter did not differ significantly from one another. Homogeneity tests of mtDNA haplotype frequencies, $F_{ST}$ values, analysis of molecular variance (AMOVA), and comparisons of pairwise $\Phi_{ST}$ distances were consistent with the hypothesis that (at least) two subpopulations (stocks) of greater amberjack exist in U.S. waters: one in the northern Gulf and one along the U.S. Atlantic coast. The latter subpopulation includes individuals from the Florida Keys. There was no evidence of phylogeographic structure among mtDNA haplotypes or among sample localities, suggesting either that restricted gene flow between the subpopulations is fairly recent or that gene flow between the two is relatively infrequent. No significant spatial autocorrelations of mtDNA haplotypes was found among samples of greater amberjack from the Gulf, indicating continuous gene flow across the northern Gulf. Long-term effective (female) population sizes of both subpopulations were estimated to be in the range of 90,000–95,000 individuals. The estimates were commensurate with estimates in other, economically important marine fish. Based on suggested differences in mtDNA evolutionary rates between homeothermic and poikilothermic vertebrates, the effective (female) population sizes of both stocks of greater amberjack could be in the range of 500,000 to 1,000,000 individuals.

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Fish. Bull. 96:767–778 (1998).

Greater amberjack, *Seriola dumerili*, constitute an increasingly important component of the U.S. Gulf and Atlantic commercial and recreational fisheries. Commercial landings in the Atlantic rose over twentyfold between 1981 and 1991, from under 100,000 pounds annually to nearly two million pounds (Cummings-Parrack[1]). Commercial landings in the Gulf rose similarly, reaching a peak of nearly 2.5 million pounds in 1988 that was then followed by a >50% decline in 1990 and a further decline in 1991 (McClellan and Cummings[2]). An increase in commercial landings in 1993 was followed by declines in both 1994 and 1995 (McClellan and Cummings[2]). The commercial interest in greater amberjack appears to be driven by: 1) consumer acceptance of greater amberjack as an edible fish; 2) replacement of red drum in the blackened fish market; and 3) effort displacement of king mackerel and reef-fish fishermen, especially off the coasts of Florida (Cummings-Parrack[1]). Recreational landings are smaller in both the Gulf and Atlantic and appear to have declined in recent years (Cummings-Parrack[1]; McClellan and Cummings[2]). Problems that confound landing statistics and fishery analysis of the greater amberjack resource include species misidentification and the possibility that reported landings may be small in proportion to total removals (Cummings-Parrack[1]). Current management of the greater amberjack resource in U.S. waters is based on a two-stock (management unit) model. One stock resides along the U.S. southeastern coast and includes all fishing areas north of Cape Hatteras, NC (35°00'N) southward to the Dry Tortugas and the Florida Keys (24°35'N); the other includes fishing grounds in the Gulf of Mexico off the Dry Tortugas and Florida Keys north and then westward to the U. S. Mexico border (26°00'N)

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[1] Cummings-Parrack, N. 1993. The exploitation status of the Atlantic amberjack fisheries through 1991. Miami Laboratory, SE Fisheries Sci. Center, Natl. Mar. Fish. Serv., Cont. MIA-92/93-30, Miami, FL, 98 p.

[2] McClellan, D. B., and N. J. Cummings. 1996. Stock assessment of Gulf of Mexico greater amberjack through 1995. Miami Laboratory, SE Fisheries Sci. Center, Natl. Mar. Fish. Serv., Cont. MIA-96/97-03, Miami, FL, 69 p.

(Cummings and McClellan[3]). Movement patterns inferred from mark-and-release experiments carried out between 1959 and 1994 (Cummings and McClellan[3]) are consistent with the two-stock hypothesis. In brief, over 1400 recaptures from approximately 14,000 releases revealed cyclical tag-return patterns that suggested resident stocks or subpopulations of greater amberjack along both the eastern coast of Florida and the northern Gulf. Exchange rates between the two stocks was estimated as approximately 1.5% by Cummings and McClellan[3] although, as noted by these authors, the rate estimates were not adjusted for fishing pressure or for potential biases due to mortality, tag shedding, lack of reporting, and fishing effort. It also was clear from a few tag returns that greater amberjack can migrate considerable distances, e.g. from near Charleston, South Carolina, to Texas or from northwest Florida to Virginia (Cummings and McClellan[3]).

Biological information on greater amberjack is limited to studies reported in Berry and Burch (1978), Shipp (1986), Manooch (1988), and GMFMC (1989). Thompson et al.[4] presented data on greater amberjack age, growth, and reproduction, and Cummings-Parrack[1] and McClellan and Cummings[2] summarized most of the available information on landings and other fishery statistics. Direct or indirect information on genetic stock structure is even more limited. Johnson[5] carried out a pilot study of nuclear-gene (allozyme) variation among 225 greater amberjack sampled from the Atlantic ($n$=60), eastern Gulf ($n$=84), and western Gulf ($n$=81). Of 72 putative loci examined, only one polymorphic (and noninformative) system was found. On the surface, these data do not support the concept of separate stocks. However, genetic homogeneity (*sensu stricto*) does not unequivocally establish the existence of a single breeding population (stock), but rather is simply consistent with the hypothesis that samples are drawn from a population with the same parametric allele frequencies. In addition, the almost total absence of variation effectively precluded rigorous testing of the null hypothesis (i.e. the interpretation of genetic homogeneity among samples is potentially compromised by virtue of the absence of significantly variable nuclear-gene loci).

Alternatively, the apparent absence of genetic variation raises considerable concern about the effective size of greater amberjack populations. Compared with other marine finfish (Smith and Fujio, 1980; Waples, 1987; Bohlmeyer and Gold, 1991), levels of nuclear-gene variation in greater amberjack (as reported by Johnson[5]) are low. Richardson and Gold (1993) examined mitochondrial (mt)DNA variation among 59 greater amberjack sampled primarily from the west coast of Florida. Levels of mtDNA variation in greater amberjack were low in comparison with red drum and several clupeid species (e.g. Atlantic menhaden), but higher than those found in black drum, red snapper, and red grouper (Camper et al., 1993; Gold et al., 1993; Richardson and Gold, 1993). Estimates of long-term, effective female population size (computed directly from levels of mtDNA variation) paralleled levels of mtDNA variation, suggesting that effective (female) population sizes of Gulf greater amberjack were not atypically low.

Concerns regarding greater amberjack fisheries in the Gulf and Atlantic include the following: 1) presumed decreases in average individual size in both Gulf and Atlantic fisheries; 2) apparent declines in size of the presumed Atlantic stock; 3) a trend of declining yield in both commercial and headboat fisheries in the Gulf; and 4) apparent highly erratic recruitment where success of individual year classes is quite variable (Cummings-Parrack[1]; Cummings and McClellan[3]). These concerns have intensified as the economic importance of greater amberjack has grown (GMFMC, 1989; Cummings and McClellan[3]). In this study, we employed variation in restriction sites in mitochondrial (mt)DNA of greater amberjack to determine if significant population structure (separate genetic stocks) occurs in U.S. waters, i.e. in the northern Gulf of Mexico and along the U.S. southeastern Atlantic coast. The rationale for this study is the need for accurate geographic definition when conducting stock assessments (Hilborn, 1985; Sinclair et al., 1985), in this case for greater amberjack in U.S. waters.

## Materials and methods

Appropriate tissues (heart and white muscle) were obtained from a total of 444 greater amberjack sampled from 11 offshore localities in U.S. waters (Table 1; Fig. 1). With exception of a sample of seven individuals from near Gulfport, MS, sample sizes

[3] Cummings, N. J., and D. B. McClellan. 1996. Movement patterns and stock interchange of greater amberjack *Seriola dumerili*, in the southeastern U.S. Miami Laboratory, SE Fisheries Sci. Center, Natl. Mar. Fish. Serv., Cont. MIA-95/96-14, Miami, FL, 24 p.

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[5] Johnson, A. G. 1990. Progress report: electrophoretic examination of greater amberjack (*Seriola dumerili*). Panama City Laboratory, SE Fish. Sci. Center, Natl. Mar. Fish. Serv., Panama City, FL, 34 p.

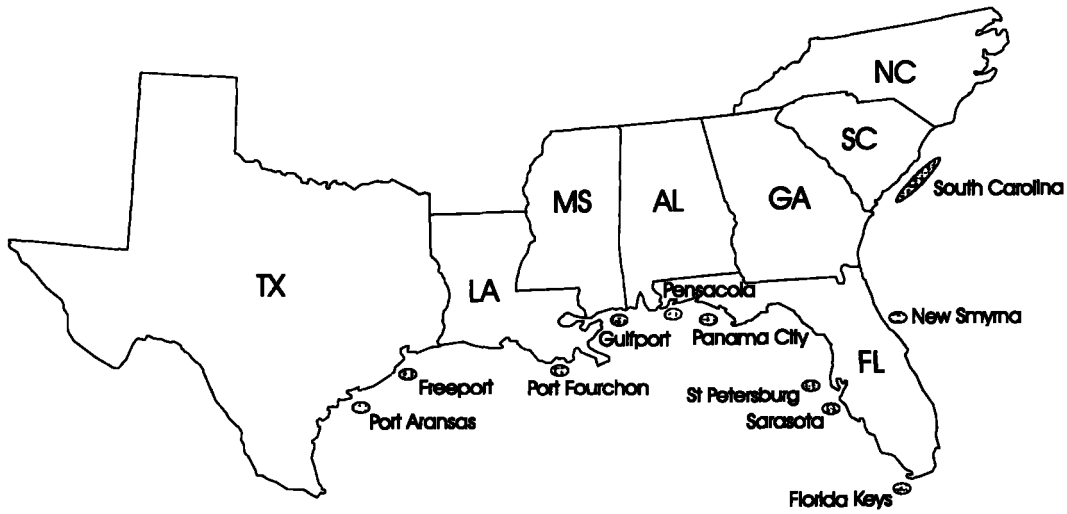


**Figure 1**

Dockside localities for greater amberjack, *Seriola dumerili*, in present study: NC = North Carolina; SC = South Carolina; GA = Georgia; FL = Florida; AL = Alabama; MS = Mississippi; LA = Louisiana; and TX = Texas.

ranged from 24 to 58 individuals. Individuals were sampled variously from charter boats, headboats, and commercial fishing boats, and from catches of recreational fishers at tournaments. Tissues were removed from each specimen, quickly frozen in liquid nitrogen, and transported to Texas A&M University where they were stored at –80°C in an ultracold freezer.

Methods (including DNA extraction, precipitation, and storage) used to assay restriction-enzyme fragment patterns of mtDNA molecules of individual fish followed those described in Gold and Richardson (1991). Sixteen, type-II restriction-endonuclease enzymes were used to digest 1.0–1.5 µg of DNA in 40 µL reactions according to manufacturer's specifications. Enzymes used were *Apa*LI, *Apa*I, *Eco*RI, *Eco*RV, *Hin*dIII, *Hpa*I, *Nco*I, *Pst*I, *Pvu*II, *Sca*I, *Sma*I, *Spe*I, *Ssp*I, *Sst*I, *Stu*I, and *Xba*I. Methods of DNA digestion, agarose electrophoresis, transfer to nylon filters (after Southern, 1975), hybridization, and autoradiography also followed those in Gold and Richardson (1991). Hybridization employed a 12.5 kilobase (kb) fragment of greater amberjack mtDNA cloned into lambda bacteriophage (Richardson and Gold, 1993). Bacteriophage lambda DNA digested with restriction enzyme *Hin*dIII was employed as a molecular weight marker on each gel. MtDNA fragments produced by single digestion of greater amberjack mtDNA were sized by fitting migration distances to a least-squares regression of lambda DNA-*Hin*dIII fragment migration distances. Single digestion mtDNA-fragment patterns were used to generate composite digestion patterns (mtDNA haplotypes).

**Table 1**

Sample localities of greater amberjack (*Seriola dumerili*).

| Locality[1] | Number of individuals |
|---|---|
| Port Aransas, Texas (PA) | 58 |
| Freeport, Texas (FP) | 44 |
| Port Fourchon, Louisiana (PF) | 43 |
| Gulfport, Mississippi (GP) | 7 |
| Pensacola, Florida (PN)[2] | 24 |
| Panama City, Florida (PC) | 50 |
| St. Petersburg, Florida (SP) | 42 |
| Sarasota, Florida (SR)[2] | 32 |
| Florida Keys (FK) | 55 |
| New Smyrna Beach, Florida (NS) | 53 |
| South Carolina (SC) | 36 |
| Total | 444 |

[1] Localities represent dock sites where individuals sampled offshore were off-loaded. Individuals from the Florida Keys were off-loaded at Islamorada; individuals from South Carolina were off-loaded at several localities.
[2] Previously examined by Richardson and Gold (1993).

Analysis of mtDNA data was facilitated by the Restriction Enzyme Analysis Package (REAP) of McElroy et al. (1992). Genotypic (nucleon) diversity within sample localities was calculated following Nei and Tajima (1981) and was based on the total number of mtDNA haplotypes identified within a local-

ity. This value represents the probability that any two individuals drawn at random will differ in mtDNA haplotype. Intrapopulational nucleotide sequence diversity within sample localities also was estimated after Nei and Tajima (1981). This value represents the average nucleotide sequence difference between any two individuals drawn at random from a given sample or locality.

Homogeneity testing of mtDNA haplotype frequencies among sample localities was carried out by using 1) a randomization (bootstrap) procedure developed by Roff and Bentzen (1989), 2) a log-likelihood ($G$) test (Sokal and Rohlf, 1969), and 3) $V$ tests that employed arcsine, square-root-transformed haplotype frequencies (DeSalle et al., 1987). Significance levels for multiple tests were adjusted after Rice (1989). $F_{ST}$ values, a measure of the variance in mtDNA haplotype frequencies, were calculated after Weir and Cockerham (1984) by using algorithms described in Weir (1990). Significance of $F_{ST}$ values was tested by the randomization procedure in version 1.4 of the analysis of molecular variance (AMOVA) program of Excoffier et al. (1992). The latter program (AMOVA) was used primarily to examine the distribution of variance in mtDNA haplotypes. AMOVA analysis generates estimates of (genetic) variance components and a set of hierarchical $F$-statistic analogs ($\Phi$ statistics) that are tested for significance through random permutation methods. The permutation approach avoids the parametric assumptions of normality and independence normally not met by molecular distance measures (Excoffier et al., 1992). Sample localities were nested into regional groupings, i.e. Gulf and Atlantic, that were input into AMOVA. In one AMOVA run, the sample from the Florida Keys was included with the Gulf group, whereas in a second run it was included in the Atlantic group.

Restriction-site presence and absence matrices for individual mtDNA haplotypes were constructed with the GENERATE program in REAP by inferring restriction site gains and losses for each enzyme. Maximum-parsimony analysis of restriction-site presence and absence matrices representing all haplotypes employed MULPARS and CONTREE options in version 3.1 of the Phylogenetic Analysis Using Parsimony (PAUP) program of Swofford (1991). Autapomorphic and symplesiomorphic characters were removed prior to PAUP runs. Nucleotide-sequence divergence values among sample localities (interpopulational divergence) were generated following Nei and Tajima (1981) and Nei and Miller (1990). MtDNA-based similarity among sample localities was assessed with the neighbor joining method (Saitou and Nei, 1987) and employed the NEIGHBOR program in Phylogenetic Inference Package (PHYLIP), version 3.4 of Felsenstein (1989).

The spatial distribution of mtDNA haplotypes was investigated by means of spatial autocorrelation analysis (SAAP; Wartenberg, 1989). This analysis determines whether haplotype frequencies at any sample locality are independent of haplotype frequencies at neighboring sample localities. Correlograms that plot autocorrelation coefficients (Moran's $I$ values) as a function of geographic distance between pairs of localities were used to summarize patterns of geographic variation of haplotype frequencies. To minimize "noise" generated by low-frequency haplotypes, Moran's $I$ values were calculated only for haplotypes occurring in eight or more individuals (10 haplotypes total). These included haplotypes 1–4, 6, 11, 13, 23, 37, and 48.

## Results

Single digestions of mtDNA molecules from the 444 individuals surveyed produced variable fragment patterns for the 16 restriction enzymes. The majority of fragment patterns observed are given in Appendix Table A2 of Richardson and Gold (1993). New fragment patterns revealed in our study are as follows (fragment sizes in base pairs; asterisks represent fragments assumed to exist but not covered by the mtDNA probe): *Eco*RI, pattern C (8700, 5025, 3175*); *Hpa*I, pattern C (8800, 5550, 2550); *Nco*I, pattern C (11050, 5850); *Sst*I, pattern C (11700, 3450, 1750); *Sca*I, pattern C (7500, 3600, 3100, 2700) and pattern D (10000, 3600, 3300); *Sma*I, pattern D (10700, 4250, 1500, 450); *Spe*I pattern D (7900, 5800, 1200, 1200*, 800); *Ssp*I, pattern C (6600, 6200, 4100); and *Xba*I, pattern D (7300, 5000, 4600) and pattern E (7300, 4600, 2600, 2275, 125*). The mean genome size of all apparently complete digestion patterns was 16.9 ±0.2 kilobase pairs. No evidence of mtDNA size variation or heteroplasmy was observed. All fragment patterns for each restriction enzyme were consistent with the hypothesis of single nucleotide substitutions. A total of 72 unique restriction sites was inferred from the digestion patterns.

A total of 49 mtDNA haplotypes was identified among the 444 individuals surveyed (Table 2). Four haplotypes (8, 14, 16, and 18) are not listed in Table 2; these were listed in Richardson and Gold (1993) and were identified by three restriction enzymes (*Cla*I, *Nsi*I, and *Pvu*I) not employed in our study. Four haplotypes (1, 4, 6, and 13) were abundant, occurring in 77, 91, 54, and 70 individuals, respectively. Two haplotypes (2 and 3) occurred in 20 and 22 individuals, respectively, whereas the remainder occurred in 10 or fewer individuals. Twenty haplotypes were found in only one individual each. Estimates of

**Table 2**

Spatial distribution of mitochondrial (mt)DNA haplotypes of greater amberjack (*Seriola dumerili*). Letters (from left to right) are digestion patterns for *Apa*LI, *Apa*I, *Eco*RI, *Eco*RV, *Hin*dIII, *Hpa*I, *Nco*I, *Pst*I, *Pvu*II, *Sca*I, *Sma*I, *Spe*I, *Ssp*I, *Sst*I, *Stu*I, and *Xba*I.

| Haplotype no. | Composite mtDNA genotype | Samples | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | PA | FP | PF | GP | PN | PC | SP | SR | FK | NS | SC |
| 1 | AAAAAAAAAAAAAAAA | 7 | 10 | 8 | 2 | 5 | 8 | 12 | 7 | 4 | 8 | 6 |
| 2 | AAAABBAAAAAAAAAA | 4 | 4 | 3 | — | 1 | 2 | 3 | — | 3 | 2 | 1 |
| 3 | AAAAABAAAAAAAABA | 3 | 2 | 3 | — | 3 | 1 | 1 | — | 4 | 4 | 1 |
| 4 | AAAAABAAAAAAAAAA | 15 | 9 | 10 | 1 | 5 | 11 | 4 | 10 | 10 | 9 | 7 |
| 5 | AABBABAAAABAABAA | — | 1 | — | — | 3 | — | — | 1 | — | — | — |
| 6 | AAAAAAAAAAAAAABA | 8 | 4 | 2 | 1 | — | 4 | 4 | 5 | 10 | 6 | 10 |
| 7 | AAAAAAAAAAABAAAA | — | — | — | — | — | — | — | 1 | — | — | — |
| 9 | BABAAAAAAACAAABA | — | — | — | 1 | — | — | — | 1 | 1 | — | — |
| 10 | BAAAABBBAAAAAAAA | — | — | 1 | — | — | 2 | — | 1 | — | — | — |
| 11 | BABAAAAAAAAAAABA | 1 | 1 | 2 | — | — | 1 | 1 | 1 | — | 1 | 1 |
| 12 | AAAAAAAAABACAAAA | — | — | — | — | — | — | — | 1 | — | 2 | — |
| 13 | AAAAAAAAABABAAAA | 7 | 4 | 4 | 2 | 1 | 12 | 7 | 2 | 10 | 15 | 6 |
| 15 | AAAAAAAAAAAABABA | — | — | 1 | — | — | 1 | — | 1 | — | — | — |
| 17 | AAAAABAABAAAAAAC | — | — | — | — | 1 | — | — | — | — | — | — |
| 19 | AAAAABACAAAAAAAA | — | — | — | — | 1 | — | — | — | — | — | — |
| 20 | AAAAAAAAAAAAAABB | — | — | — | — | 1 | — | — | — | — | — | — |
| 21 | AAAAABABAAAAAAAA | — | 1 | — | — | 1 | 1 | — | — | — | — | — |
| 22 | ABAACAAACBAAAABA | — | — | — | — | 1 | — | — | — | — | — | — |
| 23 | AABAABAAAAAAAAAA | 3 | 1 | 2 | — | 1 | 1 | — | — | — | — | — |
| 24 | BAAAAAAAAAAABABA | — | 1 | — | — | — | — | — | — | — | — | — |
| 25 | AAAAAAAAACABCAAA | — | — | — | — | — | — | — | — | 2 | — | — |
| 26 | BAAABAAAAAAAAAAA | — | 1 | — | — | — | — | — | — | — | — | — |
| 27 | ABAACAAACAAAACBA | 1 | — | — | — | — | — | — | — | — | — | — |
| 28 | AAAAAAAAABAAAAAA | — | 2 | — | — | — | — | 1 | — | — | — | — |
| 29 | AAAACAAAAAAAAABA | — | 1 | — | — | — | — | — | — | — | — | — |
| 30 | AAAABBAAAAAAACAA | — | — | 1 | — | — | — | — | — | — | — | — |
| 31 | AAAAABBAAAAAAAAA | — | 1 | — | — | — | — | — | — | — | — | — |
| 32 | AAAACAAAADDDAABD | — | 1 | 1 | — | — | — | — | — | — | — | — |
| 33 | AAABAAAAAAAAAAAA | 1 | — | — | — | — | 1 | — | — | — | — | — |
| 34 | AACAAAAAABABAAAA | 2 | — | — | — | — | — | — | — | — | — | — |
| 35 | AAAAABAAAAAAAACA | 1 | — | — | — | — | — | 1 | 1 | 1 | — | — |
| 36 | BABAABAAAAAAAABA | 1 | 1 | — | — | — | — | — | — | — | — | — |
| 37 | ABAACAAACAAAAABA | 1 | — | 2 | — | — | — | 2 | — | 4 | 1 | — |
| 38 | AAAAAAAAACABAAAA | 1 | — | — | — | — | 1 | — | — | — | 1 | — |
| 39 | AABACCAAADDDAABD | — | — | — | — | — | — | — | — | — | 1 | — |
| 40 | AAAAABAAAAAACAAA | — | — | — | — | — | — | 1 | — | — | 1 | — |
| 41 | ABAAAAAAABABAAAA | — | — | — | — | — | — | — | — | — | 1 | — |
| 42 | AAAAABAAAAAABAAA | — | — | — | — | — | — | — | — | 1 | — | — |
| 43 | AAAAABAAAAAAAAAE | — | — | — | — | — | 1 | — | — | — | — | — |
| 44 | AAAAABCAAAAAAABA | — | — | 1 | — | — | 1 | — | — | — | — | — |
| 45 | AAAAABCAAAAAAAAA | — | — | 1 | — | — | 1 | — | — | — | — | — |
| 46 | AAAACCAAADDDCABD | 1 | — | — | — | — | 1 | — | — | — | — | — |
| 47 | AAAAABAAAABAABAA | — | — | — | — | — | — | — | — | 1 | — | — |
| 48 | AAAAABAAAAAAACAA | 1 | 2 | — | — | — | — | 2 | — | 2 | 1 | — |
| 49 | AAAAABAAABABAAAA | — | — | 1 | — | — | — | — | — | — | — | — |
| 50 | AAAAABAAABAAAAAA | — | — | — | — | — | — | 1 | — | — | — | — |
| 51 | AAAACAAACAAAAABA | — | — | — | — | — | — | 1 | — | — | — | 1 |
| 52 | AABAABAAAABAABAA | — | — | — | — | — | — | — | — | — | — | 1 |
| 53 | AAAACAAAAAADAAAD | — | — | — | — | — | — | 1 | — | — | — | — |

the percentage nucleotide-sequence divergence among the 49 haplotypes ranged from 0.156 to 2.623 (mean ±SE=0.980 ±0.015). MtDNA nucleon diversity was 0.905, and intrapopulational nucleotide sequence diversity was 0.548 ±0.412 (mean ±SD). The latter estimates were based on all 444 individuals surveyed. Nucleon diversity within samples (Table 3) ranged from 0.845 in the sample from Sarasota, Florida, to

**Table 3**

Mitochondrial (mt)DNA nucleon and intrapopulational nucleotide sequence diversities among samples of greater amberjack (*Seriola dumerili*) from the Gulf of Mexico and Atlantic Ocean

| Locality | Number of individuals | Number of haplotypes | Nucleon diversity | Nucleotide sequence diversity (±SD)[1] |
|---|---|---|---|---|
| Port Aransas, TX | 58 | 17 | 0.886 | 0.561 ± 0.443 |
| Freeport, TX | 44 | 18 | 0.899 | 0.515 ± 0.387 |
| Port Fourchon, LA | 43 | 16 | 0.901 | 0.579 ± 0.435 |
| Gulfport, MS | 7 | 5 | 0.905 | 0.587 ± 0.415 |
| Pensacola, FL | 24 | 12 | 0.906 | 0.601 ± 0.449 |
| Panama City, FL | 50 | 17 | 0.872 | 0.525 ± 0.415 |
| St. Petersburg, FL | 42 | 15 | 0.879 | 0.519 ± 0.395 |
| Sarasota, FL | 32 | 12 | 0.845 | 0.483 ± 0.370 |
| Florida Keys | 55 | 14 | 0.893 | 0.619 ± 0.419 |
| New Smyrna, FL | 53 | 14 | 0.861 | 0.537 ± 0.427 |
| South Carolina | 36 | 10 | 0.846 | 0.502 ± 0.342 |
| Total | 444 | 49 | 0.905 | 0.548 ± 0.412 |

[1] In per cent.

0.906 in the sample from Pensacola, Florida. Intrapopulational nucleotide sequence diversity within samples (Table 3) ranged (mean ±SD) from 0.483 ±0.370 in the sample from Sarasota, Florida, to 0.619 ±0.419 in the sample from the Florida Keys. The latter values are all within one standard error (estimated from bootstrap analysis) of one another, indicating that levels of mtDNA variation are essentially identical throughout the geographic area surveyed. Levels of mtDNA variability, as measured by nucleon diversity and intrapopulational nucleotide sequence diversity, are commensurate with those estimated for several other marine fish of commercial or recreational value (Gold et al., 1993).

Results of bootstrap analyses and log-likelihood tests of spatial homogeneity in mtDNA haplotype frequencies are shown in Table 4. Tests were carried out 1) among all sample localities, 2) among samples from the Gulf, and 3) between defined groups where samples were pooled. In the last category, defined groups were based on region, i.e. Gulf and Atlantic. Gulf samples included the following: Port Aransas, TX; Freeport, TX; Port Fourchon, LA; Gulfport, MS; Pensacola, FL; Panama City, FL; and Sarasota, FL. Atlantic samples included New Smyrna, FL, and South Carolina. Two sets of pooled comparisons were carried out: in one, the sample from the Florida Keys was included with Gulf samples; in the other, the sample from the Florida Keys was included with Atlantic samples. We used this approach because the sample from the Florida Keys is located on the geographic boundary between the two putative stocks of greater amberjack (Cummings and McClellan[3]), and we could not place *a priori* the sample from the Florida Keys into either stock before testing the two-stock hypothesis. Significant heterogeneity was found only in the pooled comparison of samples from the Atlantic and Florida Keys versus samples from the Gulf; tests of homogeneity among all samples, among samples from the Gulf, and between pooled samples from the Atlantic versus those from the Gulf plus the Florida Keys were nonsignificant (Table 4). Estimates of $F_{ST}$ revealed the same pattern; the $F_{ST}$

**Table 4**

Tests for spatial homogeneity in mtDNA haplotype frequencies among greater amberjack (*Seriola dumerili*) from the Gulf of Mexico and U.S. southeastern Atlantic. $F_{ST}$ is a measure of variance in haplotype frequencies. Number of samples is in parentheses.

| Test group | Number of haplotypes | Homogeneity tests[1] $P_{RB}$ | $P_G$ | $F_{ST}$ |
|---|---|---|---|---|
| All samples (11) | 49 | 0.158 | >0.050 | 0.005 |
| Gulf samples (8) | 45 | 0.250 | >0.050 | 0.003 |
| Pooled comparisons | | | | |
| Gulf + Florida Keys vs. Atlantic (2) | 49 | 0.627 | >0.050 | 0.004 |
| Atlantic + Florida Keys vs. Gulf (2) | 49 | 0.042 | ~0.002 | 0.009[2] |

[1] $P_{RB}$ is probability from randomization (bootstrap) approach of Roff and Bentzen (1989); $P_G$ is probability from log-likelihood ($G$) test (Sokal and Rohlf, 1969).
[2] Value differs significantly ($P$=0.007) from 0.00; all other $F_{ST}$ values are nonsignificant.

**Table 5**

Hierarchical analysis of molecular variation (AMOVA) among mtDNA haplotypes of greater amberjack (*Seriola dumerili*) from the Gulf of Mexico and U.S. southeastern Atlantic.

| Variance component | Observed partition | | $P^1$ | $\Phi$ values |
|---|---|---|---|---|
| | Variance | % total | | |
| Gulf + Florida Keys vs. Atlantic | | | | |
| Between regions | 0.00127 | 0.29 | 0.259 | $\Phi_{CT} = 0.003$ |
| Among samples within regions | 0.00160 | 0.36 | 0.190 | $\Phi_{SC} = 0.004$ |
| Within samples | 0.43974 | 99.35 | 0.121 | $\Phi_{ST} = 0.006$ |
| Atlantic + Florida Keys vs. Gulf | | | | |
| Between regions | 0.00398 | 0.90 | 0.001 | $\Phi_{CT} = 0.009$ |
| Among samples within regions | 0.00011 | 0.03 | 0.444 | $\Phi_{SC} = 0.000$ |
| Within samples | 0.43974 | 99.07 | 0.113 | $\Phi_{ST} = 0.009$ |

[1] Probability of finding a more extreme variance component by chance alone (5000 permutations).

value of 0.009 in the pooled comparison of samples from the Atlantic and Florida Keys versus samples from the Gulf differed significantly from zero, whereas $F_{ST}$ values in all other comparisons were nonsignificant (Table 4).

For AMOVA, where the variance in mtDNA haplotypes was partitioned by region, we also performed two separate analyses: one where the sample from the Florida Keys was included with Gulf samples, and one where the sample from the Florida Keys was included with Atlantic samples. In both analyses, the majority of the variance (>99%) was distributed within samples, and in both, the among-samples-within-groups component ($\Phi_{SC}$) was nonsignificant (Table 5). The between-region component ($\Phi_{CT}$) in the comparison of Atlantic and Florida Keys versus the Gulf was highly significant ($P<0.001$); whereas $\Phi_{CT}$ in the comparison of Atlantic versus the Gulf plus Florida Keys was not (Table 5). These results paralleled results of the homogeneity tests and the $F_{ST}$ values. Finally, we employed pairwise $\Phi_{ST}$ values (i.e. between pairs of samples) to generate average "distance" values between samples from the Gulf (eight total), between samples from the Atlantic plus the sample from the Florida Keys (three total), and between samples from the Gulf versus samples from the Atlantic (and the Florida Keys). The average (±SE) $\Phi_{ST}$ values for these comparisons were 0.004 ±0.001 (samples from the Gulf), 0.002 ±0.002 (samples from the Atlantic and the Florida Keys), and 0.012 ±0.002 (samples from the Gulf versus samples from the Atlantic and the Florida Keys).

Homogeneity ($V$) tests were carried out on the ten haplotypes (1–4, 6, 11, 13, 23, 37, and 48) that were found in at least six individuals. Over all 11 samples, only haplotype 6 differed significantly ($P$~0.048) in frequency. This result is not significant when corrections for multiple testing (Rice, 1989) are applied. We then pooled samples into two groups (one that included the eight samples from the Gulf, and one that included the two samples from the Atlantic and the sample from the Florida Keys). Significant $V$ tests (again, prior to corrections for multiple testing) were found for haplotype 6 ($P$~0.011) and haplotype 13 ($P$~0.024). Frequency plots by sample of these two haplotypes (Fig. 2) revealed a clinal pattern to variation in haplotype 6, with frequencies generally increasing eastwardly in the Gulf and into the Atlantic; no pattern was apparent for variation in haplotype 13.

Maximum-parsimony (MP) analysis of individual mtDNA haplotypes and neighbor-joining (NJ) analysis of the matrix of interpopulational (genetic) distances revealed no evidence of phylogeographic structure. MP analysis generated an unresolved multichotomous topology where a few clades of individual mtDNA haplotypes were supported at 90% or greater in bootstrap analysis (100 replicates). In each case, haplotypes within such clades were not geographically cohesive. Examples included a clade of haplotypes 5, 52, and 47, which were found, respectively, in waters off Texas and west Florida (5), South Carolina (52), and the Florida Keys (47) (Table 2); a clade of haplotypes 32, 39, and 46, which were found, respectively, in waters off Texas and Louisiana (42), east Florida (39), and Texas and west Florida (46) (Table 2); and a clade of haplotypes 22, 27, 37, and 51, which were found, respectively, in waters off west Florida (22), Texas (27), several localities (37), and west Florida and South Carolina (51) (Table 2). No "deep" subdivisions, in the sense of multiple restriction sites identifying a clade of haplotypes, were evident. The NJ topology (Fig. 3) indicated relatively

long terminal branches to individual samples, but short internodal branches linking samples. Samples did not necessarily cluster geographically, and in no case did geographically proximate samples form a cluster.

Spatial autocorrelation analyses generated 40 Moran's $I$ values in each run (10 haplotypes × four distance classes). Four significant ($P<0.05$) values were obtained when equal numbers of pairwise comparisons were used: two were positive and occurred in the first and third distance classes, and two were negative and occurred in the third and fourth distance classes. Two significant values ($P<0.05$) were obtained when equal geographic distances were used: one in the first distance class was positive, and one in the third distance class was negative. Mean $I$ values were negative in all four distance classes in both runs and did not differ significantly from expected values of $I$ in the absence of autocorrelation (Fig. 4).

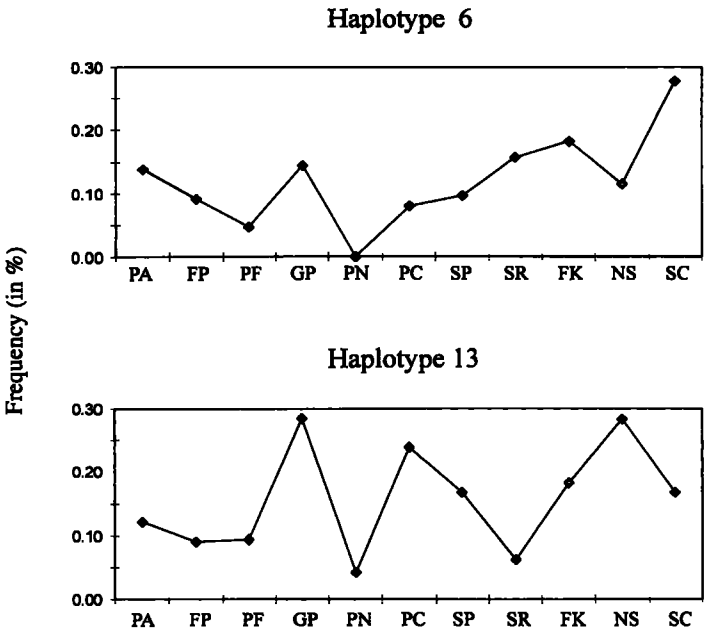


**Figure 2**

Frequency of mtDNA haplotypes 6 and 13 among greater amberjack (*Seriola dumerili*) sampled from 11 localities in the northern Gulf of Mexico and southeastern (U.S.) Atlantic. Acronyms are defined in Table 1.

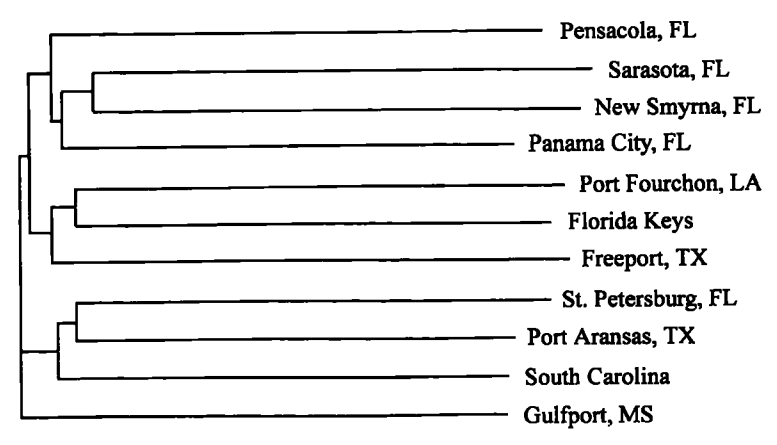


**Figure 3**

Neighbor-joining topology generated from matrix of pairwise, interpopulational (mtDNA) nucleotide sequence divergence among samples of greater amberjack, *Seriola dumerili*.

## Discussion

Variation of mtDNA in greater amberjack is consistent with the hypothesis that one subpopulation (stock) exists in the northern Gulf of Mexico (Gulf), whereas a second subpopulation (stock) exists along the U.S. southeast Atlantic coast (Atlantic). The latter (Atlantic) subpopulation includes the sample from the Florida Keys. Evidence supporting this hypothesis includes 1) significant heterogeneity in the distribution of pooled haplotypes (and of haplotype 6) from the Gulf versus those from the Atlantic (and the Florida Keys); 2) a significant (nonzero) $F_{ST}$ value in the same comparison; 3) a highly significant ($P<0.001$) between-region component ($\Phi_{CT}$ value) in AMOVA, when regions were defined as the Gulf versus the Atlantic (and the Florida Keys); and 4) comparison of pairwise $\Phi_{ST}$ "distances" where samples from the Gulf or from the Atlantic were at least three times more similar to one another than were samples from the Gulf versus those from the Atlantic (and the Florida Keys).

Neither maximum-parsimony (MP) analysis of individual mtDNA haplotypes nor neighbor-joining analysis of a matrix of interpopulational (intersample) nucleotide-sequence distances revealed phylogeographic patterns indicative of population structuring. A few, well-supported clades of individual haplotypes were detected in MP analysis, but in no case were haplotypes within individual clades from the same or geographically proximate

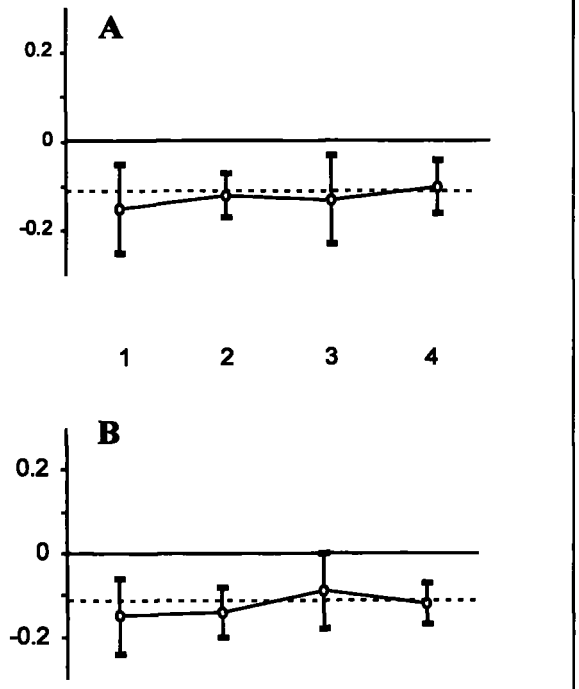


**Figure 4**

Correlograms based on frequencies of mtDNA haplotypes found in eight or more individuals among samples of greater amberjack, *Seriola dumerili*, from the northern Gulf of Mexico. Abscissas: distance classes 1–4 (left to right); ordinates: mean autocorrelation coefficients (Moran's *I* values) for each distance class (±SE). (**A**) Equal frequencies/distance class; (**B**) equal distances between distance classes.

sample localities. Absence of structure in MP analysis is not inconsistent with results of homogeneity testing, $F_{ST}$ values, and AMOVA analysis, in that 1) presumed restrictions in gene flow between subpopulations could be relatively recent, i.e. there has been insufficient time for haplotypes (e.g. haplotype 6) that differ in frequency between subpopulations to become reciprocally monophyletic, or 2) there may be limited gene flow between subpopulations. Finally, there was no indication of spatial autocorrelation (positive or negative) in common haplotypes among samples from the Gulf. This finding indicates the absence of an isolation-by-distance effect among greater amberjack in the Gulf and is consistent with the hypothesis of continuous gene flow across the northern Gulf.

Divergence in mtDNA between Gulf and Atlantic subpopulations has been documented for a variety of marine species. In some (e.g. American oysters, toadfish, black sea bass, and to a lesser extent, horseshoe crabs), major phylogeographic discontinuities between Gulf and Atlantic subpopulations were found, leading to the hypothesis that the similar vicariant patterns may have stemmed from episodic changes in environmental conditions during Pleistocene glaciation (Avise, 1992). In addition, the presence of phylogeographic structure was taken to indicate that current-day gene flow between subpopulations is very restricted, if it occurs at all. In species such as red drum (Gold et al., 1993), king mackerel (Gold et al., 1997), and greater amberjack (our study), mtDNA differences between Gulf and Atlantic subpopulations are documented but are limited to either a frequency difference in a single mtDNA haplotype, a small (but significant) difference in mtDNA haplotype distribution, or both. The relatively small genetic differences observed between subpopulations in these species, along with the absence of phylogeographic structure, both between regions and among haplotypes, suggest either that limited gene flow occurs between subpopulations or that separation between subpopulations is fairly recent. In the case of greater amberjack, the former is consistent with mark-and-recapture data that suggest exchange rates of 1.5% between Gulf and Atlantic stocks (Cummings and McClellan[3]).

For greater amberjack, the boundary between Gulf and Atlantic subpopulations appears to be between the Florida Keys (included in the Atlantic subpopulation) and somewhere off the central-western Florida coast, possibly the Florida Middle Ground, a series of north-south reef structures located about 150 km south of the north Florida coast and about 160 km northwest of Tampa Bay (Hopkins et al.[6]), and the primary source for amberjack fishermen located in Sarasota and St. Petersburg. Separation between Gulf and Atlantic subpopulations (stocks) of greater amberjack could stem from a number of causes that involve historical or recent interactions between dispersal capability and impediments to gene flow, or both. Among present-day alternatives are 1) offshore currents that are not conducive to unrestricted movement between regions; and 2) absence of suitable habitat or difference in ecological (biogeographic) provinces between regions. A third (historical) possibility might be that subpopulations were separated (e.g. during Pleistocene glaciations) and have only recently (in geological time) begun exchanging genes. Rates of approach to genetic homogeneity under this last hypothesis are, in part, time-dependent, and one could speculate that there has been insufficient time for accumulated genetic differences to disappear.

[6] Hopkins, T. 1981. Florida Middle Ground. *In* R. Rezak and T. J. Bright (eds.), Final report: northern Gulf of Mexico topographic features study, p. 1–5. Tech. Rep. No. 81-2-T, Dep. Oceanography, Texas A&M University, College Station, TX.

There is at least suggestive evidence for each of the above three possibilities in greater amberjack. First, measurements of offshore current velocities are consistent with increased passive movement of individuals from the Florida Keys into the Atlantic rather than northward along the west Florida coast. Mean current velocities (145 m below the surface) eastward from the Keys through the Florida Straits are approximately 75 cm/sec, and along the southeast Florida coast, these currents can be as fast as 95 cm/sec (SAIC[7]). Because current velocities are expected to be greater nearer the surface, and because greater amberjack have been observed spawning in the Florida Keys (Cummings and McClellan[3]), buoyant eggs and larvae would likely be impacted and have little opportunity to move northward along the west coast of Florida. Second, in terms of habitat, the southern half of the Florida peninsula represents a transition zone between temperate and tropical forms, where the southern ranges of many temperate species terminate in tropical southern Florida (Briggs, 1974). There also is relatively little reef habitat or sharp topography between the Florida Middle Ground and the Keys; most of the area has a relatively smooth bottom comprising shell, sand, and quartz (Rezak et al., 1985; Rezak and Bright[8]). Because greater amberjack exhibit a marked preference for reefs, rock outcrops, and wrecks (Shipp, 1986; Manooch, 1988), it is possible that the paucity of significant reef or other major structure on the Outer Continental Shelf off southwestern Florida may inhibit movement of greater amberjack between the Florida Middle Ground and the Keys. Finally, although relatively little is known about the early life history of greater amberjack, spawning is thought to occur from mid-spring to early summer both along the southeastern coast of Florida (including the Florida Keys) and in the northern Gulf off Louisiana (Cummings and McClellan[3]; Thompson[9]). This spawning time suggests that warmer water temperatures may trigger onset of reproductive activity. One might then hypothesize that during the late Pleistocene Epoch, when waters of the northern Gulf were much cooler (Rezak et al., 1985), subpopulations of greater amberjack were isolated in warm-water refugia, perhaps off the Florida Keys (or in the Caribbean) and off the Yucatan Peninsula (Campeche Banks) where considerable reef habitat exists (Rezak et al., 1985). Following glacial retreat, the (putatively) isolated subpopulations could then have returned to the northern Gulf. Because the rate of approach to genetic homogeneity would be partly a function of time and gene flow, genetic differences between present-day subpopulations of greater amberjack could simply be historical artifacts, reflecting insufficient time (or restricted gene flow) relative to genetic homogenization.

Our finding that the sample of greater amberjack from the Florida Keys was included in a grouping (subpopulation) with samples from the Atlantic differs from a recent study in king mackerel (Gold et al., 1997), where a sample from the Florida Keys was placed in a grouping with samples from the Gulf. King mackerel are highly migratory, and the sample of king mackerel from the Florida Keys was taken during late winter when the majority of king mackerel in the Keys are thought to be from the Gulf Migratory Unit or stock (Williams and Godcharles[10]). The sample of greater amberjack from the Keys, however, was obtained during late March–early April, a time when the majority of king mackerel in the Keys are considered to be from the Atlantic Migratory Unit or stock (Williams and Godcharles[10]). Although greater amberjack are not migratory in the same way as king mackerel, it would be of more than passing interest to examine winter samples of greater amberjack from the Florida Keys and ask whether the Florida Keys constitute a mixing zone in greater amberjack as in king mackerel. Along these lines, it also would be important to examine both summer and winter samples of greater amberjack in the area between the Florida Middle Ground and the Florida Keys. A better definition of the geographic limits of the two subpopulations is critical for assessment and allocation of the greater amberjack resources along the west coast of Florida.

Avise et al. (1988) presented models that allow estimation of evolutionary (long-term) effective female-population size ($N_{fe}$ values) based on mtDNA intrapopulational nucleotide sequence diversities. Assuming that the generation time in greater amberjack is three years (Wilson[11]), we estimated $N_{fe}$ for the two subpopulations (stocks) of greater amberjack to be 90,000 (Gulf of Mexico) and 93,500 (U.S. southeastern Atlantic, including the Florida Keys).

[7] SAIC (Science Applications International Corporation). 1992. Straits of Florida physical oceanographic field study, final interpretative report, volume II: technical report. OCS Report/MMS 92-0024. U. S. Dep. Interior, Minerals Mgmt. Serv., Gulf of Mexico OCS Regional Office, New Orleans, LA, 179 p.

[8] Rezak, R., and T. J. Bright (eds.). 1981. Final report: northern Gulf of Mexico topographic features study. Tech. Rep. No. 81-2-T, Dept. Oceanography, Texas A&M University, College Station, TX, 150 p.

[9] Thompson, B. A. 1997. Coastal Fisheries Institute, Louisiana State University, Baton Rouge, LA 70803. Personal commun.

[10] Williams, R. O., and M. F. Godcharles. 1984. Completion report, king mackerel tagging and stock assessment. Project 2-341-R. Florida Dep. Natural Resources., St. Petersburg, FL.

[11] Wilson, C. A. 1997. Coastal Fisheries Institute, Louisiana State University, Baton Rouge, LA 70803. Personal commun.

The two estimates do not differ significantly from one another and are larger than those reported in a more limited (in terms of sample size and geographic coverage) study of greater amberjack (Richardson and Gold, 1993). They also are commensurate with $N_{f(e)}$ estimates for several other marine fish of commercial or recreational value (Gold et al., 1993). Although a positive correlation exists between effective population sizes and census sizes, the latter are generally an order of magnitude or two larger than the former (Avise et al., 1988). One reason for this difference, at least in estimates of $N_{f(e)}$ values for poikilothermic vertebrates, is that the models of Avise et al. (1988) employ (estimated) mtDNA evolutionary rates for homeothermic vertebrates. Estimated mtDNA evolutionary rates for poikilothermic vertebrates may be 5–10 times less than those for homeothermic vertebrates (Martin and Palumbi, 1993), suggesting that long-term effective population sizes of each subpopulation of greater amberjack could be on the order of 500,000 to 1,000,000 females.

According to results of this project, current stock boundaries for assessment and allocation of greater amberjack resources in U.S. waters appear appropriate except possibly for the west coast of Florida, south of the Florida Middle Ground. Depending on present or future importance of the greater amberjack fishery in this area, it would be useful to know both the geographic limits of the two subpopulations and whether the Florida Keys constitute a mixing zone for greater amberjack as for species such as king mackerel.

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# Age, growth, and reproduction of the tropical squid *Nototodarus hawaiiensis* (Cephalopoda: Ommastrephidae) off the North West Slope of Australia

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**Abstract.**—The age, growth, and reproduction of the tropical Indo-Pacific ommastrephid squid *Nototodarus hawaiiensis* was studied on the North West Slope of Australia. The weight, mantle length (ML), gonad weight, and nidamental gland length were measured for 37 males and 52 females captured in January and February 1992 and ranging in size from 42 mm ML to 214 mm ML. Statolith increments were counted, as a proxy for age. The number of statolith increments, counted on 42 of the squid, ranged from 49 to 195. The relation between increment number (i.e. age) and ML was linear for both sexes. The relation between increment number and ovary weight, and between increment number and testis weight, had greater variability than did ML versus ovary weight, and ML versus testis weight, indicating a large range in age at maturity in individuals of similar size. Some statoliths showed two prominent zones, the origins of which are uncertain. Back-calculated hatch dates indicated that all squid hatched between July and December 1991 and that the majority hatched between August and October (Austral spring).

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Fish. Bull. 96:779–787 (1998).

*Nototodarus hawaiiensis* (Berry, 1912) was thought originally to be restricted to the Hawaiian Islands in the central Pacific (Roper et al., 1984). However, studies by Dunning (1988a, 1988b) revealed that this species is also distributed in the Indo-Pacific including the Philippines (previously referred to as *N. sloani philippinensis* [Voss, 1962]), northern Australia, South China Sea, western Indian Ocean, and off Chile (Dunning and Förch, in press). In Australian waters, postparalarval *N. hawaiiensis* inhabit slope waters at depths between 200 and 500 m off the North West Slope and between 100 and 600 m off the north east coast to southern Queensland (Dunning, 1988b) in bottom temperatures of 12.4°C. Recent trawl surveys on the North West Slope of Australia have shown that *N. hawaiiensis* is the dominant species of cephalopod in commercial catches from demersal trawlers (Wadley, 1993). The recent identification and dominance of *N. hawaiiensis* in waters off the North West Slope of Australia necessitates understanding the biology and role of this species in deepwater marine communities in tropical Australian waters.

This study was carried out to obtain preliminary age, growth, and reproductive parameters for *N. hawaiiensis* not previously reported. Statolith age analysis, a valuable tool in squid growth and life history studies (Jackson, 1994), was carried out as an indication of age and growth. Previous statolith ageing work on tropical Australian squid species has been restricted to shallow water loliginids that predominantly complete their life span in less than 200 d (Jackson, 1990; Jackson and Choat, 1992; Jackson and Yeatman, 1996). However, no growth information has been available to date for deepwater tropical species of other families. It was therefore of interest, for comparative purposes, to obtain life history parameters of this deepwater tropical ommastrephid.

Statoliths of *N. hawaiiensis* were studied to assess if periodic increments might be useful for ageing this species. Owing to the difficulty of obtaining live specimens from deep water, age information has to be inferred (as in this study), rather than validated on living squid. Increment structure was considered in relation to the validation evidence available for other ommastrephids.

## Material and methods

### Squid collection and analysis

Individuals were collected day and night, 20 January to 14 February 1992, off the North West Slope of Australia, between about 12°S and 22°S (Wadley, 1993) and 385 to 555 m. This study was composed of 89 individuals of which 42 individuals were used for age analysis. Specimens were obtained from the RV *Southern Surveyor* and commercial vessels, which trawled with demersal gear (45-mm mesh net) on soft sandy substrates.

The fresh *N. hawaiiensis* were identified by using field characters from Wadley (1990). Other ommastrephids were captured (Wadley, 1993) but *Nototodarus gouldi* was absent in the area. Specimens were sampled at random from the range of sizes available in the trawl catches. The squid were frozen at sea and subsequently defrosted in the laboratory for reproductive and statolith analysis. Measurements taken included mantle length (ML), total wet weight (W), testis weight for males and ovary weight and nidamental gland length (NGL) for females. Hectocotylisation of the ventral arm and presence of spermatophores in Needham's sac were used as indicators of sexual maturity in males. In females, development of the nidamental gland and presence of mature oocytes in the ovaries were used as indicators of sexual maturity.

### Statolith removal and analysis

Statoliths were removed through an incision in the cephalic cartilage, placed singly on microscope slides, and rinsed with 100% ethanol. The dried statoliths were mounted in thermoplastic cement (Crystal Bond, Jackson, 1990). Statoliths were taken for age analysis from 42 individuals selected from the full size range available.

To observe the increment structure, statoliths were ground and polished, usually on both the anterior and posterior surfaces. The complete increment sequence was usually visible only on the posterior (convex) surface, which was preferred for routine counting. In many of the statoliths, the crystal structure obstructed a view of the increments in the nuclear region of the anterior surface. Some statoliths were ground from the anterior (concave) surface through the obstructing crystals until the nucleus was revealed and all the increments could be observed (terminology according to Lipinski et al., 1991).

Statoliths were viewed on a computer monitor with a video camera attached to a compound microscope. Increments were counted by following the increment sequence with a cursor while using a hand counter. The number of increments on each statolith was counted at least three times and the mean was taken. Counts that varied more than 10% from the mean were repeated or rejected. The increments were similar in structure to daily statolith increments observed in other ommastrephid species (e.g. Hurley et al., 1985; Villanueva, 1992; Arkhipkin, 1996).

## Results

### Length-weight relationship

Weight and length parameters were measured for 37 males and 52 females. Males ranged in size from 42 mm ML and 6.6 g to 176 mm and 211.7 g; females ranged from 48 mm ML and 5.3 g to 214 mm ML and 381.6 g (Fig. 1).

### Increment number

The relation between the number of statolith increments and ML was linear for both males and females over the size range available, although there was considerable variability in the data (Fig. 2). The regression equations were

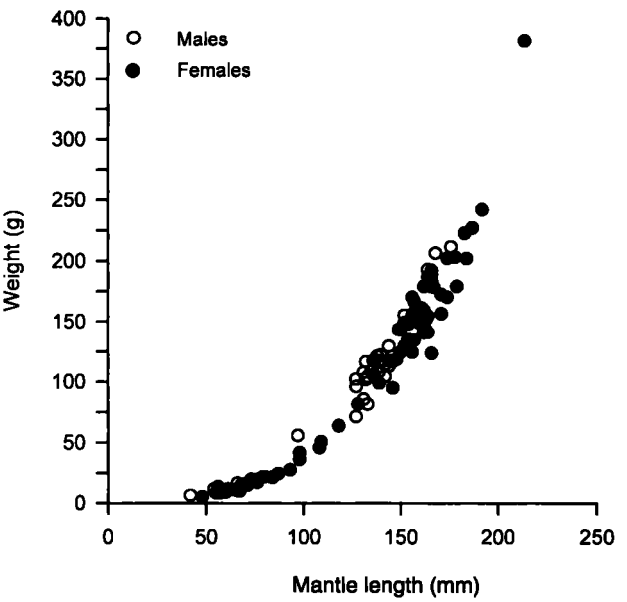


**Figure 1**

The relation between mantle length and weight for males and females of *Nototodarus hawaiiensis*.

$$y = 0.95x - 7.75 \qquad (r^2 = 0.75)$$

and

$$y = 1.08x - 14.915 \qquad (r^2 = 0.78),$$

for males and females respectively,
where $x$ = increment number; and
$y$ = mantle length (mm).

The increment count for males ranged from 71 (42 mm ML) to 192 (164 mm ML). Statolith increments in the largest male collected (176 mm ML) could not be counted owing to overgrinding of the statolith. The increment count for females ranged from 49 (48 mm ML) to 195 (183 mm ML). The largest female (214 mm ML) had an increment count of 179.

## Male maturation patterns

The largest immature male was 127 mm ML and had 167 statolith increments. Males appeared to mature as early as 100 d and 90 mm ML. Mature males showed considerable range in weights of testis (from 0.92 g to 2.84 g, Fig. 3A).

On the basis of ML alone, testis weight appeared to increase rapidly with growth (Fig. 3A), and there was some evidence of testis regression (on the basis of reduced testis weight relative to ML) at larger sizes. However, when testis growth was compared with increment number, there was no clear pattern. Plotting testis weight against increment number showed that mature individuals varied widely in age and individuals of similar age varied widely in testis weight (Fig. 3B).

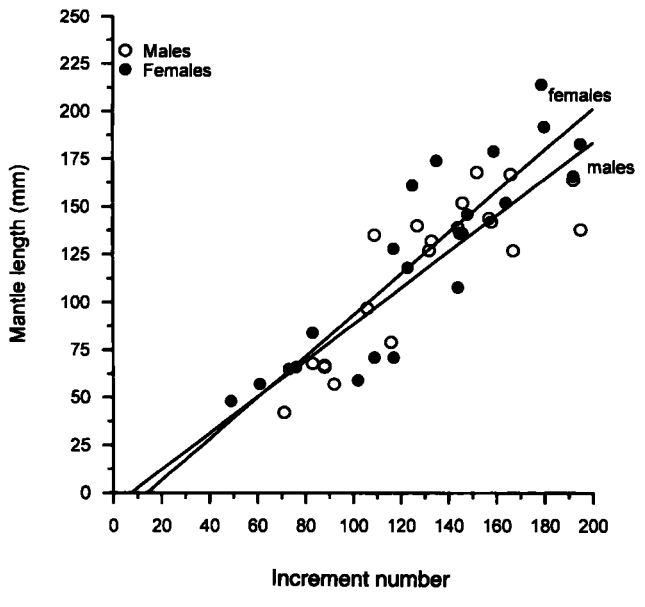


**Figure 2**

The relation between statolith increment number and mantle length for males and females of *Nototodarus hawaiiensis*. Regression equations are given in the text.

## Female maturation patterns

The largest immature female was 166 mm ML and had 192 statolith increments, whereas the smallest mature female was 136 mm ML and had 146 statolith increments. All females larger than 166 mm ML were mature on the basis of the presence of mature oocytes. On the basis of ML (Fig. 4A), females reached full maturity over a narrow length range between approximately 136 and 170 mm ML. However, as with testis weight for the males, ovary weight plotted against increment number (Fig. 4B) showed considerably more variability than did ovary weight plotted against ML (Fig. 4A). The youngest mature female was 125 d. It appeared that there was little growth in the ovary before 100 d.

The largest immature female (166 mm ML) had a NGL of 48 mm ML. Whereas the smallest mature female (136 mm ML) had a NGL of 51 mm, all mature females had a NGL greater than 38 mm. All immature individuals had a NGL less than 50 mm.

The trend in growth of the nidamental gland followed a similar pattern for either ML or increment number (Fig. 5, A and B).

## Hatching dates

On the assumption that statolith increments are formed daily, hatching dates were backcalculated. All individuals that were aged hatched between July and December 1991; the majority (83%) hatched between August and November, and 71% hatched in August, September, and October (Fig. 6). Most squid hatched during the austral spring (September–November), although there was some hatching in late winter (July) and early summer (December).

## Statolith microstructure and growth zones

The statoliths of *N. hawaiiensis* generally had clear increments that could be counted from the nucleus to the outer margin of the dorsal dome (Fig. 7). There was a pattern in the zonation in nine of the 42 statoliths examined (Fig. 7, A and B). Some individuals had a distinct inner opaque zone followed by an outer translucent zone (Fig.

7). No obvious opacity was observed in any of the juvenile (<110 mm ML, $n$=14) statoliths. Opaque zone increment counts on the nine individuals ranged between 89 and 135.

The crystal structure obscuring increments in some statoliths of *N. hawaiiensis* resembled crystals in other squid statoliths. They appeared similar to structures in *Illex illecebrosus*, described as "nodules" by Lipinski (1981) or "occulting crystals" by Dawe et al. (1985). Similar crystals were also observed in the statolith microstructure of the Antarctic squid *Mastigoteuthis psychrophila* (Jackson and Lu, 1994).

## Discussion

### Maturation

*Nototodarus hawaiiensis* matures at a relatively young age (<150 d). According to our study of trawl-caught specimens, *N. hawaiiensis* may have a life span of less than 200 d. This is in contrast to its temperate-water conspecifics *Nototodarus gouldi* and *N. sloanii*, which do not reach maturity until 200 d in New Zealand waters (Uozumi et al., 1995). Maturation in *N. hawaiiensis* appears to be more closely tied

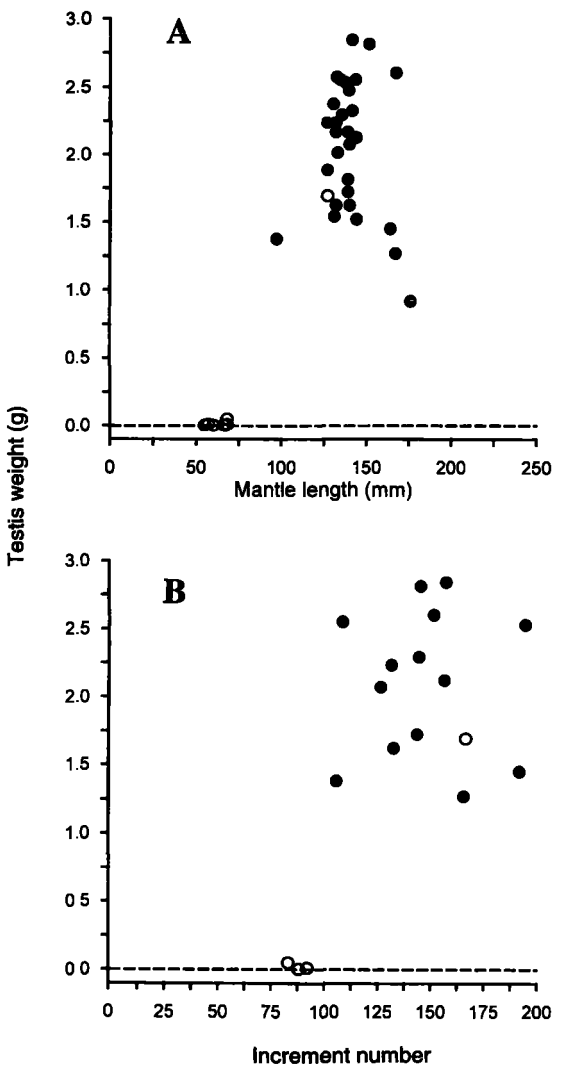


**Figure 3**

The relation between (**A**) mantle length and testis weight, and (**B**) increment number and testis weight for *Nototodarus hawaiiensis*. Filled circles represent mature individuals; hollow circles represent immature individuals.

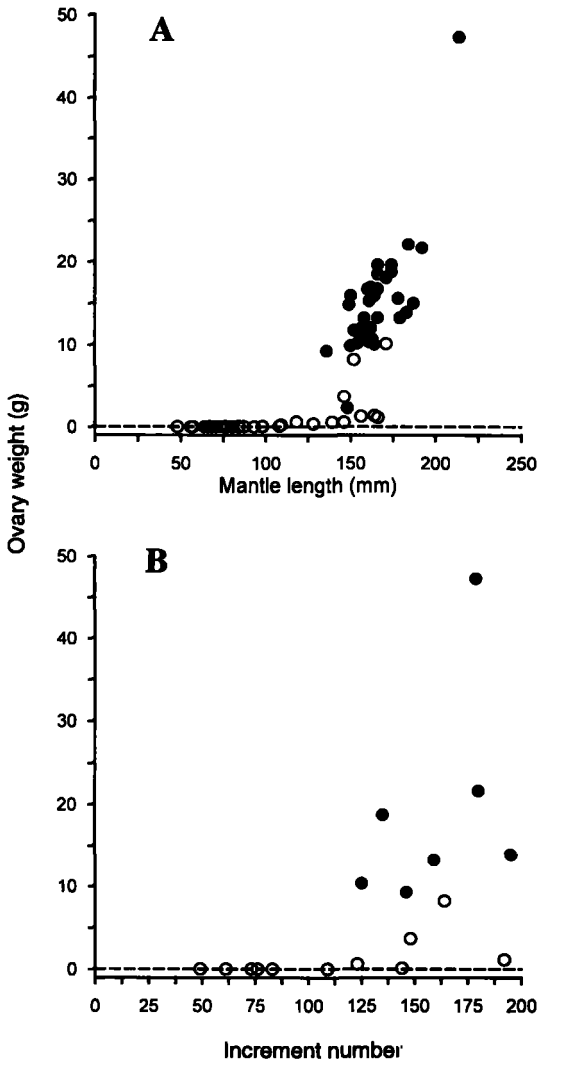


**Figure 4**

The relation between (**A**) mantle length and ovary weight, and (**B**) increment number and ovary weight for *Nototodarus hawaiiensis*. Filled circles represent mature individuals; hollow circles represent immature individuals.

to body size than to age, suggesting that there is a minimal physical or physiological size threshold to be reached before maturity can take place, regardless of age. This pattern has also been found in shallow-water *Photololigo* sp. (referred to as *Loligo chinensis* in Jackson, 1993a) and *Lolliguncula brevis* (Jackson et al., 1997), as well as in males of the deepwater onychoteuthid *Moroteuthis ingens* (Jackson, 1997). Guerra and Castro (1994) found that female reproductive organs of *Loligo gahi* generally required a minimum body size before increasing substantially in size. Such a trend may be a common strategy in squids. *Illex argentinus* in the South Atlantic (Rodhouse and Hatfield, 1990) likewise shows considerable variability in the timing of maturation in relation to age. Rodhouse and Hatfield (1990) postulated that for *I. argentinus*, maturity and gonad growth does not occur at the expense of somatic growth. This also appears to be the case for *N. hawaiiensis*. However, this pattern of maturation contrasts with the deepwater onychoteuthid squid *Moroteuthis ingens*, which undergoes degradation of somatic tissues with maturation (Jackson and Mladenov, 1994).

Size of the nidamental gland relative to body length in *N. hawaiiensis* appears to be a useful indication of female maturity because growth of this organ is closely associated with growth of the ovary (Ikeda et al., 1991, Collins et al., 1995). Uozumi et al. (1995) found a close association in growth of the nidamental gland and ovary size and ovulation in the closely related *Nototodarus sloanii* and *N. gouldi* in New Zealand.

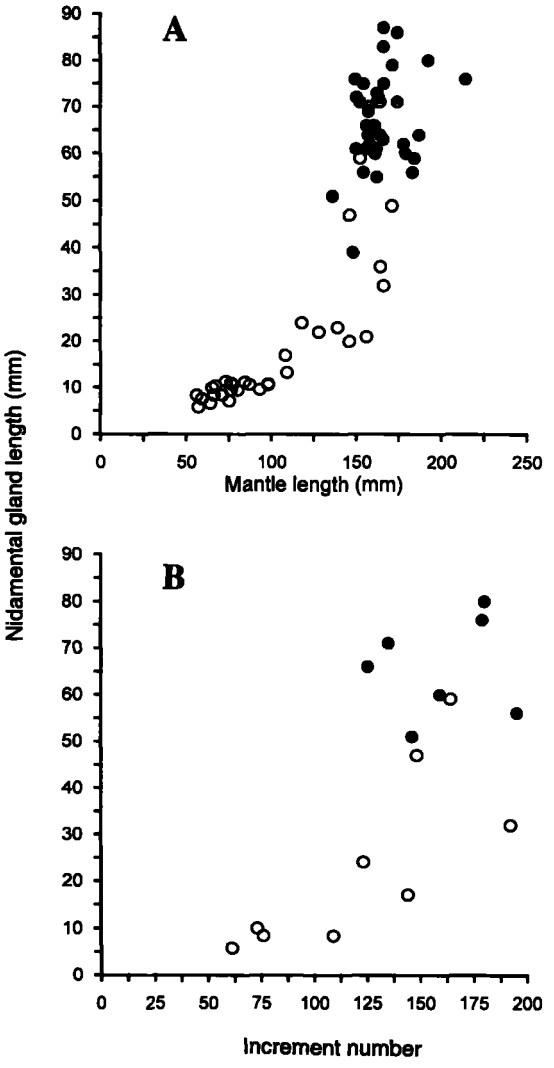


**Figure 5**

The relation between (**A**) mantle length and nidamental gland length and (**B**) increment number and nidamental gland length for *Nototodarus hawaiiensis*. Filled circles represent mature individuals; hollow circles represent immature individuals.

## Hatching

Ageing data suggest that some ommastrephids have extended spawning periods (e.g. *Illex argentinus*, Arkhipkin, 1993; *Todarodes pacificus*, Nakamura and Sakurai, 1993; *Todarodes sagittatus*, *Nototodarus sloanii*, Uozumi and Ohara, 1993; *Ommastrephes bartramii*, Bower, 1996). Other ommastrephids, such as *Illex illecebrosus*, which hatches predominantly in spring (Dawe and Beck, 1997), appear to have peaks of spawning. In some instances, spawning peaks may be regionally influenced; *Martialia hyadesi* captured on the Patagonian Shelf Edge had

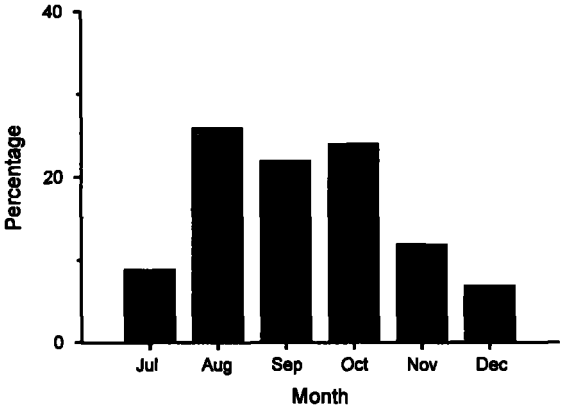


**Figure 6**

The hatching-date distribution of all individuals ($n$=42) of *Nototodarus hawaiiensis* aged in this study.

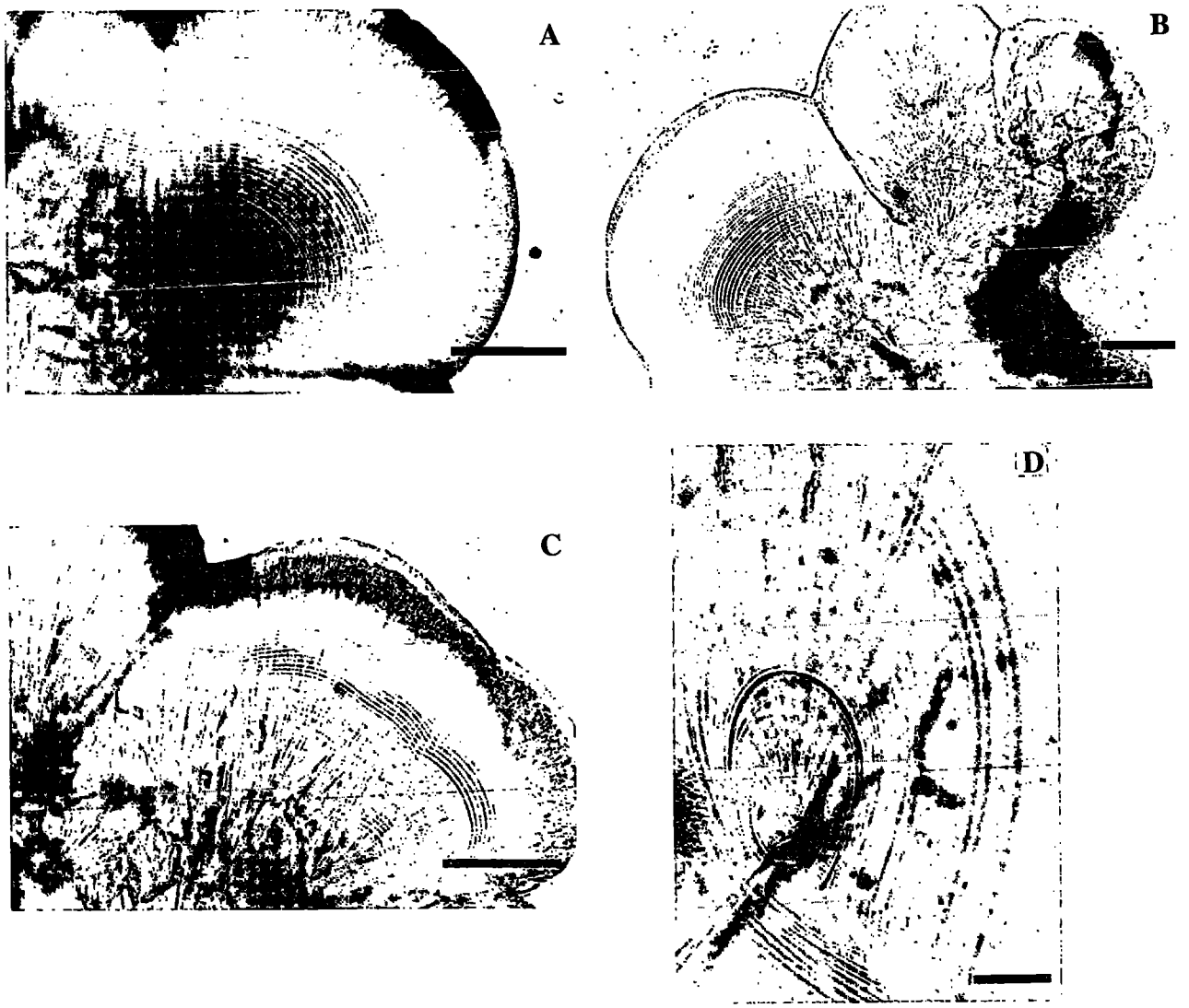


**Figure 7**

Statolith microstructure of *Nototodarus hawaiiensis* (**A**) dorsal dome region of statolith male (132 increments, 127 µm ML)—note the distinct inner opaque zone followed by the outer translucent zone, scale bar = 100 µm (**B**) dorsal dome region of statolith of female (166 µm ML, increment count not taken) —note the less distinct opaque and translucent zones, scale bar = 100 µm (**C**) dorsal dome region of statolith of female (146 increments, 136 µm ML)— note lack of any obvious opaque zone and the unusual overlapping increment structure shown to the right of the photograph, scale bar = 100 µm (**D**) nuclear region of statolith of juvenile female (61 increments, 57 µm ML), scale bar = 25 µm.

a spring peak, whereas individuals captured at the Antarctic Polar Front hatched in winter (Rodhouse et al., 1994). This preliminary data indicates a late winter–spring to early summer hatching for *N. hawaiiensis* in this study. Wadley (1993) collected 50-mm-ML juveniles of *N. hawaiiensis* off the North West Slope in August and 70–80 mm ML juveniles in April, suggesting hatching at different times of the year. From plankton surveys and collection of mature females in North West Slope waters, Dunning (1988a) concluded that *N. hawaiiensis* spawned year-round because paralarvae and juveniles were captured in September and October, and mature females were captured in February, April, August, and late September.

## Statolith zones

The origin of the opaque and translucent zones within the statolith microstructure of some of the *N.*

*hawaiiensis* specimens is unclear. Similar zones that occur in statoliths of the deepwater onychoteuthid *Moroteuthis ingens* might be related to a habitat shift from a pelagic to demersal environment (Jackson, 1993b). The number of increments in the opaque zone was similar for the two species. No zonation was observed in any of 43 statoliths examined from *Nototodarus sloanii* in New Zealand (senior author's personal observ.) which is predominantly a pelagic species. *Nototodarus hawaiiensis* adults are trawled day and night on the seafloor and might be demersal. Pelagic tows at discrete depths would be useful for establishing the ontogenetic descent in this species.

### Age and life span of *Nototodarus hawaiiensis*

The deepwater habitat of *N. hawaiiensis* may prevent validation of statolith increment periodicity because of the difficulty of carrying out experiments on live individuals from this habitat. However, some evidence is available on the periodicity of statolith increments in other ommastrephids. Experimental maintenance with chemical markers has shown that statolith increments are laid down daily in the temperate north Atlantic *Illex illecebrosus* (Dawe et al., 1985; Hurley et al., 1985) and in *Todarodes pacificus* in the north Pacific (Nakamura and Sakurai, 1990, 1991). Furthermore, increment counts on successive cohorts suggest that statolith increments are laid down daily in both *Illex argentinus* in the south Atlantic (Uozumi and Shiba, 1993) and in *Nototodarus sloanii* in southern New Zealand waters (Uozumi and Ohara, 1993). We therefore assume that statolith increment periodicity is also daily in *N. hawaiiensis*.

If the assumption of daily periodicity in increment formation for *N. hawaiiensis* is correct, this suggests that the squid matures early and has a short life span. The species reaches maturity in less than 200 d off the Australian North West Slope, considerably earlier than its conspecifics *Nototodarus gouldi* and *N. sloanii* in New Zealand waters, which live for about a year (Uozumi and Ohara; 1993, Uozumi et al., 1995). However, specimens obtained from trawls in this study were smaller than the maximum size recorded for *N. hawaiiensis*. The largest individuals recorded from Australia were 248 mm ML for a female captured off the Northwest Shelf, and 215 mm ML for a male off southern Queensland (Dunning, 1988b; Dunning and Förch, in press). Based on the regressions in Figure 2, and assuming linear growth throughout the life span, the total number of increments even in these larger individuals would be less than 250. However, *N. hawaiiensis* females have been reported to reach 290 mm ML in the western Indian Ocean and 318 mm ML in the southeastern Pacific. In contrast, individuals of *N. hawaiiensis* are much smaller in the Hawaiian and Philippine waters, with maximum sizes of 180 mm and 160 mm ML, respectively (Dunning and Förch, in press). There thus appear to be regional differences in maximum size (and possibly age) attained by this species.

On the basis of statolith analysis of *N. hawaiiensis* in Australia, this species may complete its life cycle in less than one year. It has a growth rate and life span comparable to tropical Australian shallow-water loliginids, which complete their life cycle in less than 200 d (Jackson, 1990; Jackson and Choat; 1992; Jackson and Yeatman 1996). *Nototodarus hawaiiensis* spends a considerable proportion of its adult life in deeper, cooler waters compared with the loliginids. However, many oceanic squids spend a proportion of their early life phase in the epipelagic zone (Roper and Young, 1975; Vecchione, 1987; Bigelow, 1992) Therefore, a considerable proportion of the life span of *N. hawaiiensis* is probably spent in warmer, epipelagic waters. The youngest individual captured at depth in this study was 49 d, which suggests that perhaps the first 50 days (approximately 25% of the life span) might be spent in the epipelagic zone. Forsythe (1993) proposed a model of squid growth that predicted that increased temperature during a squid's early growth phase can dramatically increase its growth rate, resulting in a much larger adult size. This model has recently been validated by seasonal growth data for *Lolliguncula brevis* (Jackson et al., 1997). *Nototodarus hawaiiensis* may therefore reach a larger size more quickly than if it spent most of its life span in cooler waters at depth.

The statolith analysis of *N. hawaiiensis* on the North West Shelf of Australia suggests a much shorter life span than that of other ommastrephids in tropical waters, e.g. *Todarodes angolensis* in the northern Benguela upwelling (Villanueva, 1992) and *Sthenoteuthis pteropus* in the tropical Atlantic (Arkhipkin and Mikheev, 1992) which have estimated life spans of around one year.

## Acknowledgments

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**Abstract.**—Pigmentation patterns, meristic characters, morphometric measurements, and head spination were recorded and illustrated for the developmental series of larval and pelagic juvenile (10.0–27.7 mm SL) grass rockfish, *Sebastes rastrelliger*. Larvae were identified by the presence of strong dorsal and postanal ventral midline pigment and by the presence of pigment on the lateral midline. Juveniles became highly pigmented over most of their body and fin surfaces at a length of 27.7 mm. Pigment patterns were sufficiently distinct and consistent to differentiate larval and juvenile *S. rastrelliger* from other *Sebastes* species occurring off central California. Otolith characters were also useful in identification of this species. Larval and juvenile *S. rastrelliger* grew at a rate of 0.36 mm/day, similar to the growth rates observed in other species of *Sebastes*.

# Description of pelagic larval and juvenile grass rockfish, *Sebastes rastrelliger* (family Scorpaenidae), with an examination of age and growth

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Rockfishes (*Sebastes* spp.) support important commercial and recreational fisheries in the northeastern Pacific Ocean. During 1995, they accounted for approximately 12.6% of the commercial groundfish catch in weight (PFMC[1]) and 19.4% of all species in the recreational landings off California, Oregon, and Washington (Witzig et al., 1992). Management of rockfishes has been difficult owing to the large number of species within this genus. Sixty-one species of rockfish are reported from California alone (Eschmeyer et al., 1983). The need to identify and separate adult rockfish landed by the fishery has long been recognized (Phillips, 1964; Chen, 1971). Larvae and juveniles are far more difficult to differentiate than adults, but the need for their accurate identification is growing with their use in biomass estimates and recruitment studies (Moser and Butler, 1987; Hunter and Lo, 1993; Ralston et al.[2]). Here we provide means to identify the larvae and juveniles of grass rockfish, *S. rastrelliger*.

*Sebastes rastrelliger* is a thick-bodied, medium-size (maximum size, 56 cm), bottom-dwelling rockfish that inhabits shallow, rocky areas (maximum depth, 46 m) from central Baja California to Yaquina Bay, Oregon (Eschmeyer et al., 1983). This species accounts for less than 1% of the commercial groundfish catch by weight (Pearson[3]). However, in recent years landings have increased from 1.5 metric tons (t) in 1991 to 52 t in 1995. This may be attributed to a relatively new live fish fishery for this species in southern California (Love, 1996). Additionally, *Sebastes rastrelliger* is also an important part of the nearshore recreational catch (Love, 1996).

Manuscript accepted 11 February 1998.
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Only a few studies have been conducted on the development of *S. rastrelliger*. Moreno (1990) described the pigmentation patterns of laboratory-reared larvae up to 53 days old and 7.2 mm in length. Laroche[4] described the pigmentation of a 27.0-mm individual. The purpose of this study is to describe the development of *S. rastrelliger* from larvae to the pelagic juvenile stage and to examine the age and growth of larvae and juveniles.

## Methods

Specimens of pelagic larval and juvenile *S. rastrelliger* were obtained from research cruises conducted aboard the NOAA RV *David Starr Jordan*. Specimens were collected with a 26 × 26-m midwater trawl (12.7-mm stretched mesh codend liner). Surveys were conducted in the spring of 1990, 1992–94, and 1996. Specimens from midwater trawls were frozen for later analysis. All samples were collected off central California between Cypress Point (36°35'N) and Salt Point (38°35'N).

We examined pigmentation patterns and physical characteristics of 18 *S. rastrelliger* larvae and pelagic juveniles. Standard length (SL) was measured for each individual, and sizes ranged from 10.0 mm to 27.7 mm. Specimens greater than 19.9 mm were identified by meristic characters (Chen, 1986; Matarese et al., 1989; Moreland and Reilly, 1991; and Laroche[4]), and pigment patterns were recorded. Specimens less than 20 mm were initially identified from pigment patterns developed from a size series based on the patterns observed by Moreno (1990) and the pigment patterns of the smallest, positively identifiable individuals with complete meristic characters. Whenever possible, dorsal, anal, and pectoral-fin ray counts and the number of gill rakers on the first gill arch were recorded and subsequently used in identifications. Gill-raker counts were obtained only from fish larger than 15 mm in length.

Snout to anus length, head length, snout length, eye diameter, body depth at the pectoral-fin base, body depth at anus, and pectoral-fin length were measured on 17 specimens ranging from 10.0 to 27.7 mm. Terminology for morphometrics follows Richardson and Laroche (1979).

Fifteen specimens (ranging from 10.0 to 27.7 mm) were stained with alizarin red-S and examined for head spination. Terminology for head spination follows Richardson and Laroche (1979).

Otoliths were removed from 16 larvae and juveniles (10.0 to 27.7 mm) and ages were determined following the procedures in Laidig et al. (1991). Additionally, extrusion check radius was measured following the procedures in Laidig and Ralston (1995). Transformation from the larval stage to the juvenile stage was ascertained by the presence of secondary primordia in the otolith (Laidig et al., 1991).

## Results

### General development

At 10.0 mm, *S. rastrelliger* larvae had already undergone flexion, and a full complement of adult fins rays was present (13 dorsal, 6 anal, and 19 pectoral-fin rays), although the spinous dorsal rays were not quite fully developed (Table 1; Fig. 1C). Meristic counts were similar to those reported by Laroche[4] and Moreland and Reilly (1991). In our sample, the earliest signs of transformation were observed in a specimen 20.9 mm in length, and all specimens 27.7 mm or larger had completed transformation. Lateral line pores were present only in the largest individual; therefore a full complement was never observed during this study.

### Morphometrics

Notable changes in body proportion for *S. rastrelliger* occurred between lengths of 10.0 and 13.8 mm and during juvenile transformation (Table 2). At 10.0 mm, larvae had large heads in relation to their body size, whereas larger larvae became more elongate and thus decreased the proportion of head size in relation to body

**Table 1**

Frequency of occurrence of dorsal, anal, and pectoral-fin ray, and gill-raker counts in larval and juvenile grass rockfish, *Sebastes rastrelliger*.

| Character | Count | Frequency of occurrence | Percent occurrence |
|---|---|---|---|
| Dorsal-fin rays | 12 | 2 | 11.1 |
| | 13 | 16 | 88.9 |
| Anal-fin rays | 6 | 18 | 100 |
| Pectoral-fin rays | 18 | 2 | 11.8 |
| | 19 | 15 | 88.2 |
| Gill rakers | 21 | 2 | 16.7 |
| | 22 | 6 | 50.0 |
| | 23 | 3 | 25.0 |
| | 24 | 1 | 8.3 |

[4] Laroche, W. A. 1987. Guide to larval and juvenile rockfishes (*Sebastes*) of North America. Box 216, Enosburg Falls, VT 05450. Unpubl. manuscript, 311 p.

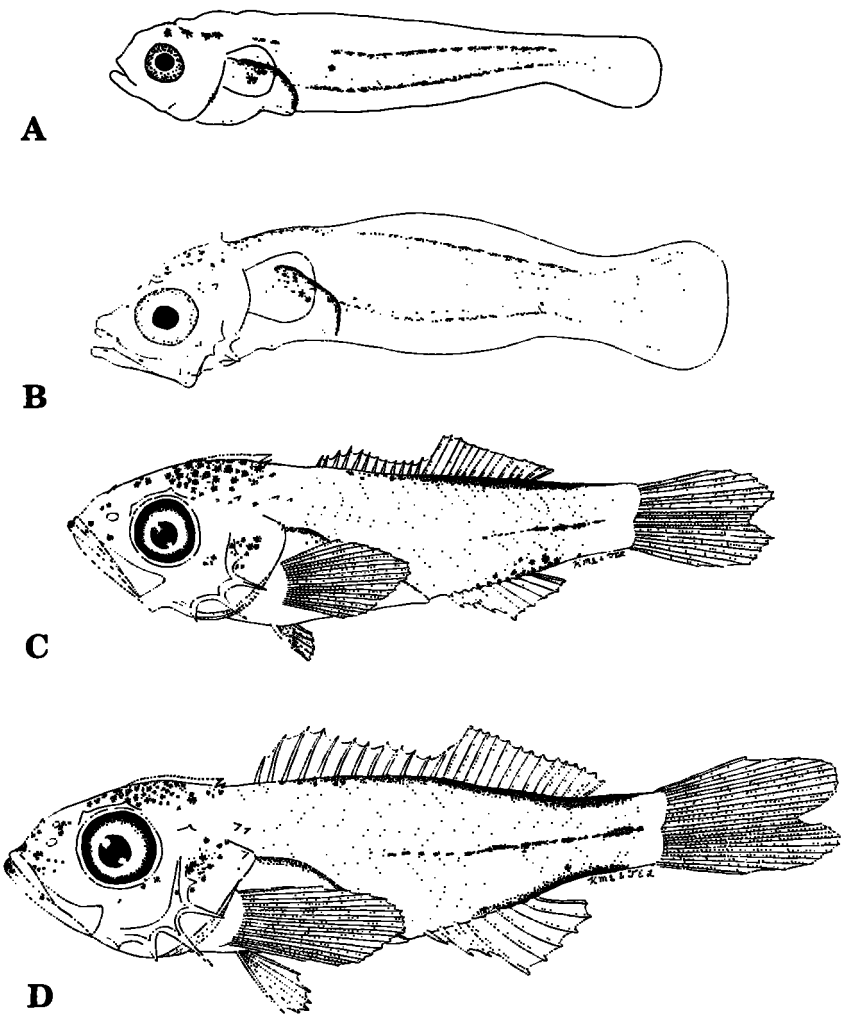


**Figure 1**

Developmental series of grass rockfish, *Sebastes rastrelliger*. (**A**) 4.6 mm SL yolksac preflexion larva; (**B**) 7.2 mm SL flexion larva; (**C**) 10.0 mm SL larva; (**D**) 13.8 mm SL larva; (**E**) 18.3 mm SL larva; (**F**) 21.6 mm SL transforming larva; (**G**) 27.7 mm SL pelagic juvenile. Illustrations A and B (4.6 and 7.2 mm SL, respectively) from Moreno, 1993.

length. After transformation, the fish became more thick-bodied, as evidenced by the increase in body depth at the pectoral-fin ray base and at the anus.

## Head spination

Several head spines had already developed by a length of 10.0 mm (Table 3). The nasal, postocular, parietal, nuchal, pterotic, inferior posttemporal, supracleithral, opercular, and preopercular were all well formed, whereas the 1st inferior and 1st superior infraorbital were barely perceptible at 10.0 mm. By 13.8 mm, the preocular, 2nd inferior infraorbital, and the superior posttemporal were developed. At 18.8 mm, the 4th superior infraorbital was formed. The tympanic formed at 19.7 mm. The pterotic became overgrown and embedded by 21.6 mm. The supraocular, coronal, 3rd inferior infraorbital, and 2nd and 3rd superior infraorbital were not apparent at any length examined.

## Body pigmentation

A distinct pattern of heavy dorsal and postanal ventral midline pigment, along with strong lateral midline pigment, was characteristic at a length of 10.0

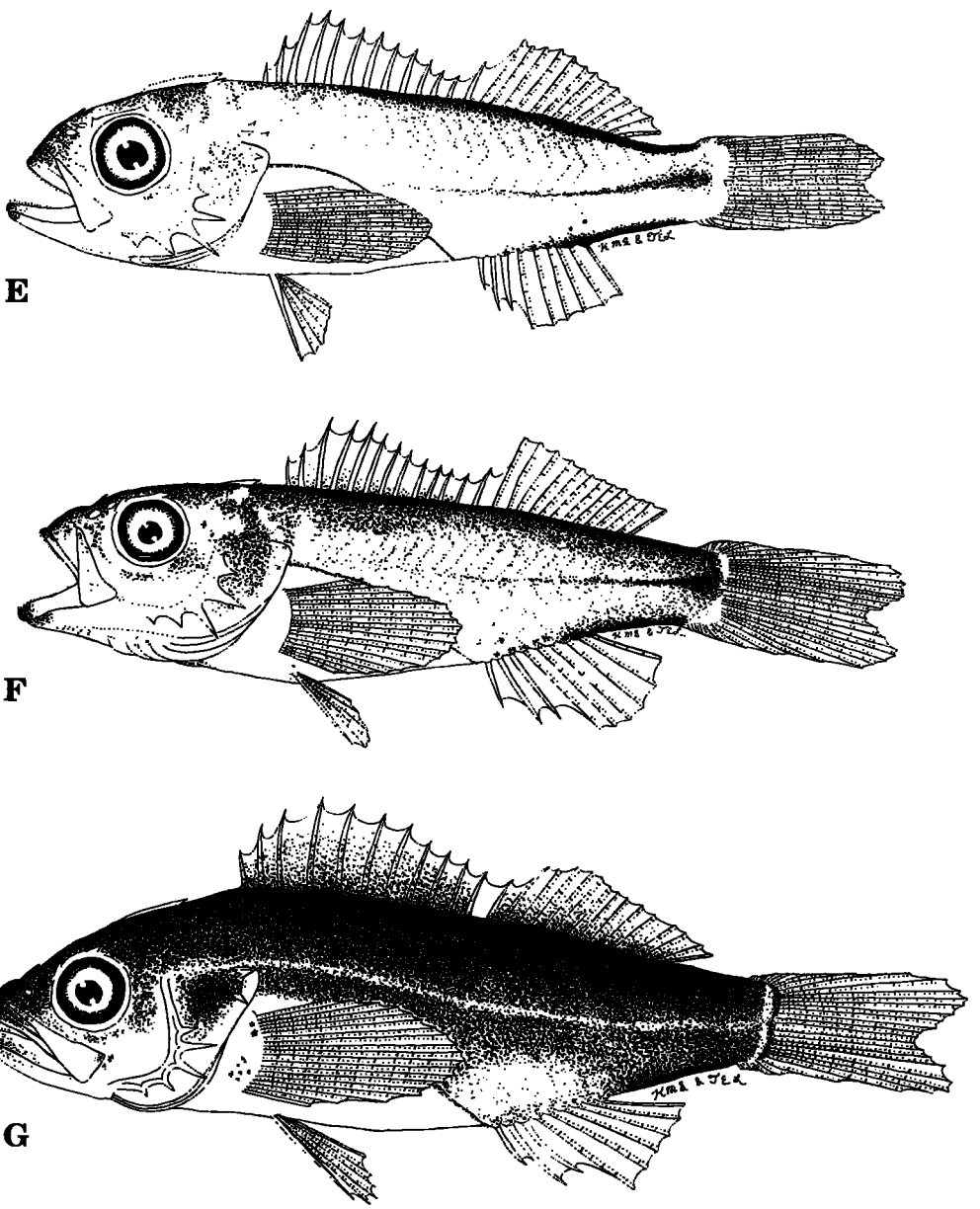


**Figure 1 (continued)**

mm (Fig. 1C; Table 4). Pigment was also evident along the anterior tip of the lower jaw, on the snout anterior to the eye orbit, on the top of the cranium, on the operculum, and along the dorsal and posterior margin of the gut cavity.

Pigmentation patterns at a length of 13.8 mm were similar to, but more intensely developed than, those at 10.0 mm (Fig. 1D). Pigment advanced in the anterior direction along the postanal ventral and lateral midline, and to a lesser degree along the dorsal midline. In addition, pigment along the posterior-ventral portion of the eye orbit had begun to form.

At a length of 18.3 mm, the dorsal half of the fish had become highly pigmented (Fig. 1E). Nape pigment had developed and merged with the dorsal midline pigment, forming a continuous band from the parietal and nuchal spines to the beginning of the caudal fin at this size. Snout and cranial pigment also had merged to form a solid line of pigment from the upper jaw to the parietal and nuchal spines at a

**Table 2**

Morphometric measurements (in mm) of grass rockfish, *Sebastes rastrelliger*.

| SL (mm) | Snout–anus length | Head length | Snout length | Eye diameter | Body depth at pectoral-fin ray base | Body depth at anus | Pectoral fin length |
|---|---|---|---|---|---|---|---|
| 10.0 | 6.4 | 3.7 | 1.2 | 1.2 | 2.9 | 2.4 | 1.7 |
| 13.8 | 7.9 | 4.5 | 1.5 | 1.6 | 3.4 | 3.1 | 2.9 |
| 16.7 | 8.4 | 5.0 | 1.7 | 1.8 | 3.8 | 3.3 | 3.4 |
| 16.7 | 8.4 | 5.0 | 1.7 | 1.8 | 3.8 | 3.3 | 3.4 |
| 16.8 | 8.9 | 5.4 | 1.8 | 1.9 | 3.8 | 3.4 | 3.4 |
| 17.4 | 10.2 | 5.8 | 2.1 | 1.9 | 3.9 | 3.3 | 3.6 |
| 18.0 | 10.5 | 5.9 | 2.2 | 2.0 | 4.3 | 3.4 | 3.8 |
| 18.3 | 10.5 | 6.2 | 2.2 | 2.0 | 4.3 | 3.9 | 3.7 |
| 18.8 | 10.8 | 6.3 | 2.3 | 2.1 | 4.5 | 3.9 | 3.8 |
| 19.2 | 10.9 | 6.5 | 2.4 | 2.1 | 4.6 | 3.7 | 4.0 |
| 19.3 | 11.1 | 6.8 | 2.5 | 2.2 | 4.6 | 3.8 | 4.2 |
| 19.7 | 11.4 | 6.9 | 2.5 | 2.2 | 4.8 | 3.9 | 4.3 |
| 20.9 | 11.7 | 7.2 | 2.7 | 2.3 | 5.1 | 4.4 | 4.5 |
| 21.6 | 12.8 | 7.5 | 2.9 | 2.4 | 5.9 | 5.2 | 4.8 |
| 22.7 | 13.7 | 7.9 | 3.0 | 2.5 | 6.2 | 5.5 | 5.2 |
| 24.3 | 14.0 | 8.7 | 2.5 | 2.7 | 6.7 | 5.7 | 5.8 |
| 27.7 | 15.9 | 9.0 | 2.6 | 2.9 | 7.6 | 6.5 | 6.7 |

length of 18.3 mm. An unpigmented section was conspicuous between the nape and cranial regions. Pigment on the flanks of the dorsal body intensified, especially in between the myomeres. Lateral midline pigment extended from the caudal peduncle to the gut cavity. Pigment on the lateral midline near the caudal peduncle coalesced into a large pigmented area, which decreased in intensity anteriorly. Much of the dorsal half of the operculum was covered with pigment.

At 18.3 mm, the ventral half of the body remained mostly unpigmented, except for the presence of a series of melanophores on the ventral surface anterior to the gut cavity and between the branchiostegals (Fig. 1E). Pigment at the anterior tip of the lower jaw remained similar in intensity to that of the 13.8-mm specimen. Postanal ventral midline pigment became reduced, especially at the base of the anal fin. Pigment was also absent between the ventral myomeres.

By 21.6 mm, pigmentation increased over the entire body surface (Fig. 1F). The dorsal midline pigment merged with the nape, head, snout, and anterior tip of the upper jaw pigment to form a solid line along the dorsal surface of the body from the mouth to the caudal fin. Pigment formed on the ventral half of the membranes of the spinous dorsal fin. Pigment increased around the ventral surface of the eye orbit. Nape, head, and operculum pigment merged to form a vertical bar from the operculum to the dorsal midline, except for a small unpigmented area near the nuchal and parietal spines. Hypural pigment began to form, and the caudal peduncle became highly pigmented. The ventral surface of the body remained only lightly pigmented. A few pigment spots were observed at the base of the pelvic fin.

Juvenile *S. rastrelliger* became highly pigmented throughout most of their body surface by 27.7 mm (Fig. 1G). The entire dorsal surface of the body was completely pigmented. Pigment also covered much of the ventral surface of the body. The gut cavity, the ventral surface of the head, and the area just above the anal fin still remained largely unpigmented. Some pigment was observed at the base of the pectoral fin. A line of light pigment occurred along the lateral midline. Hypural pigment became intense, but an area of decreased pigment was evident just anterior to the hypural area. The spinous and soft dorsal fins were highly pigmented, except for the membrane between spine 11 and 12 which was completely devoid of pigment. A few pigment spots occurred on the anal and caudal fins.

## Otolith examination

A linear model provided a good fit for the relationship of total otolith radius versus SL ($r^2$=0.94)(Fig. 2). The growth rate of *S. rastrelliger* was estimated by a linear model fitted to the relationship of SL and age (coefficient of determination, $r^2$=0.88)(Fig. 3). This model estimated a growth rate of 0.36 mm/day and an extrusion SL of 0.15 mm. The extrusion check radius for *S. rastrelliger* ranged from 13.3 to 14.6 μm, averaging 14.0 μm (SD=0.39). Secondary primordia

**Table 3**

Development of head spines in grass rockfish, *Sebastes rastrelliger*. "1" means spine present and "0" means spine absent.

| | Standard length (mm) | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Spines | 10.0 | 13.8 | 16.7 | 17.4 | 18.0 | 18.3 | 18.8 | 19.2 | 19.3 | 19.7 | 20.9 | 21.6 | 22.7 | 24.3 | 27.7 |
| Nasal | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Preocular | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Supraocular | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Postocular | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Coronal | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Tympanic | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 |
| Parietal | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Nuchal | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Pterotic | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 0 | 0 | 0 |
| Posttemporals | | | | | | | | | | | | | | | |
| Superior | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Inferior | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Supracleithral | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Opercular | | | | | | | | | | | | | | | |
| Superior | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Inferior | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Preopercular | | | | | | | | | | | | | | | |
| 1st anterior | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 2nd anterior | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 3rd anterior | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 1st posterior | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 2nd posterior | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 3rd posterior | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 4th posterior | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 5th posterior | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Infraorbitals | | | | | | | | | | | | | | | |
| 1st inferior | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 2nd inferior | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 3rd inferior | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 1st superior | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 2nd superior | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 3rd superior | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 4th superior | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |

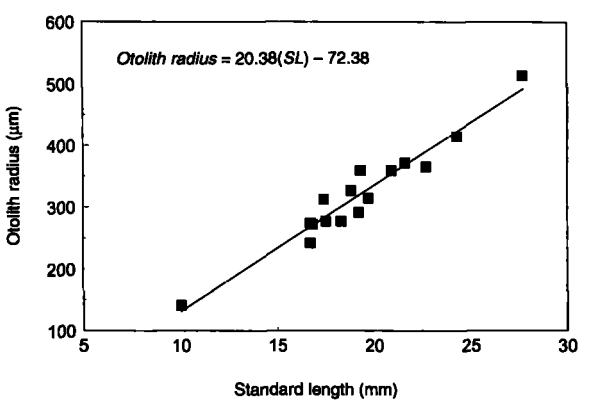


**Figure 2**

Plot of total otolith radius and standard length of grass rockfish, *Sebastes rastrelliger* ($n$=16). Solid line indicates predicated values from linear model.

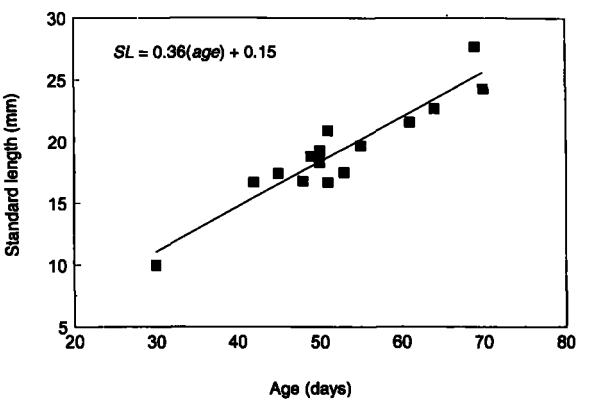


**Figure 3**

Plot of standard length and age of grass rockfish, *Sebastes rastrelliger* ($n$=16). Solid line indicates predicated values from linear model.

**Table 4**

Pigment occurrence at various pigment loci for grass rockfish, *Sebastes rastrelliger*. SL = standard length in mm. Definitions of pigment loci are given below. 0.0 = no pigment, 1.0 = some pigment present, and 2.0 = area heavily pigmented. LJ = anterior tip of the lower jaw, EYE = posterior-ventral edge of the eye orbit, HEAD = cranial surface, FACE = dorsal surface anterior to the eyes, OPER = operculum, CHK = radiating cheek bars, NAPE = nape pigment, DORS = dorsal body surface, VENT = ventral body surface, MID = along the lateral midline, HYP = hypural region, DFIN = spinous dorsal fin, AFIN = anal fin, PEC = blade of the pectoral fin.

| SL | LJ | EYE | HEAD | FACE | OPER | CHK | NAPE | DORS | VENT | MID | HYP | DFIN | AFIN | PEC |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 10.0 | 2.0 | 0.0 | 2.0 | 2.0 | 2.0 | 0.0 | 1.0 | 2.0 | 2.0 | 1.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 13.8 | 2.0 | 2.0 | 2.0 | 2.0 | 2.0 | 0.0 | 1.0 | 2.0 | 2.0 | 2.0 | 1.0 | 0.0 | 0.0 | 0.0 |
| 16.7 | 2.0 | 2.0 | 2.0 | 2.0 | 2.0 | 0.0 | 2.0 | 2.0 | 2.0 | 2.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 16.7 | 2.0 | 2.0 | 2.0 | 2.0 | 2.0 | 0.0 | 2.0 | 2.0 | 2.0 | 2.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 16.8 | 2.0 | 2.0 | 2.0 | 2.0 | 2.0 | 0.0 | 2.0 | 2.0 | 2.0 | 2.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 17.4 | 2.0 | 2.0 | 2.0 | 2.0 | 2.0 | 0.0 | 2.0 | 2.0 | 2.0 | 2.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 17.5 | 2.0 | 2.0 | 2.0 | 2.0 | 2.0 | 0.0 | 2.0 | 2.0 | 2.0 | 2.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 18.0 | 2.0 | 2.0 | 2.0 | 2.0 | 2.0 | 0.0 | 2.0 | 2.0 | 2.0 | 2.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 18.3 | 2.0 | 2.0 | 2.0 | 2.0 | 2.0 | 0.0 | 2.0 | 2.0 | 2.0 | 2.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 18.8 | 2.0 | 2.0 | 2.0 | 2.0 | 2.0 | 0.0 | 2.0 | 2.0 | 2.0 | 2.0 | 0.0 | 1.0 | 0.0 | 0.0 |
| 19.2 | 2.0 | 2.0 | 2.0 | 2.0 | 2.0 | 0.0 | 2.0 | 2.0 | 2.0 | 2.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 19.3 | 2.0 | 2.0 | 2.0 | 2.0 | 2.0 | 0.0 | 2.0 | 2.0 | 2.0 | 2.0 | 0.0 | 1.0 | 0.0 | 0.0 |
| 19.7 | 2.0 | 2.0 | 2.0 | 2.0 | 2.0 | 0.0 | 2.0 | 2.0 | 2.0 | 2.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 20.9 | 2.0 | 2.0 | 2.0 | 2.0 | 2.0 | 0.0 | 2.0 | 2.0 | 2.0 | 2.0 | 1.0 | 1.0 | 0.0 | 0.0 |
| 21.6 | 2.0 | 2.0 | 2.0 | 2.0 | 2.0 | 0.0 | 2.0 | 2.0 | 2.0 | 2.0 | 1.0 | 2.0 | 0.0 | 0.0 |
| 22.7 | 2.0 | 2.0 | 2.0 | 2.0 | 2.0 | 0.0 | 2.0 | 2.0 | 2.0 | 2.0 | 1.0 | 2.0 | 0.0 | 0.0 |
| 24.3 | 2.0 | 2.0 | 2.0 | 2.0 | 2.0 | 0.0 | 2.0 | 2.0 | 2.0 | 2.0 | 1.0 | 2.0 | 0.0 | 0.0 |
| 27.7 | 2.0 | 2.0 | 2.0 | 2.0 | 2.0 | 0.0 | 2.0 | 2.0 | 2.0 | 2.0 | 2.0 | 2.0 | 1.0 | 0.0 |

first appeared in the otoliths of the 20.9-mm specimen and was subsequently observed in the otoliths of all specimens larger than 20.9 mm. By 27.7 mm, the otolith was completely encircled by secondary primordia, signaling the end of juvenile transformation.

## Discussion

*Sebastes rastrelliger* have developed a unique pigment pattern by 10 mm (Fig. 1C), which allows them to be distinguished from other *Sebastes* spp. At this size, the presence of dorsal, ventral, and lateral body midline pigment is distinctive for only three species (*S. dallii* [Moser and Butler, 1981], *S. rufus* [Moser and Butler, 1987], and *S. saxicola* [Laidig et al., 1996]) that co-occur with *S. rastrelliger* off California. All four species have anterior lower jaw, snout, and opercular pigments, which could add to the confusion between these species. One major difference in pigmentation between these species is that *S. dallii* and *S. rufus* have pectoral-fin pigment. We found no pectoral-fin pigmentation in *S. rastrelliger* larger than 10.0 mm, and Moreno (1990) found no pectoral-fin pigment for individuals smaller than 8 mm. *Sebastes saxicola* also lacks pectoral-fin pigment in fish smaller than 20 mm (Laidig et al., 1996). *Sebastes saxicola* and *S. rastrelliger* can exhibit similar pigmentation at 10 mm. This similarity occurs until approximately 18 mm, when *S. saxicola* develops hypural and dorsal fin pigment and when saddling along the dorsal surface eventually changes into a barred pattern. *Sebastes rastrelliger* was also found to have a relatively small pectoral fin for its SL (Table 2) in comparison with other *Sebastes* spp. (Moser et al., 1977; Richardson and Laroche, 1979; Laroche and Richardson, 1980, 1981; Sakuma and Laidig, 1995; Laidig et al., 1996)

Meristics can aid in differentiating *S. rastrelliger* from other species. The average counts of 13 dorsal, 6 anal, and 19 pectoral-fin rays (Table 1) are similar to those observed by Moreland and Reilly (1991) and Laroche.[4] Moreland and Reilly (1991) found this combination of fin-ray counts typical for only two species: *S. rastrelliger* and *S. babcocki*. *Sebastes babcocki* has a distinct barred pigmentation pattern and typical gill-raker counts of 30–31. *Sebastes rastrelliger* had no barred pattern and average gill-raker counts of 22. This count is lower than that observed by Moreland and Reilly (1991) (an average of 25) and Laroche[4] (an average of 24). Gill-raker counts may be low in our study because the gill rakers may not have fully developed in some of our specimens (Sakuma and Laidig, 1995). Therefore, the use of pigment patterns in conjunction with meristics should aid in the identification of *S. rastrelliger*.

Otolith characters can also be useful in separating *Sebastes rastrelliger* from some other *Sebastes* species. Laidig et al. (1996) showed that the extrusion check radius of *S. rastrelliger* (14.0 μm) was significantly different from those of *S. saxicola*, *S. maliger*, *S. atrovirens*, and the copper complex (*S. carnatus*, *S. caurinus*, and *S. chrysomelas*). It was not different from those of *S. auriculatus* or *S. semicinctus*. However, these latter two species have distinctly different meristic counts and pigmentation patterns. In addition, the extrusion check radii found by Laidig and Ralston (1995) for *S. paucispinis*, *S. flavidus*, *S. entomelas*, and *S. mystinus* were smaller (10.93–12.20 μm) than that for *S. rastrelliger*, whereas the extrusion check radii for *S. jordani* and *S. goodei* were much larger (15.15–16.96 μm).

Postflexion *Sebastes rastrelliger*, from 10.0 to 27.7 mm, grew at a rate of 0.36 mm/day. Moreno (1990) found that the growth rate for reared preflexion *S. rastrelliger* less than 8 mm was 0.07 mm/day. This slow growth rate may be attributed to laboratory rearing of the fish. However, slow growth rates have been shown for the first few weeks in *S. goodei* (Sakuma and Laidig, 1995), *S. saxicola* (Laidig et al., 1996), and *S. jordani* (Laidig et al., 1991). Sakuma and Laidig (1995) observed growth rates of 0.135 mm/day in *S. goodei* less than 40 days old whereas Woodbury and Ralston (1991) noted growth rates of 0.399–0.555 mm/day in specimens 35–170 days old. Laidig et al. (1996) observed growth rates of 0.125 mm/day in *S. saxicola* less than 40 days old, whereas larvae and juveniles older than 40 days exhibited increased growth rates of 0.367 mm/day. Laidig et al. (1991) determined that in *S. jordani* there were large fluctuations in growth rates associated with flexion, with relatively slow growth prior to flexion, almost no growth during flexion, and relatively rapid growth after flexion. Because the *S. rastrelliger* in this study had already undergone flexion, we expected a faster growth rate than that of smaller fish as recorded by Moreno (1990). For this reason, our growth curve does not accurately express the growth in the first few weeks of life; this lack of fit is consistent with the smaller than expected estimate of SL at extrusion (0.15 mm). Therefore, extrapolating growth rates for flexion and preflexion larvae from our model would not be advised.

## Acknowledgments

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# Changes in the sex ratio and size at maturity of gag, *Mycteroperca microlepis*, from the Atlantic coast of the southeastern United States during 1976–1995*

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**Abstract.**—Gag, *Mycteroperca microlepis*, is a large, slow-growing, protogynous grouper that probably makes annual migrations to specific locations to aggregate for spawning. During 1976–82, male gag constituted 19.6% of the sexually mature individuals taken during fishery-dependent and fishery-independent sampling along the southeast coast of the United States. A similar percentage of males was found in the Gulf of Mexico from 1977 to 1980; however, males made up only 1.9% of the population in the Gulf of Mexico during 1992. To assess the current sex ratio of gag along the southeast U.S. coast, an emergency rule was enacted by the Department of Commerce in January 1995 that required commercial vessels from North Carolina to southeast Florida to land gag with gonads intact. Histological examination of 2613 gonads of sexually mature gag collected from 18 January through 18 April 1995 revealed that 5.5% of the gag from the southeast Atlantic were male. There was a weak trend indicating that females reached maturity at a smaller size in 1994–95 than in 1976–82. Very few transitional specimens were collected during the spawning season. Most transitional individuals (79%) were taken during April through June immediately after the 1995 spawning season. Gag in spawning condition were landed during December through mid-May by fishermen working offshore from North Carolina to southeast Florida. In addition, gag in spawning condition were taken during research cruises documenting the occurrence of spawning north of Florida (off South Carolina and Georgia at depths ranging from 49 to 91 m).

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Fish. Bull. 96:797–807 (1998).

Gag, *Mycteroperca microlepis*, is a large, slow-growing serranid associated with inshore-reef and shelf-break habitats in the western Atlantic from New York to Brazil and in the Gulf of Mexico (Smith, 1971; Huntsman, 1976; Hardy, 1978; Collins et al., 1987). Gag are protogynous and probably make annual late-winter migrations to specific locations to form spawning aggregations (Collins et al., 1987; Keener et al., 1988; Van Sant et al., 1994). Recent evidence indicates that males may be selectively removed because they are the largest and most aggressive individuals in a spawning aggregation and are the first to be taken by fishing gear (Gilmore and Jones, 1992). Effects of fishing on spawning aggregations in other grouper species have been found to be deleterious on population size, sex ratio, genetic diversity, and behavior of individuals (Nelson and Soulé, 1987; Smith et al., 1991; Carter et al., 1994; Coleman et al., 1996).

Histological examination of gonads of 498 gag collected throughout the year during 1976–82 along the southeast coast of the United States revealed that 84% were females, 15% males, and 1% were undergoing transition from female to male (Collins et al., 1987). Hood and Schlieder (1992) found similar sex ratios (14.0% male) for Gulf of Mexico gag collected from 1977 to

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1980. In both of these earlier studies, immature females were included in the sex ratio. In 1992, Coleman et al. (1996) determined that males made up a smaller percentage (1.9%) of the Gulf of Mexico adult (sexually mature) population than did males in the earlier study by Hood and Schlieder (1992). No current estimate of sex ratio is available for gag along the southeast coast of the United States.

In 1993, the South Atlantic Fishery Management Council (SAFMC) and the Florida Marine Fish Commission considered a closure for fishing of gag along the southeast coast during the gag spawning season to prevent the possibility that fishing on aggregations could severely decrease spawning output and affect sex ratios for future spawning seasons and generations (SAFMC, 1993). Much of the impetus for the proposed closure was the heavy fishing pressure exerted by recreational and commercial fishermen on spawning aggregations along the narrow Florida shelf. However, the SAFMC elected to take no action because it was unknown if gag spawned north of Florida and because the impacts of a spawning season closure for the entire southeast coast might be an unnecessary hardship on fishermen. In addition, no recent data were available on the sex ratio of gag along the southeast coast. Owing to the paucity of data on the current reproductive status of gag, the U.S. Department of Commerce followed recommendations from SAFMC and the National Marine Fisheries Service (NMFS) and enacted an emergency rule requiring all commercial vessels along the Atlantic coast of the southeastern United States to land gag in whole condition so that sex ratios and reproductive condition could be assessed. In this paper we compare current sex ratio and maturity data (1994–95) with historical information (1976–82). An additional objective of this work was to determine if gag spawn north of Florida.

## Methods

Gag reproductive data were collected during 1976–82 and 1994–95 by the Marine Resources Monitoring Assessment and Prediction (MARMAP) program at South Carolina Department of Natural Resources (SCDNR). Data collected from 1976 to 1982 were obtained from the commercial hook and line fishery or research cruises conducted by the MARMAP program. These data (1976–82) were published by Collins et al. (1987), but raw data were available to us for comparison with recent information. During 1994–95, the collection of most gag resulted from an emergency rule that required commercial fishermen along the southeast Atlantic coast to land all gag with gonads intact from 18 January through 18 April 1995. The rule was extended through 17 July 1995 but applied only to gag larger than 889 mm (TL). Upon reaching the dock, fishermen were instructed to contact a NMFS or state port sampler assigned to the region. The port samplers recorded date, port, approximate area of fishing, and total length (TL) and weight of specimens. All length measurements in our study refer to TL. Gonads were obtained from each specimen, packed in ice or preserved in formalin, and shipped to personnel of the MARMAP program. Additional samples were collected by MARMAP during 1994 and 1995 with chevron traps and hook-and-line gear at randomly chosen reef areas off the southeastern United States (Collins and Sedberry, 1991; Cuellar et al., 1996) and through port sampling efforts.

To assess sex and reproductive state, all gonads collected during 1994–95 were prepared for histological examination. The posterior portion of the gonad was removed and preserved in 10% formalin buffered with seawater. After a 2–6 week fixation, the tissue samples were transferred to 50% isopropanol, processed and vacuum infiltrated in a modular vacuum tissue processor, and blocked in paraffin. The resulting imbedded samples were sectioned at 7 μm, stained with double-strength Gill hematoxylin, and counter-stained with eosin-y. A similar technique was used for the 1976–82 samples (Collins et al., 1987).

Sex and reproductive stage were assessed by one reader according to histological criteria (Table 1). Sections from 100 randomly selected specimens were examined by a second reader early in the study to verify the assessments. Specimens with developing, ripe, spent, or resting gonads were considered to be sexually mature. For females, this definition of sexual maturity included specimens with oocyte development at or beyond the cortical granule (alveoli) stage and specimens with beta, gamma, or delta stages of atresia. To ensure that females were correctly assigned to the immature and resting categories, the length-frequency histogram for immature females was compared to the histograms for resting females and females with evidence of certain maturity (e.g. developing, ripe, or spent). If there was little or no overlap between the two histograms representing mature individuals and the histogram for immature females, it was assumed that immature and resting individuals were not being confused.

To produce a sex ratio for the adult portion of the population, only data for mature gag were included in analyses. Data from Collins et al. (1987) and Hood and Schlieder (1992) were analyzed again to determine a sex ratio based on mature gag so that the results of these studies and the present study could

**Table 1**

Histological criteria used to determine reproductive state in gag, *Mycteroperca microlepis* (based on Moe, 1969; Hunter and Macewicz, 1985; Hunter al. 1986; Collins et al., 1987; West, 1990; Ferreira, 1993; Shapiro et al., 1993a, 1993b).

| Reproductive state | Male | Female |
|---|---|---|
| Immature | No primary males found. "Immature males" in Moe (1969) considered late transitional because sex transition is not yet completed. | No evidence of atresia. In comparison to resting female, oogonia more abundant along the margin of lamellae, most previtellogenic oocytes <80 μm in diameter, area of transverse section of ovary is smaller, lamellae lack muscle and connective tissue bundles, lamellae are not as elongate, and ovarian wall is thinner. |
| Developing | Development of cysts containing primary and secondary spermatocytes through some accumulation of spermatozoa in lobular lumina and peripheral sinuses within gonadal wall. | Oocytes undergoing cortical granule (alveoli) formation through nucleus migration and partial coalescence of yolk globules. |
| Running ripe | Predominance of spermatozoa in lobules and peripheral sinuses. Little or no occurrence of spermatogenesis. | Completion of yolk coalescence and hydration in the most advanced oocytes. Zona radiata becomes thin. Postovulatory follicles sometimes present. |
| Spent | No spermatogenesis. Some residual spermatozoa in lobules and peripheral sinuses. | More than 50% of vitellogenic oocytes in alpha or beta stage of atresia. |
| Resting | Little or no spermatocyte development. Empty lobules and sinuses evident. | Traces of atresia. In comparison to immature female, oogonia less abundant along margin of lamellae, most previtellogenic oocytes >80 μm in diameter, area of transverse section of ovary is larger, lamellae have muscle and connective tissue bundles, lamellae are more elongate and convoluted, and ovarian wall is thicker. |
| Developing, recent spawn | Not assessed. | Developing stage as described above plus presence of postovulatory follicles. |
| Mature specimen, state unknown | Mature, but inadequate quantity of tissue or postmortem histolysis prevent further assessment of reproductive state. | Mature, but inadequate quantity of tissue or postmortem histolysis prevents further assessment of reproductive state. |
| Transitional | | |
| Proliferation of spermatogonia through limited spermatogenesis within lamellae of resting ovary and development of peripheral sinuses in musculature of ovarian wall. | | |

be compared. The sex ratio for 1995 was based on mature individuals that were collected during the early portion of the emergency rule (18 January to 18 April 1995). Recent data were analyzed by region: North Carolina, South Carolina, Georgia, northern Florida, and southern Florida (south of New Smyrna Beach). Plots of reproductive seasonality were based on all individuals that were collected during 1994 and 1995. Females that possessed hydrated oocytes or postovulatory follicles were considered to be in spawning condition.

Data for all females collected during the two periods were used in size-at-maturity analyses. The probit procedure (SAS, 1990) was used to fit a gompit model with the Gompertz distribution function to maturity data in 5-cm-TL intervals. This procedure provided estimates of length at 50% maturity ($L_{50}$) and a comparison of size at maturity between periods. Analysis of variance (ANOVA) and the Duncan multiple range test were used to determine if there was a significant difference in the mean size of gag collected by month for mature individuals. ANOVA and the Duncan multiple range test were also used to determine if there was a significant difference in the monthly mean size of gag between 889 and 1050 mm TL to reduce the potential for bias that might result from selection of larger fishes during the latter part of the emergency rule. The results of all statistical tests were considered significant if $P$ was $<0.05$.

## Results

Histological examination of 2606 sexually mature gag (size range=517–1275 mm TL) taken during 18 January through 18 April 1995 revealed that there were significantly ($\chi^2$=66.852; $P$ <0.001) fewer males (5.5%) along the southeast coast of the United States than during 1976–82 (19.6%; Tables 2 and 3). There were no significant differences in the percentage of males captured in 1995 off North Carolina, South Carolina, Georgia, and southern Florida ($\chi^2$ =4.926; $P$>0.05; Table 4). However, the percentage of males taken in northern Florida (14.9%) was significantly greater than in all other regions combined ($\chi^2$ =133.160; $P$<0.001). Four collections accounted for over 35% of the males that were collected in northern Florida.

The size range of gag captured during 1994 and 1995 was similar to those caught from 1976 to 1982; however, there were some differences in size between periods for both sexes (Tables 3 and 5). Larger mature female gag were collected in 1994–95, although the mean lengths for the two periods were similar (1976–82: $\bar{x}$ TL=831 mm, SD=92; 1994–95: $\bar{x}$ TL = 832 mm, SD=82). The smallest mature female was

**Table 2**

Sex ratio of gag, *Mycteroperca microlepis*, (M=Male; F=Female; T=Transitional) taken during various studies in the northeast Gulf of Mexico and southeastern United States between 1976 and 1995. Sex ratios based on sexually mature individuals.

| Study | Dates | Area | No. of M | % M | No. of F | % F | No. of T | % T |
|---|---|---|---|---|---|---|---|---|
| This study | 1976–1982 | SE Atlantic | 104 | 19.6 | 419 | 78.9 | 8 | 1.5 |
| Hood and Schlieder (1992) | 1977–1980 | NE Gulf of Mexico | 125 | 15.6 | 659 | 82.5 | 15 | 1.9 |
| Coleman et al. (1996) | 1992 | NE Gulf of Mexico | 9 | 1.9 | 457 | 97.3 | 3 | 0.6 |
| This study | 18 Jan–18 April 1995[1] | SE Atlantic | 143 | 5.5 | 2468 | 94.4 | 2 | 0.1 |
| This study | 1994–1995 | SE Atlantic | 256 | 6.4 | 3720 | 92.7 | 39 | 0.9 |

[1] Period of emergency rule when fishermen were required to land all gag with gonads intact.

**Table 3**

Number of sexually mature gag, *Mycteroperca microlepis*, collected by size class during 1976–82 and 18 January to 18 April 1995 when fishermen were required to land all gag with intact gonads (TL=total length). Trans = transitional specimens.

| Size (mm TL) | 1976–1982 | | | 1995 | | |
|---|---|---|---|---|---|---|
| | Female | Male | Trans | Female | Male | Trans |
| 450–499 | — | — | — | — | — | — |
| 500–549 | 2 | — | — | 2 | — | — |
| 550–599 | 1 | — | — | 12 | — | — |
| 600–649 | 10 | — | — | 19 | — | — |
| 650–699 | 14 | — | — | 79 | — | — |
| 700–749 | 31 | — | — | 171 | — | — |
| 750–799 | 64 | 1 | 2 | 437 | — | |
| 800–849 | 94 | 1 | 1 | 709 | — | 1 |
| 850–899 | 79 | 1 | 2 | 580 | 5 | 1 |
| 900–949 | 42 | 4 | 1 | 271 | 3 | — |
| 950–999 | 7 | 13 | 1 | 99 | 26 | — |
| 1000–1049 | 13 | 14 | — | 48 | 48 | — |
| 1050–1099 | 5 | 27 | — | 27 | 36 | — |
| 1100–1149 | — | 14 | — | 6 | 13 | — |
| 1150–1199 | — | 2 | — | 1 | 7 | — |
| 1200–1249 | — | 1 | — | — | 5 | — |
| 1250–1299 | — | — | — | | — | — |
| No length | 47 | 25 | 1 | 7 | | |
| Total | 419 | 104 | 8 | 2468 | 143 | 2 |
| Percent | 78.9 | 19.6 | 1.5 | 94.4 | 5.5 | 0.1 |

**Table 4**

Number of sexually mature gag, *Mycteroperca microlepis*, females (F), males (M), and transitionals (T) taken in North Carolina, South Carolina, Georgia, northern Florida, and southern Florida during 18 January to 18 April 1995 when fishermen were required to land all gag with intact gonads (TL=total length).

| Size (mm TL) | North Carolina | | | South Carolina | | | Georgia | | | North Florida | | | South Florida | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | F | M | T | F | M | T | F | M | T | F | M | T | F | M | T |
| 450–499 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| 500–549 | — | — | — | 2 | — | — | — | — | — | — | — | — | — | — | — |
| 550–599 | 1 | — | — | 10 | — | — | — | — | — | 1 | — | — | — | — | — |
| 600–649 | 3 | — | — | 12 | — | — | 1 | — | — | — | — | — | 3 | — | — |
| 650–699 | 13 | — | — | 39 | — | — | 16 | — | — | 4 | — | — | 7 | — | — |
| 700–749 | 37 | — | — | 87 | — | — | 35 | — | — | 6 | — | — | 6 | — | — |
| 750–799 | 53 | — | — | 199 | — | — | 113 | — | — | 46 | — | — | 26 | — | — |
| 800–849 | 64 | — | — | 234 | — | 1 | 214 | — | — | 111 | — | — | 86 | — | — |
| 850–899 | 64 | — | — | 160 | 3 | — | 148 | 1 | — | 155 | — | — | 53 | 1 | 1 |
| 900–949 | 23 | — | — | 66 | 1 | — | 43 | 1 | — | 112 | — | — | 27 | 1 | — |
| 950–999 | 19 | 1 | — | 11 | 3 | — | 16 | 1 | — | 44 | 18 | — | 9 | 3 | — |
| 1000–1049 | 7 | 3 | — | 4 | 5 | — | 10 | 4 | — | 26 | 33 | — | 1 | 3 | — |
| 1050–1099 | 3 | 1 | — | 2 | 4 | — | 7 | 3 | — | 14 | 27 | — | 1 | 1 | — |
| 1100–1149 | — | — | — | 3 | 1 | — | — | 1 | — | 2 | 9 | — | 1 | 2 | — |
| 1150–1199 | — | — | — | — | 3 | — | 1 | 1 | — | — | 3 | — | — | — | — |
| 1200–1249 | — | 1 | — | — | 1 | — | — | 2 | — | — | 1 | — | — | — | — |
| 1250–1299 | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| No lengths | | | | 2 | | | 2 | | | 2 | | | 1 | | |
| Total | 287 | 6 | — | 831 | 21 | 1 | 606 | 14 | — | 523 | 91 | — | 221 | 11 | 1 |
| Percent | 97.9 | 2.1 | — | 97.4 | 2.5 | 0.1 | 97.7 | 2.3 | — | 85.1 | 14.9 | — | 94.8 | 4.7 | 0.5 |

508 mm in 1976–82 and 517 mm in 1994–95. All gag >683 mm in the 1976–82 samples and those >750 mm in the 1994–95 samples were sexually mature. During 1994–95, 266 males ($\bar{x}$ TL=1041 mm, SD=68) were collected and no gag less than 875 mm was male (Table 5). During 1976–82, 104 males ($\bar{x}$ TL=1041 mm, SD=73) were collected with the smallest specimen at 795 mm. The transitional specimens collected during 1994–95 were larger than those from 1976 to 1982.

The length at 50% maturity ($L_{50}$) was similar during 1978–82 (641 mm; 95% confidence interval (CI) =616–658 mm) and 1994–95 (622 mm; 95% CI=611–631 mm (Fig. 1); however, the probit analysis with period and total length as independent variables (Pearson $\chi^2$, $P$=0.9953, df=27) indicated that the size at maturity was likely decreasing (Table 6). The negative coefficient for period indicated that overall a smaller proportion of specimens in each size class was mature during 1976–82. The overlap in the histograms of female gag that were developing, ripe, or spent and females that were resting indicated that reproductive tissue was correctly assigned to the immature and resting categories (Fig. 2).

Female gag were in spawning condition from December 1994 through mid May 1995 on the basis of

**Table 5**

Number of mature gag, *Mycteroperca microlepis*, taken during 1994–95 (TL=total length). Trans = transitional specimens.

| Size (mm TL) | Female | Male | Trans |
|---|---|---|---|
| 450–499 | 0 | — | — |
| 500–549 | 2 | — | — |
| 550–599 | 16 | — | — |
| 600–649 | 35 | — | — |
| 650–699 | 121 | — | — |
| 700–749 | 267 | — | — |
| 750–799 | 650 | — | 1 |
| 800–849 | 1021 | — | 2 |
| 850–899 | 790 | 7 | 5 |
| 900–949 | 386 | 14 | 12 |
| 950–999 | 132 | 46 | 10 |
| 1000–1049 | 70 | 82 | 8 |
| 1050–1099 | 33 | 68 | — |
| 1100–1149 | 7 | 28 | — |
| 1150–1199 | 2 | 15 | — |
| 1200–1249 | — | 5 | 1 |
| 1250–1299 | 1 | — | — |
| No Lengths | 41 | 1 | — |
| Total | 3574 | 266 | 39 |
| Percent | 92.1 | 6.9 | 1.0 |

occurrence of hydrated oocytes or postovulatory follicles (Fig. 3). Spawning individuals were caught from North Carolina to Florida by commercial fishermen and fishery-independent sampling (MARMAP). Approximate fishing locations provided by commercial fishermen indicated that gag were spawning from the border between North Carolina and South Carolina to a point east of Ft. Lauderdale, Florida. Spawning individuals were captured on research cruises off South Carolina and Georgia at depths ranging from 49 to 91 m. The spawning season appeared to be more protracted in southern Florida than in other areas, with spawning beginning in December and extending into mid May. Peak spawning occurred from March through mid-April (Fig. 4). When the data were stratified by area, the highest percentage of spawning females was found in northern Florida during March and April (Fig. 4).

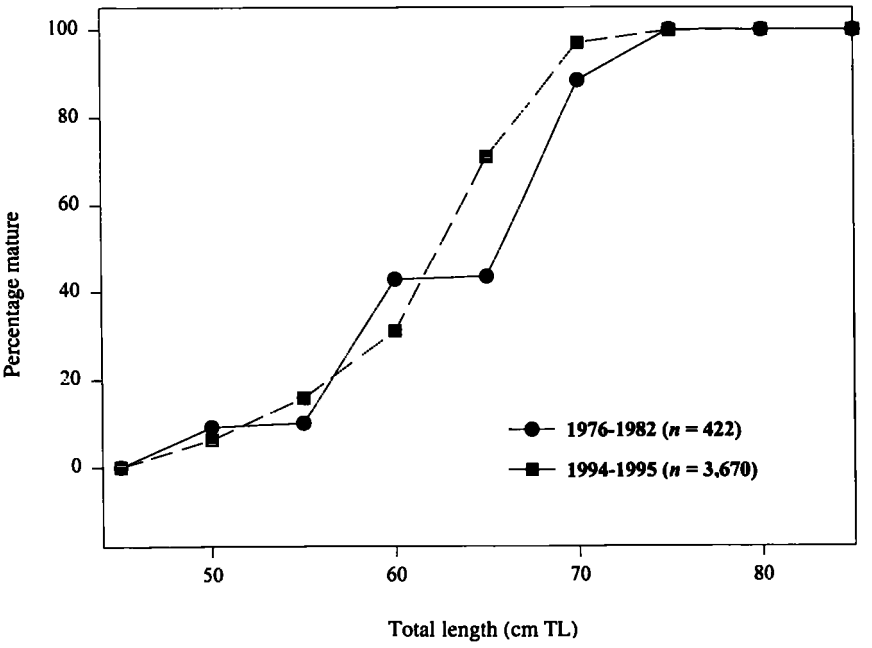


**Figure 1**

Percentage of mature specimens by size class for female gag, *Mycteroperca microlepis*, collected during 1976–82 and 1994–95. Individuals >85 cm are not included in the plot; $n$ = the total number of fish examined.

Overall, spawning of gag declined rapidly after 8 April. Individuals undergoing sexual transition were extremely rare during most of the spawning season; only one transitional specimen was documented during February and March 1994–95, out of 2147 fish examined (Table 7). There was a sharp increase in the number of transitional individuals immediately after the spawning season. The majority of transitional fish ($n$=26) were collected during mid-April through mid-June when 1473 gag gonads were examined. ANOVA and the Duncan multiple range tests indicated that there were significant differences in the mean lengths of gag sampled between months. When the number of males, females, and transitionals between 889 mm and 1050 mm was tabulated

**Table 6**

Results of probit analysis comparing the proportions of mature females in 5-cm length intervals collected during two periods: 1976–82 and 1994–95 (TL=total length).

| Parameter | Estimate | SE | P |
|---|---|---|---|
| Intercept | −12.304 | 0.871 | <0.0001** |
| Period | −0.378 | 0.176 | 0.0320* |
| cm TL | 0.192 | 0.013 | <0.0001** |

* = significant at $P$<0.05; ** = significant at $P$<0.0001.

**Table 7**

Total number sampled ($n$), mean total length (mm TL; sexes combined), standard deviation (SD), number of males (M), number of females (F), and number of transitional specimens (T) by month for mature gag captured during 1994 and 1995. Means with same letter are not significantly different ($P$>0.05).

| Month | $n$ | $\bar{x}$ TL | SD | M | F | T |
|---|---|---|---|---|---|---|
| Jan | 243 | 837.0$^{bcd}$ | 85.5 | 10 | 229 | 4 |
| Feb | 754 | 829.7$^{bcd}$ | 87.0 | 27 | 726 | 1 |
| Mar | 1142 | 859.0$^{b}$ | 99.2 | 87 | 1055 | — |
| Apr | 1027 | 844.8$^{bc}$ | 86.4 | 50 | 965 | 12 |
| May | 297 | 873.2$^{ab}$ | 110.8 | 48 | 235 | 14 |
| Jun | 48 | 928.1$^{a}$ | 110.7 | 11 | 32 | 5 |
| Jul | 77 | 925.9$^{a}$ | 124.1 | 19 | 56 | 2 |
| Aug | 2 | 717.0$^{f}$ | 106.1 | — | 2 | — |
| Sep | 33 | 774.8$^{ef}$ | 84.1 | 2 | 31 | — |
| Oct | 24 | 759.7$^{ef}$ | 83.6 | — | 24 | — |
| Nov | 77 | 818.5$^{de}$ | 86.8 | — | 76 | — |
| Dec | 89 | 788.5$^{cde}$ | 89.7 | 2 | 86 | 1 |

to reduce the potential for bias that might result from the selection of larger fishes after 18 April 1995, the Duncan multiple range test showed little difference in the mean size of gag collected each month (Table 8), and it was still apparent that transitional fish did not appear in the collections until immediately after the spawning season.

## Discussion

Analysis of reproductive data indicates that the gag population along the southeast coast of the United States is stressed. The percentage of males in the adult population has decreased from 19.6% (1976–82) to 5.5% (1994–95). However, the percentage of males currently in the population may actually be less than 5.5%; more recent data were collected during the spawning season when male gag are most vulnerable to fishing gear (Coleman et al., 1996). In contrast, data were collected throughout the year during 1976–82 rather than primarily during the spawning season. Had the 1995 emergency rule been put into place at a time of the year when gag were not spawning, it is possible that fewer males would have been captured.

The relative abundance of males and the length of the spawning period were greater off Florida than off other southeastern states. The highest percentage of males (14.9%) during 1995 was noted off northern Florida. However, the majority of males were taken by one fisherman on 2 March 1995, 17 March 1995, and 1 April 1995 indicating that this fisherman may have been targeting a relatively unfished spawning aggregation. Spawning aggregations of gag (Coleman et al., 1996) and red hind, *Epinephelus guttatus* (Shapiro et al., 1993a), contained a higher percentage of males than nonaggregation groups. Commercial fishermen indicate that after the spawning season (May and June), female gag move in groups to shallower water (~30 m) and the larger males become solitary and remain at depths of 50 to 90 m.

Probit analysis revealed that female gag may have been maturing at smaller sizes during 1994–95 than during 1976–82 which would further indicate that

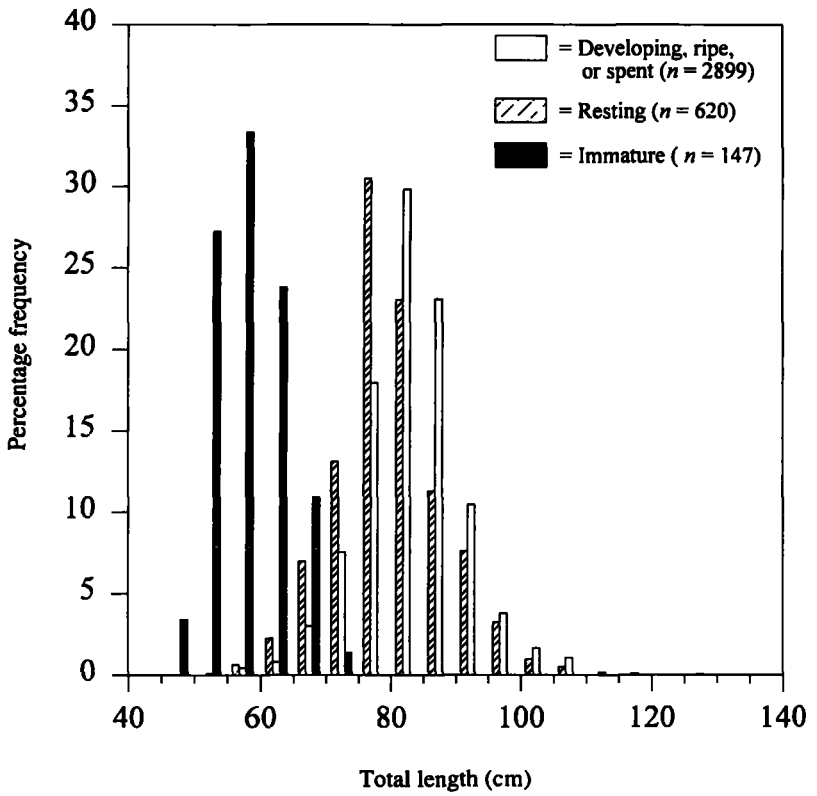


**Figure 2**

Comparison of the size frequency of immature gag, *Mycteroperca microlepis*, with the size frequencies of resting females and females with evidence of certain maturity.

**Table 8**

Total number sampled (*n*), mean total length (mm TL; sexes combined), standard deviation (SD), number of males (M), number of females (F), and number of transitional specimens (T) by month for mature gag (>889 mm and <1050 mm) captured during 1994 and 1995. Means with same letter are not significantly different ($P>0.05$).

| Month | *n* | $\bar{x}$ TL | SD | M | F | T |
|---|---|---|---|---|---|---|
| Jan | 45 | $932.4^{b}$ | 41.5 | 5 | 38 | 2 |
| Feb | 126 | $935.6^{b}$ | 42.5 | 12 | 114 | — |
| Mar | 308 | $948.3^{ab}$ | 46.4 | 51 | 257 | — |
| Apr | 219 | $939.6^{ab}$ | 43.8 | 27 | 183 | 9 |
| May | 92 | $949.8^{ab}$ | 43.4 | 24 | 54 | 14 |
| Jun | 25 | $971.0^{ab}$ | 49.7 | 7 | 13 | 5 |
| Jul | 41 | $963.1^{ab}$ | 46.7 | 10 | 30 | 1 |
| Aug | 0 | — | — | — | — | — |
| Sep | 3 | $986.7^{a}$ | 28.9 | 2 | 1 | — |
| Oct | 2 | $944.5^{ab}$ | 77.1 | — | 2 | — |
| Nov | 10 | $961.6^{ab}$ | 52.7 | 1 | 9 | — |
| Dec | 11 | $933.0^{b}$ | 47.4 | 2 | 8 | 1 |

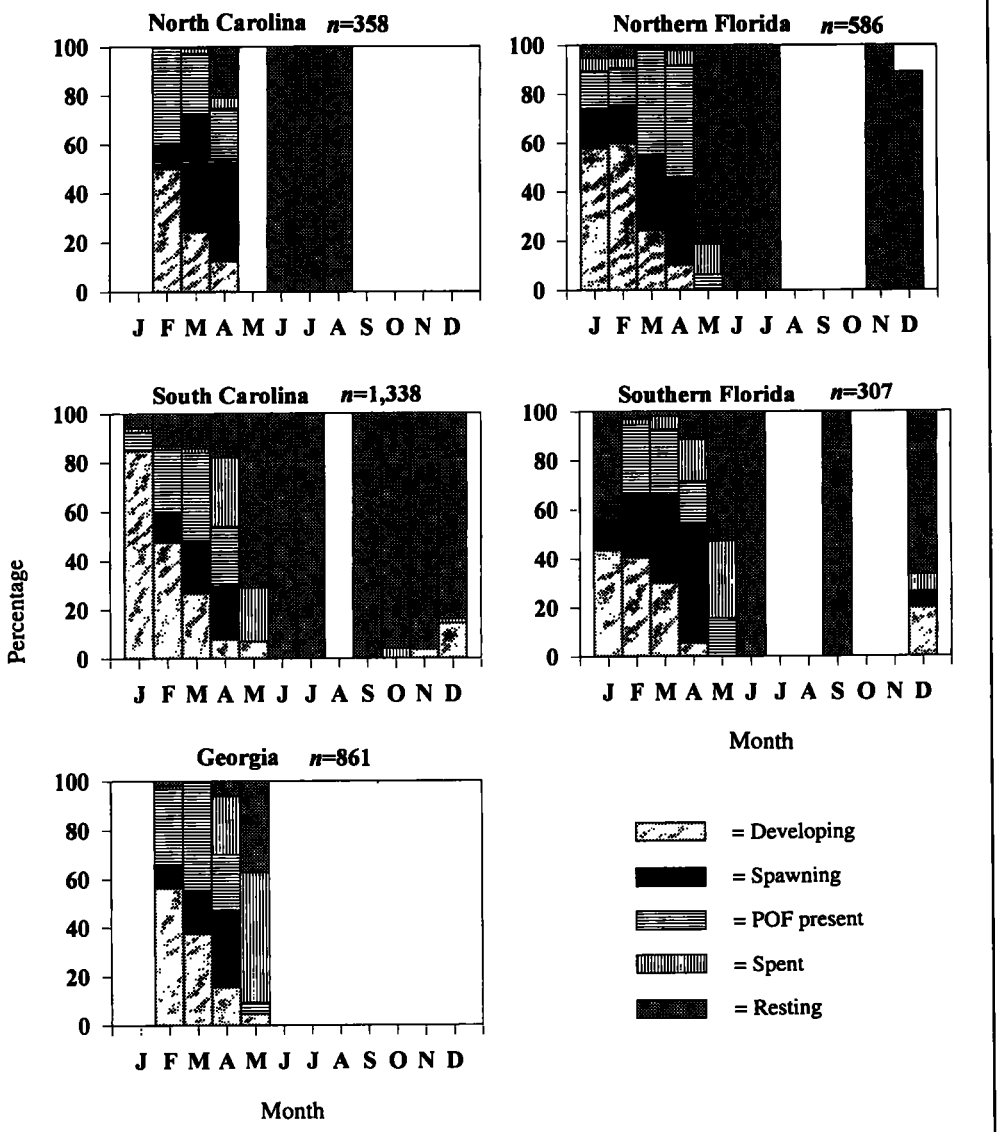


**Figure 3**

Reproductive seasonality of female gag, *Mycteroperca microlepis*, in North Carolina, South Carolina, Georgia, northern Florida, and southern Florida during 1994–95. POF = postovulatory follicles.

the gag population is stressed. Although probit analysis suggested size at maturity is decreasing, it is difficult to conclude that this is happening in the population on the basis of estimates of $L_{50}$ because there is overlap in the confidence intervals. A cautious interpretation is also warranted given the small number of females ($n$=422) sampled during 1976–82. Coleman et al. (1996) found that female gag collected in the Gulf of Mexico during 1991–93 became sexually mature and underwent transition at smaller sizes than those reported by Hood and Schlieder (1992) for the same region during 1977–80. Changes in life history aspects of gag from the Gulf of Mexico were attributed to steadily increasing fishing pressure.

Gag were in spawning condition from December through mid May in southern Florida, January through May in northern Florida, and January through April in South Carolina. Although no specimens were collected during January in North Carolina and Georgia, individuals in spawning condition were landed during February through April. Peak spawning activity occurred from March through mid-April in all areas. Collins et al. (1987) and Keener et al. (1988) also reported that peak spawning occurred

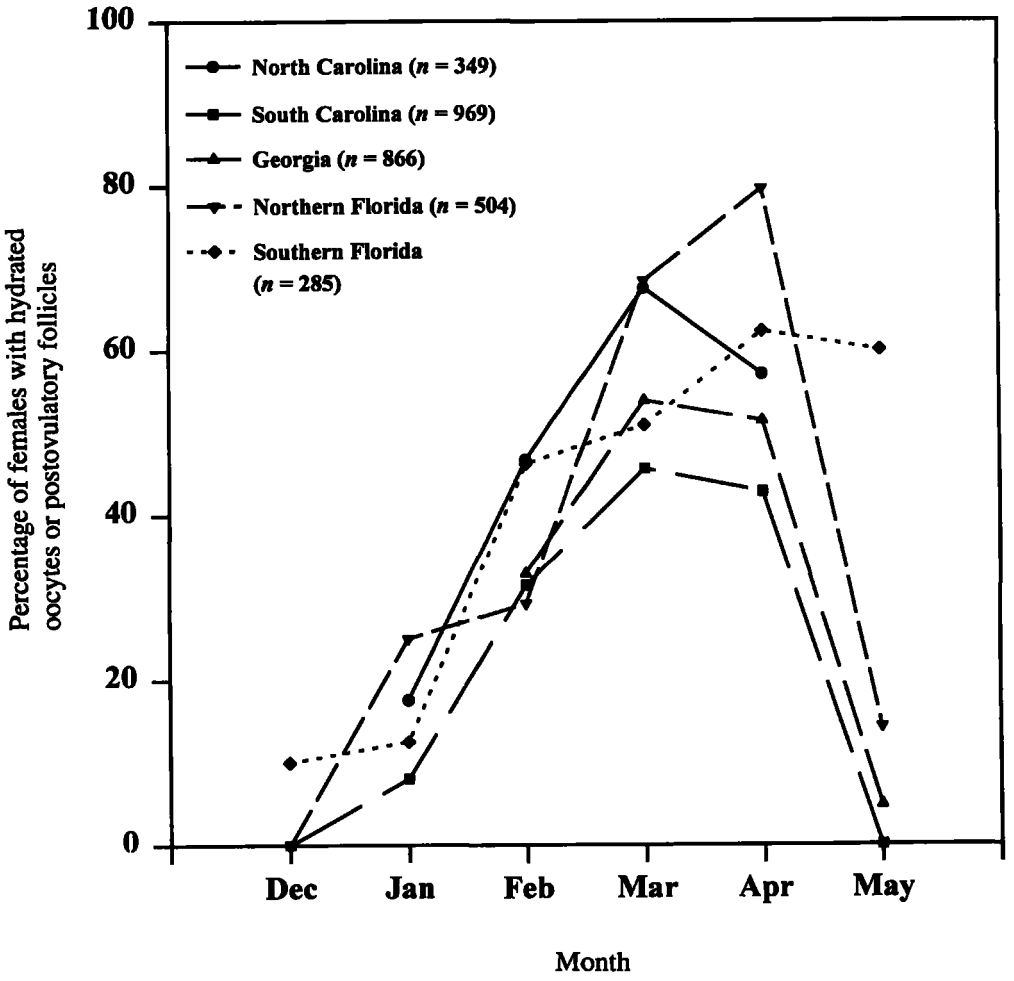


**Figure 4**

Percentage of female gag, *Mycteroperca microlepis*, in spawning condition by area during 1994–95.

in March and April along the southeast Atlantic coast. Hood and Schlieder (1992) and Coleman et al. (1996) indicated that peak spawning occurred during February and March in the Gulf of Mexico.

Despite the large number of specimens examined during 1994–95 ($n$=3879), transitional specimens ($n$=39) made up a small percentage (1.0%) of individuals collected. The low number of individuals with transitional gonads may have been due to the rapid nature of sex transition that appears to occur immediately after the spawning season. Smith (1965) and Moe (1969) suggested that other groupers may have a quick rate of sex transition. Because there was no significant monthly difference in the mean length of gag between 889 and 1050 mm TL landed during January through July, we feel that the peak in the number of transitional specimens during April and May was real and not an artifact of the emergency rule that required fishermen to land only larger fish (>889 mm TL) after 18 April. Coleman et al. (1996) stated that sex transition in gag and other grouper species may be socially mediated either through size ratio or sex ratio cues. Shapiro et al. (1993b) proposed that one function of annual spawning aggregations in red hind may be that of enabling a female to determine if it should function as a female or a male during the next spawning season. Shapiro et al. (1993b) further suggested that if this hypothesis is true, sex-changing individuals should be found soon after the aggregation has dispersed. The high percentage of males and transitionals taken during April and May in this study indicates that aggregations may remain intact for a short time after the spawning season.

Van Sant et al. (1994) and MARMAP tagging data[1] provided evidence that some gag migrate from off-

[1] 1998. Unpublished data from MARMAP tagging study. Marine Resources Research Institute, Charleston, SC.

shore areas of South Carolina and Georgia to the shelf edge off Florida, perhaps to spawn. However, the presence of hydrated oocytes and new postovulatory follicles in female gag taken from North Carolina through Florida, including specific locations off South Carolina and Georgia, shows that spawning is not restricted to Florida. Hunter et al. (1985) reported that the presence of hydrated oocytes in teleosts is an indication that individuals will spawn within 12 hours. Furthermore, Hunter et al. (1986) found that postovulatory follicles are present only in fishes that have recently spawned.

Gag off Florida are subject to intense fishing pressure by commercial fishermen, sport divers, and anglers, particularly during the late fall through early spring, because the continental shelf is very narrow and spawning aggregations are easily accessed. Therefore, even if most gag are not migrating to Florida for spawning, the vulnerability of at least part of the stock to winter fishing is of concern. This "funneling" of migratory fishes off southeastern Florida may increase fishing mortality for many species and requires further investigation.

In 1993, the SAFMC decided to take no action on a proposal to close all fishing for gag during their spawning season because insufficient data were available on sex ratios and the spatial extent of spawning along the southeast coast of the United States. The information on sex ratio and size at maturity presented here indicates that the gag population is overfished. Because there has been a reduction in the percentage of males in commercial landings and a modest decrease in the size at maturity for females, the total fishing effort should be limited, especially in the removal of males from spawning aggregations. Since gag spawn in offshore areas from North Carolina to southeast Florida, any regulation should apply to all southeastern states. However, seasonal closure to fishing may not be sufficient to protect gag from overexploitation because males will continue to be lost during the open season. Protected areas with no fishing, such as marine fishery reserves, may be a possible solution to overfishing of reef fishes along the southeast coast of the United States (PDT, 1990). Marine fishery reserves can protect population age structure, species diversity, genetic diversity, and recruitment supply to exploited areas (Bohnsack, 1993). Sedberry et al. (1996) found that marine reserves in Belize, Central America, had a higher diversity of fishes than in areas that were not protected. Top predators, such as various grouper and snapper species, were more abundant and larger in reserves. In addition, populations of herbivorous forage species were reduced to presumed natural levels in the presence of protected predators. Marine reserves in Belize appear to have a natural balance of predators and forage species in relation to fished areas. There are other species in the snapper-grouper complex that are showing signs of overfishing, in addition to gag, including red porgy (Harris and McGovern, 1997), vermilion snapper (Zhao and McGovern, 1997; Zhao et al., 1997), and black sea bass.[2] In addition, less important species in fisheries (e.g. white grunt, gray triggerfish) are increasing in abundance.[2] This trend is likely to continue unless different management regulations are imposed that will protect ecosystems and restore a natural equilibrium community.

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# Distribution and abundance of and habitat use by harbor porpoise, *Phocoena phocoena*, off the northern San Juan Islands, Washington

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**Abstract.**—Boat surveys along randomly placed line transects were conducted from June to August 1991 and June to October 1992 to determine distribution and abundance of and habitat use by harbor porpoise (*Phocoena phocoena*) off the northern San Juan Islands, Washington. There were 301 sightings (average 4.4 sightings/h) of 526 harbor porpoise during 73 random boat surveys, with group sizes of 1 to 8 individuals (mean=1.87, SE=0.06, $n$=278). An estimated 299 harbor porpoise (1.26 porpoise/km$^2$, SE=0.20) were distributed in an aggregated pattern within a 237 km$^2$ area (10% of Washington Sound), indicating that a large proportion (30%) of harbor porpoise in Washington Sound occur in the northern San Juan Islands. Harbor porpoise were distributed over a depth range from 20.1 to 235.0 m (mean= 141.6 m, SE=2.43, $n$=275) and were observed more than expected ($P$<0.05) in depths greater than 125 m and over shallow slopes (<10%) and observed less than expected ($P$<0.05) in depths less than 75 m. Porpoise occurred at sea surface temperatures of 10.1° to 16.3°C and were sighted more frequently than expected ($P$<0.05) in water temperatures of 11° to 12°C. Boat surveys along fixed location transects indicated distribution was similar between 1991 and 1992. The occurrence of harbor porpoise in deep water, at cooler sea surface temperatures, over shallow sloping seafloor, and in tidally mixed regions (owing to currents and tide rips) within our study area may, collectively, affect prey distribution and associated harbor porpoise distribution.

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Harbor porpoise (*Phocoena phocoena*) are present year-round off the coast and inland waters of Washington State. Historically, harbor porpoise have been present throughout the Strait of Juan de Fuca, Washington Sound (San Juan Island archipelago), and south in Puget Sound. Once considered the most common cetacean in southern Puget Sound (Scheffer and Slipp, 1948), harbor porpoise sightings are now rare (Everitt et al., 1980; Calambokidis et al., 1984, 1985). Although harbor porpoise have not been sighted off the central San Juan Islands in recent years (Flaherty and Stark[1]; Calambokidis et al.[2]), sightings off the northern San Juan Islands have been common (Flaherty and Stark[1]; Calambokidis et al.[2]). Reasons for the disappearance of harbor porpoise from South Puget Sound are unclear but may be due to reduced availability of prey (because of changes in environmental conditions), fishing pressure, disturbance, net entanglement, or pollution.

Many biological (e.g. prey) and physical oceanographic factors (e.g. depth, seafloor relief, tidal currents, and sea surface temperature) affect the distribution of cetaceans. Increased availability of prey in deep waters may be a factor affecting the distribution of harbor porpoise. Smith and Gaskin (1983) found a significant positive correlation between abundance of mother-and-calf pairs and bottom depth and copepod (*Calanus* spp.) density. Abundance of harbor porpoise also was positively correlated with depth and physiographic features that concentrated Atlantic herring (*Clupea harengus*) in near-surface waters (Watts and Gaskin, 1985). In Fish Harbor, New Brunswick, Canada, harbor porpoise were associated with reduced sea surface temperatures that coincided with a large influx of juvenile herring in the region (Gaskin and Watson, 1985). Tidal state affected movements of harbor porpoise in the Bay of Fundy; har-

[1] Flaherty, C., and S. Stark. 1982. Harbor porpoise (*Phocoena phocoena*) assessment in "Washington Sound." Final report for subcontract 80-ABA-3584. National Marine Mammal Laboratory, Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA, 84 p.

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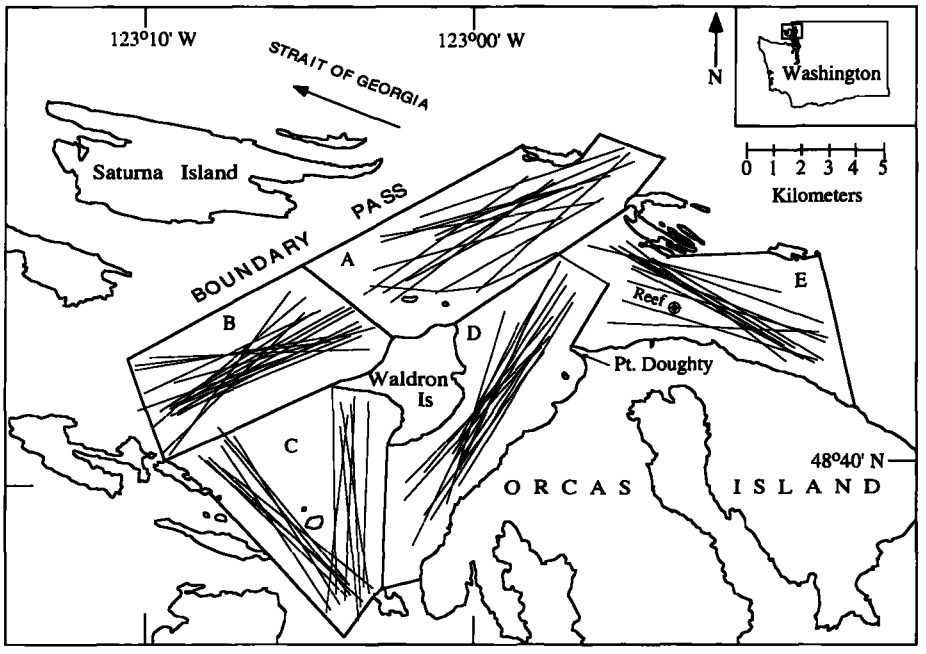


**Figure 1**

Random boat transects ($n$=73) completed from June to October 1992 within five stratified sections (A, B, C, D, E), northern San Juan Islands, Washington.

bor porpoise were observed more often during flood tide than ebb tide (Watson, 1976) and moved inshore during flood tides and offshore during ebb tides (Gaskin and Watson, 1985).

Harbor porpoise in northern Puget Sound are vulnerable to some of the same detrimental effects (disturbance, net entanglement, and pollution) that may have caused the disappearance of harbor porpoise in southern Puget Sound. It is important, therefore, to determine the abundance of harbor porpoise and identify habitat variables that may influence their distribution in northern Puget Sound. The main objectives of this study were to determine 1) the spatial and temporal distribution, density, and abundance of harbor porpoise occurring off the northern San Juan Islands and 2) the relation of harbor porpoise to depth and percentage slope of the seafloor, sea surface temperature (SST), tidal state, and time of day.

## Methods

### Study area

Washington Sound is located in the northwest corner of Washington State (48°15' to 48°50'N and 122°27' to 123°13'W), between the southern portion of Vancouver Island and the mainland, from Fidalgo Island to north of Vancouver, including the American and Canadian islands of the San Juan Archipelago (Kozloff, 1973). Mean diurnal tide heights are between 1.3 and 2.9 m (NOAA, 1991). Northern Washington Sound (northern San Juan Islands) has numerous islands and reefs with deep channels, strong currents, and tide rips. The study area off the northern San Juan Islands (Fig. 1) was selected on the basis of preliminary boat surveys conducted in 1991 to determine areas of harbor porpoise occurrence. Additionally, information was obtained from local residents and The Whale Museum, Friday Harbor, Washington.

### Random boat surveys

Randomly located boat transects ($n$=73; Fig. 1) were conducted from 27 June to 2 October 1992 within a study area composed of five strata (lettered A–E; Fig. 1) to determine harbor porpoise distribution, density, abundance, and habitat use. Eight-km transects were located within each approximately equal (42 to 50 km$^2$) stratum by using random starting points and random compass bearings. Strata were originally chosen so that transects would adequately cover the entire study area. Because placement of straight 8-km transects was constrained by the boundaries of strata and islands or reefs within strata, however, some regions of each strata were not adequately sampled. When sea conditions permitted, the five

strata, hereafter referred to as sections, were surveyed on the same day. Sections were chosen in a random starting order and every attempt was made to complete all sections before surveying the same sections again.

Harbor porpoise were surveyed from a 7.3-m aluminum marine patrol vessel during Beaufort sea state 0 (wind speed=0–1.8 km/h), 1 (wind speed=1.8–5.6 km/h), or rarely Beaufort 2 (wind speed=7.4–11 km/h). Each transect was completed in approximately 52 min, at an average boat speed of 9 km/h. Date, time, and tidal phase (flood or ebb) were recorded before each transect was surveyed. At the beginning and end of each transect, Secchi disk readings were recorded to the nearest 0.1 m and SST was recorded (by a calibrated thermometer located on the transducer of the survey vessel) to the nearest 0.1°C. During surveys, two observers divided the field of view across the forward 180° of the transect path. Observations were made from the roof of the vessel (height above the waterline=2.68 m, measured to the observers' eyes in surveying position) with unaided eyes and with Fujinon 7 × 50 reticle and compass binoculars. When an individual or group of harbor porpoise was located, an observer recorded time; group size and composition; compass bearing to the porpoise; ocular reticle marks from the horizon to the porpoise; Beaufort sea state; number of boats, birds, and marine mammals within 1 km of vessel; and direction of harbor porpoise travel. A group of harbor porpoise was defined as two or more porpoise visible at the water's surface within three body lengths (5 m) of each other, having nearly synchronous diving patterns (<15 seconds between sightings of each individual). Observers were trained and tested in the use of reticle binocompasses and in calibrating their readings on buoys and points of land and comparing distance accuracy to National Oceanic and Atmospheric Administration (NOAA) navigational charts and vessel's radar. Compasses on binoculars were also tested and were found not to be significantly affected by metal on the survey vessel. Although not common, the horizon was sometimes obscured by land in the observers' viewing area. To compensate for this, we estimated the number of reticles from the land-water interface (directly beyond the porpoise) to the porpoise sighting, then carefully rotated the binoculars from the land to the horizon. We then determined the number of reticles the horizon was beyond the land and added this amount to the reticle reading of the harbor porpoise sighting. Loran coordinates, Beaufort sea state, visibility, SST, and number of boats within 1 km of the vessel were recorded every ten minutes during surveys and for each harbor porpoise sighting. Depth and seafloor slope (at each harbor porpoise sighting) were determined from NOAA navigational charts and bathymetric charts.

Locations of harbor porpoise were determined with the aid of Fujinon 7 × 50 reticle (one reticle=17 min or 0.283°) and compass binoculars. Vertical angle was calculated as the angle between the horizon and the harbor porpoise. Distance to harbor porpoise was calculated as

$$D_r = \frac{H}{\tan(\alpha)},$$

where $D_r$ = the radial distance from the vessel to the porpoise;
$H$ = the eyeheight of observers; and
$\alpha$ = the vertical angle between the horizon and porpoise.

Locations were plotted on NOAA navigational charts by using Loran (latitude and longitude) coordinates of the vessel at the time harbor porpoise were sighted, and distance and bearing to the sighting.

Perpendicular distance from the trackline to harbor porpoise was determined by using

$$D_p = D_r \times \sin(\alpha),$$

where $D_p$ = perpendicular distance;
$D_r$ = the radial distance to the harbor porpoise; and
$\alpha$ = the angle off the trackline (the difference between the trackline heading and the bearing to porpoise).

Seafloor depth and slope were determined by using a NOAA navigational chart and bathymetric map. Percentage slope was calculated as

$$\%\,slope = \frac{dz}{ds} \times 100\%,$$

where $dz$ = the difference between the two closest depths (m) printed on the chart on either side of a harbor porpoise location (with contour lines drawn among depths); and
$ds$ = the distance (m) between those two depths.

Bathymetric charts with contour intervals of 10 m were used to verify angle of slope between depths.

To determine if harbor porpoise occurred over depths and slopes in proportion to available depths

and slopes in the study area, eight random points were plotted within a 2-km strip along the length of each 8-km transect ($n$=73 transects, 584 points) and depth and slope were determined for each point. The number of random points chosen was determined by plotting precision (standard deviation/mean) against sample size until there was little variability in this measure (i.e. a plateau and subsequent leveling of the curve).

Density and abundance estimates were calculated by using the line transect method as described by Burnham et al. (1980) and the computer program DISTANCE (Laake et al., 1993). Each transect was considered a replicate. Density and variance estimates of harbor porpoise sightings ($n$=250) were calculated by replicate for each section ($n$=12 to 15 transects) and by replicate for all sections combined ($n$=70 transects). Transects with Beaufort sea state of 2 ($n$=3) were deleted from analyses because sighting rates of harbor porpoise in Beaufort 2 are less than Beaufort 0 or 1 (Barlow, 1988). Density was calculated as

$$D = \frac{n \times f(0) \times s}{2L},$$

where $n$ = number of individual harbor porpoise sightings;
$f(0)$ = the probability density function of distances from the trackline evaluated at zero distance;
$s$ = average group size of harbor porpoise sightings, and
$L$ = total length of the trackline.

Abundance was calculated as density multiplied by area of each section (A–E) and all sections (237 km$^2$). The parameter $f(0)$ is essentially a measure of sighting efficiency and should not vary with porpoise abundance as long as sighting conditions (e.g. Beaufort sea state, visibility) remain the same. Because we surveyed only during optimal sighting conditions (Beaufort ≤1, no rain or fog) within all sections and because relatively large sample sizes are required to estimate $f(0)$ accurately, values of $f(0)$ for each section were estimated by pooling all sightings in all sections. Effective strip width is defined as $1/f(0)$, which equals one-half the transect width, such that as many objects are detected outside the strip as remain undetected within it (Buckland et al., 1993). Because group size was independent of distance from the trackline (determined through size-bias regression analysis with DISTANCE software), average group size was used to calculate density. Average group size was estimated by section and for all sightings combined.

Uniform, half-normal (hermite), hazard rate, and negative exponential models were compared with the frequency distributions of perpendicular sighting distance of harbor porpoise to trackline with DISTANCE. Several groupings and truncation points were investigated to achieve the best model fit. Buckland et al. (1993) recommend truncating 5 to 10% of objects detected at the greatest distances from the trackline. The half-normal (hermite) model, grouped into 50 m intervals and truncated at 750 m (deleting 5% of sightings), was chosen on the basis of lowest Akaike Information Criterion (AIC; Buckland et al., 1993) score for all sections combined.

The probability of detection at zero perpendicular distance, $g(0)$, was assumed to be one (all harbor porpoise on the trackline were assumed to be seen) because we were unable to estimate perception bias (bias resulting from animals available to be seen but that were not; Marsh and Sinclair, 1989). We did not have an independent observer to watch the trackline for porpoise that were missed by our two observers, therefore, a correction was not applied to $g(0)$. It is likely $g(0)$ was less than one but it is probably high (slow boat speed and excellent sighting conditions). Because $g(0)$ was constant over the survey time period, the habitat correlations are valid; however, the abundance estimate is underestimated by an unknown amount.

Seafloor depth and slope available in the study area in relation to areas of harbor porpoise occurrence were compared by using chi-square goodness-of-fit analyses. To test whether the frequency of occurrence of harbor porpoise was independent of frequency of tidal currents and surface temperature, we also used chi-square goodness-of-fit analyses. More surveys were conducted during flood tide ($n$=52) than during ebb tide ($n$=17); therefore, the number of harbor porpoise observed per minute during flood or ebb tide was used to standardize the data. A Mann-Whitney $U$, nonparametric two-sample test was conducted to examine differences in number of harbor porpoise observed per minute for each transect ($n$=73) during flood and ebb tides.

Power analyses (Cohen, 1988) were conducted on nonsignificant categories of chi-square goodness-of-fit analyses. Randomization statistics with the program Resampling Stats (Resampling Stats, 1995) were performed to assess the probability of detecting a difference between flood and ebb tides when the difference was determined to be nonsignificant. Additionally, power analyses were used to estimate the probability of detecting trends in abundance over time (Gerrodette, 1987).

Not all times of day were sampled equally; therefore, abundance of harbor porpoise in relation to time of day was compared by using number of porpoise observed per minute to standardize the data. Mean number of harbor porpoise observed per minute for each hour of daylight was compared with Kruskal-Wallis nonparametric analysis of variance and Kolmogorov-Smirnov goodness-of-fit analyses (Zar, 1984). Nonparametric statistics were used for data with non-normal distributions or unequal variances.

### Fixed boat surveys

To determine temporal changes in harbor porpoise distribution between 1991 and 1992, six 8-km transect lines (hereafter called fixed transects; Fig. 2), placed in areas of harbor porpoise occurrence (preliminary harbor porpoise surveys and information from Orca Hotline, The Whale Museum, Friday Harbor, Washington), were surveyed regularly from 27 July to 26 August 1991 and from 24 July to 28 August 1992. In 1991, there was only one observer per survey; therefore, only one half the transect (bow out to 90° port or starboard) was completed during each survey. To be consistent in 1992, one observer surveyed from bow to 90° port while the other surveyed from bow to 90° starboard so that one half of each transect could randomly be compared to 1991 transects.

Harbor porpoise were counted from the same 7.3-m vessel as in random surveys during a Beaufort sea state of 0 or 1. Each fixed transect survey was conducted at an average speed of 11 km/h and completed in 40 to 45 minutes. This vessel speed was chosen in 1991, and to be consistent, 1992 fixed transect surveys were conducted at the same speed (instead of 9 km/h as in random boat surveys). Harbor porpoise locations were calculated as in random boat survey methods.

Mean number of sightings of harbor porpoise per survey between 1991 and 1992 was compared by using a $t$-test. Because both sides of the vessel were observed during a single survey in 1992, each side could not be considered an independent sample. Therefore, one side of the vessel was randomly chosen from each survey in 1992 to compare with 1991. Power tests (Cohen, 1988) were performed when results were not significant.

## Results

### Random boat surveys

There were 301 sightings of 526 harbor porpoise (Fig. 3) during random boat surveys. Of these, 20 sightings (39 porpoise) were possible resightings (i.e. observer believed the porpoise had already been seen during that survey, given the location and direction of travel of porpoise), therefore, these possible resightings were not used in analyses. An average of 4.4 harbor porpoise sightings were recorded per hour (8.1 harbor porpoise per hour), with group sizes of 1 to 8 (mean=1.87, SE=0.06, $n$=278) individuals. Thirteen cow and calf pairs were observed between June and September. Harbor porpoise were sighted during 75% of surveys at a mean perpendicular distance of 237 m (SE=13.89, $n$=250, range: 0 to 1060 m) from the trackline. The half-normal (hermite) model, truncated at 750 m, best fitted the frequency distribution of perpendicular distance of harbor porpoise sighted from the trackline (Fig. 4). Using harbor porpoise sightings ($n$=250) for all sec-

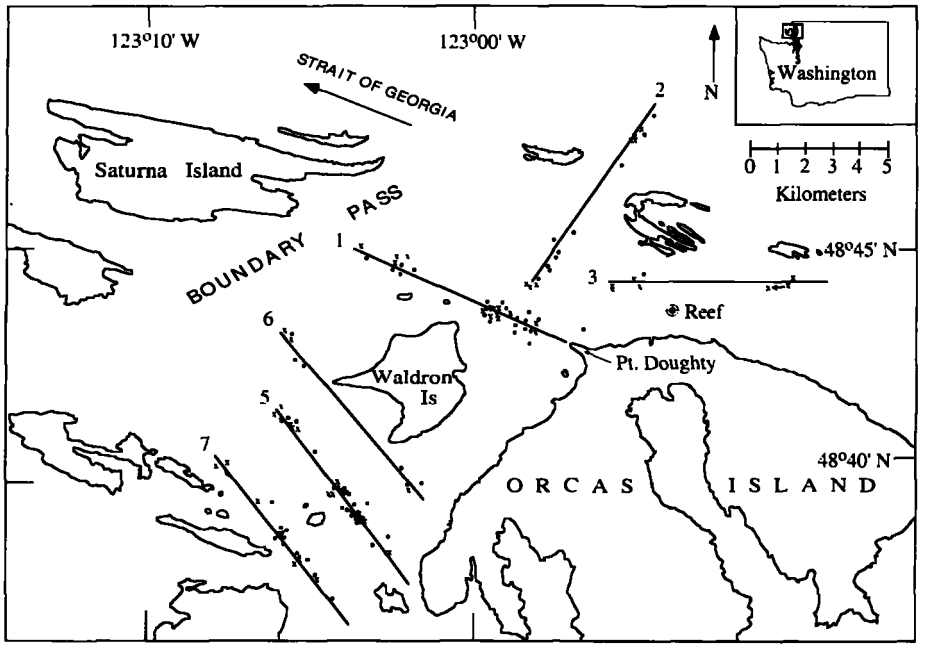


**Figure 2**

Harbor porpoise locations along fixed boat transects (1, 2, 3, 5, 6, 7) in 1991 and 1992 off the northern San Juan Islands, Washington. The "x" denotes locations of harbor porpoise sighted in 1991; the "•" denotes locations in 1992.

tions combined, we estimated that the effective half-strip width (ESW) was 337 m (95% CI=307–371 m; coefficient of variation, CV=0.048), with an $f(0)$ of 2.96/km (SE=0.14, CI=2.70–3.25, CV=0.048).

No significant correlation ($r$=0.097, $n$=250, $P$=0.938) was detected between harbor porpoise group size and perpendicular distance from the trackline. For surveys conducted during Beaufort ≤1 ($n$=70) in all sections (A–E), the mean group size was 1.91 harbor porpoise (SE=0.07, $n$=250; Table 1) and mean density was 1.26 harbor porpoise/km$^2$ (SE=0.20; Table 1). Harbor porpoise densities were least in section A (0.60 porpoise/km$^2$, SE=0.21) and greatest in section D (2.3 porpoise/km$^2$, SE=0.74; Table 1). There were an estimated 299 harbor porpoise (CI=219–409) in all sections (Table 1), ranging from 30 harbor porpoise (CI= 5–60) in section A to 116 harbor porpoise (CI=62–221) in section D (Table 1). The pooled estimate of harbor porpoise abundance (299 porpoise) for all sections yielded the same abundance estimate as adding the estimates for each individual strata (A–E; Table 1).

If the present surveys were conducted annually with a similar sampling regime that produced an equally low CV (0.159), there would be sufficient power (80%) to detect a 14% annual change ($\alpha$=0.05; 12% change for $\alpha$=0.10) after five years.

Mean number of harbor porpoise per survey was greatest in section D and least in section E (Fig. 5A). Mean depth throughout the study area was 108.1 m (SE=21.68, $n$=584); section D had the greatest mean depth and section E the least (Fig. 5B). Harbor porpoise were distributed over a depth range of 20.1 to 235.0 m (mean=141.6 m, SE=2.43, $n$=275), with 83% of harbor porpoise sightings occurring over depths greater than 100 m. Significantly ($P$<0.05) fewer than expected harbor porpoise occurred in depths less than 75 m and significantly ($P$<0.05) more than expected in depth categories greater than 100 m (Fig. 6). The effect size (degree to which depths differed among categories) was small and the power to detect a difference was

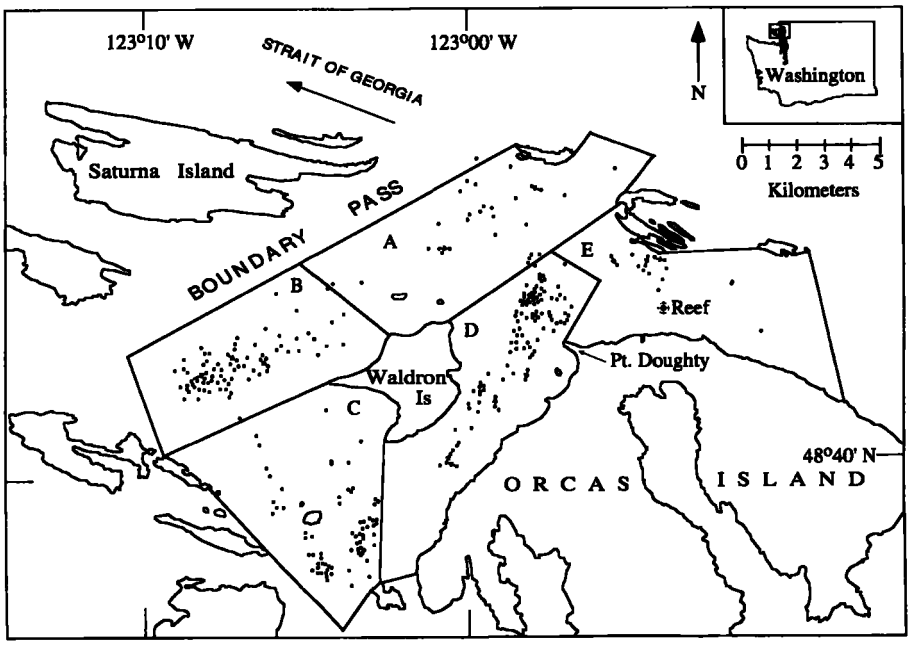


**Figure 3**

Location of 301 harbor porpoise sightings made during 73 random boat surveys completed from June to October 1992 within five stratified sections (A, B, C, D, E).

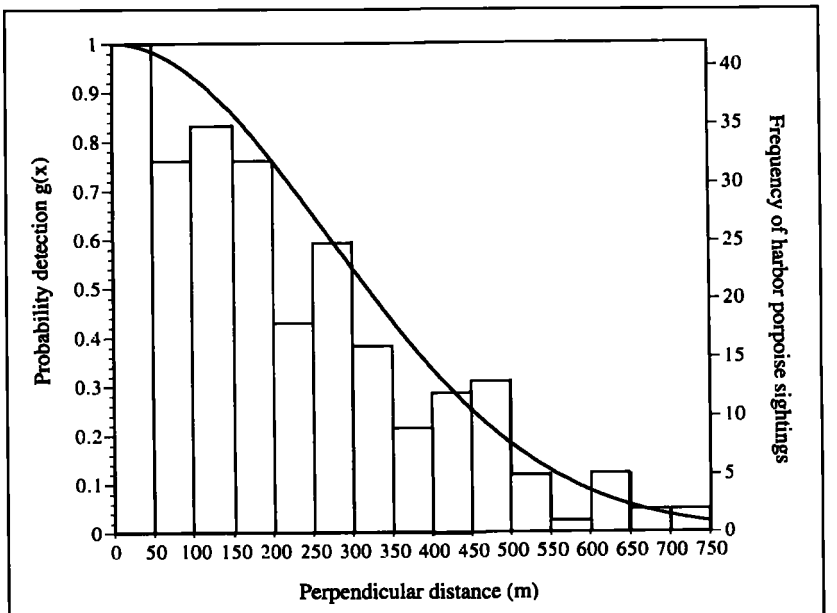


**Figure 4**

Probability detection distribution for perpendicular sighting distances of harbor porpoise. Bars represent frequency of sightings and the line represents the half-normal (hermite) model of best fit.

**Table 1**

Survey effort, line transect model parameters, density, and abundance estimates of harbor porpoise for each section (A–E) and all sections combined surveyed within the northern San Juan Islands, Washington, from June to October 1992.

| Parameter | Section A | Section B | Section C | Section D | Section E | All sections |
|---|---|---|---|---|---|---|
| Area ($km^2$) | 50.26 | 43.12 | 50.40 | 50.47 | 42.43 | 237 |
| Effort (km) | 112 | 120 | 120 | 112 | 96 | 560 |
| Transect lines | 14 | 15 | 15 | 14 | 12 | 70 |
| Truncation width (m) | 750 | 750 | 750 | 750 | 750 | 750 |
| Probability density $f(0)$/km | 2.96 | 2.96 | 2.96 | 2.96 | 2.96 | 2.96 |
| Sightings of harbor porpoise | 26 | 62 | 67 | 80 | 15 | 250 |
| Mean group size | 2.19 | 1.94 | 1.81 | 1.90 | 1.80 | 1.91 |
| Standard error (SE) of group size | 0.32 | 0.15 | 0.11 | 0.11 | 0.26 | 0.07 |
| Density (porpoise/$km^2$) | 0.60 | 1.03 | 1.55 | 2.33 | 0.76 | 1.26 |
| 95% confidence intervals (porpoise/$km^2$) | 0.30–1.21 | 0.60–1.75 | 0.77–3.10 | 1.24–4.4 | 0.35–1.66 | 0.92–1.73 |
| SE of density | 0.21 | 0.27 | 0.52 | 0.74 | 0.30 | 0.20 |
| % coefficient of variation (CV) of density | 35.09 | 26.00 | 33.86 | 31.55 | 39.16 | 15.86 |
| Abundance | 30 | 44 | 77 | 116 | 32 | 299 |
| 95% confidence interval (abundance) | 15–60 | 26–75 | 39–155 | 62–221 | 15–70 | 217–406 |
| SE of abundance | 10.53 | 11.43 | 26.07 | 36.91 | 12.53 | 47.0 |

low (37%) for categories that were not significantly different (Fig. 6). Given the small effect size, a power of 80% would require 358 locations of harbor porpoise in these three depth categories (there were 122 in this study). It is, therefore, unlikely that harbor porpoise occur in depths within these nonsignificant categories in different proportions than those available.

Mean seafloor slope for all sections combined was 9.85% (SE=0.656, $n$=584). Section B had the least slope and section C the greatest (Fig. 7). Harbor porpoise were sighted over a mean slope of 6.90% (SE=0.51, $n$=275, range: 0.37% to 45.75%). The greatest number of harbor porpoise sightings (79%) occurred over shallow slopes (<10%). There were significantly ($P$<0.05) greater numbers of harbor porpoise sightings than expected in category 0 to 2% slope, and significantly ($P$<0.05) fewer numbers of harbor porpoise than expected in categories 6 to 8%, 18 to 20%, and >26% slope (Fig. 8). The power to detect a difference was fairly high (69%) for categories that were not significantly different (Fig. 8). To increase power to 80%, we would need 151 samples within these ten categories (we had 126 samples).

Mean sea surface temperature (SST) recorded during all transects was 12.6°C (SE=0.081, $n$=427, range: 10.1° to 17.5°C). Little variability was found among the five sections. Section E had the greatest mean SST (mean=13.5°C, SE=0.22, $n$=69) and section B the least (mean=12.3°C, SE=0.14, $n$=97). Mean SST recorded during harbor porpoise sightings was 12.1°C (SE=0.09, $n$=267, range: 10.1° to 16.3°C). Harbor porpoise were sighted more frequently than expected ($P$<0.05) in water temperatures of 11° to 12°C and less frequently than expected ($P$<0.05) in water temperatures >16° C (Fig. 9). The power to detect a difference was moderate (50%) for categories that were not significantly different (Fig. 9). To increase power to 80%, we would need 180 samples within these ten categories (we had 171 samples).

There was no significant difference between number of harbor porpoise observed per minute during flood and ebb tides ($U$=315.5, $n$=69, $P$=0.076, $\alpha$=0.05). Bootstrap estimates (resampling statistics; 10,000 iterations) indicated an 86% chance of correctly rejecting the null hypothesis that mean number of sightings was equal between flood and ebb tides. Fifty samples in each tide stage (we sampled 52 in flood and 17 in ebb tide) were required to reject the null hypothesis at $\alpha$ = 0.05.

Mean Secchi reading for all harbor porpoise sightings was 9.3 m (SE=0.09, $n$=275, range: 5.7 to 11.9 m).

Greatest numbers of harbor porpoise were observed in mid-morning (1000 h) and afternoon (1400 to 1500 h) throughout the study area (Fig. 10). Fewer harbor porpoise were observed at midday (1100 to 1300 h; Fig. 10), although there was no significant difference ($H$=10.99, $n$=274, $P$=0.276) among mean number of harbor porpoise observed per minute and each hour of daylight surveyed (0900 to 1800 h).

Density estimates were calculated over all four months of the survey period rather than by month, which would have yielded too low of a sample size. If abundance estimates of porpoise had varied greatly among months during our survey period, we should have observed a higher CV (ours was relatively low: 0.159).

### Fixed boat surveys

Fifty-six sightings of 92 harbor porpoise were recorded during 33 surveys (port or starboard) in 1991, and 69 sightings of 118 harbor porpoise during 24 surveys (both sides of vessel surveyed) in 1992 (Fig. 2). Harbor porpoise were sighted during 79% of surveys in 1991 and 75% in 1992. Mean group size was 1.6 harbor porpoise (SE=0.09, $n$=56) in 1991 and 1.7 harbor porpoise (SE=0.127, $n$=69) in 1992. Distribution of harbor porpoise was patchy but similar between 1991 and 1992 (Fig. 2).

The greatest number of harbor porpoise sightings recorded per survey were along transects 1, 2, and 5 in 1991 and transects 1 and 5 in 1992 (Table 2; Fig. 2). The least number of sightings were recorded for transects 3 and 6 in 1991 and 1992 (Table 2; Fig. 2). Mean number of harbor porpoise sightings per survey was not significantly different ($P$>0.05) between 1991 and 1992 for any of the fixed transects (Table 2). Sample sizes for all transects were low because of the limited survey period (July to August). Given our low sample size (Cohen, 1988, requires a sample size of eight or more), we were unable to determine power. If eight samples of each fixed transect line had been taken, power to detect a difference in density between 1991 and 1992 would still have been low (power<27% for all fixed transects except transect three which had<6% power).

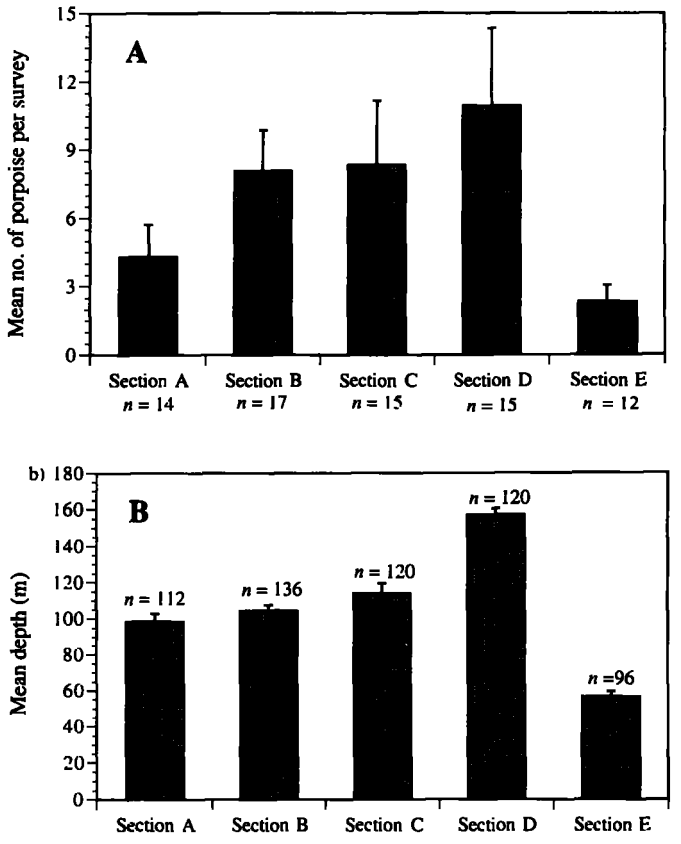


**Figure 5**

Mean number of harbor porpoise (**A**) and mean water depth (**B**) of each section (A–E) determined during random boat surveys (June–October 1992). Vertical lines represent standard error and "$n$" represents number of transects completed in each section (A; total=73) and random depth locations plotted within each section (B); total=584).

## Discussion

Population and density estimates of harbor porpoise were based on several assumptions of line transect theory. Relevant assumptions included the following: 1) study area was sampled randomly (transect lines placed randomly with respect to the distribution of objects) or animals were randomly distributed; 2) all animals on the trackline were detected; 3) group size was estimated without error; 4) locations were measured accurately for each individual or group; and 5) animals did not move in response to the survey vessel or were detected before they moved (Burnham et al., 1980).

The first assumption of line transect theory was met by employing a stratified random sampling design within the study area. This design was chosen so that the 8-km transects would adequately cover the entire study area. By using fixed length straight transects, however, certain areas of sections B and C were not adequately sampled. The habitat features of these areas were similar to the rest of the study area, and portions of section C not sampled during random surveys were sampled during fixed transect surveys 5 and 6. A study design that incorporated shorter transects (4 km) would allow more complete coverage of all areas within strata. If this study were replicated, we recommend incorporating 4-km transects to cover the areas that we missed. We do not believe, however, that our study design affected the results of the habitat correlates. By randomly surveying within a defined region off the northern San Juan Islands, we adequately sampled oceanographic features of interest (depth, seafloor slope, surface temperature, tides).

The assumption that all animals are detected on the trackline is often violated during marine mammal surveys. Animals with long durations of submer-

gence have a high probability of remaining undetected during the passage of an aircraft or vessel, resulting in availability bias (Marsh and Sinclair, 1989). Several studies (e.g. Marsh and Sinclair, 1989) of harbor porpoise have indicated, on the basis of perception bias, that the probability of detecting a harbor porpoise on the trackline, $g(0)$, is less than one (Barlow, 1988; Palka, 1993; Calambokidis[3]). Using an independent team of three observers, Barlow (1988) reported an estimated 22% of harbor porpoise that surfaced on the trackline were missed by a team of five observers (perception bias) traveling on a vessel at 18.5 km/h. Using three observers per survey, Calambokidis[3] and Palka (1993) estimated the probability of observing a group of harbor porpoise on the trackline, $g(0)$, was less than 0.5. We assumed $g(0)$ was one during our study because we were unable to determine availability or perception bias. It is probable that some porpoise did avoid the vessel and might have been submerged for up to five minutes (Raum-Suryan, 1995). It is, therefore, likely that $g(0)$ is less than one and harbor porpoise abundance is underestimated.

The ability to estimate group size can vary by the number of animals within the group and by the species of interest. Data from land-based calibration studies off the Washington coast indicated that observers on ves-

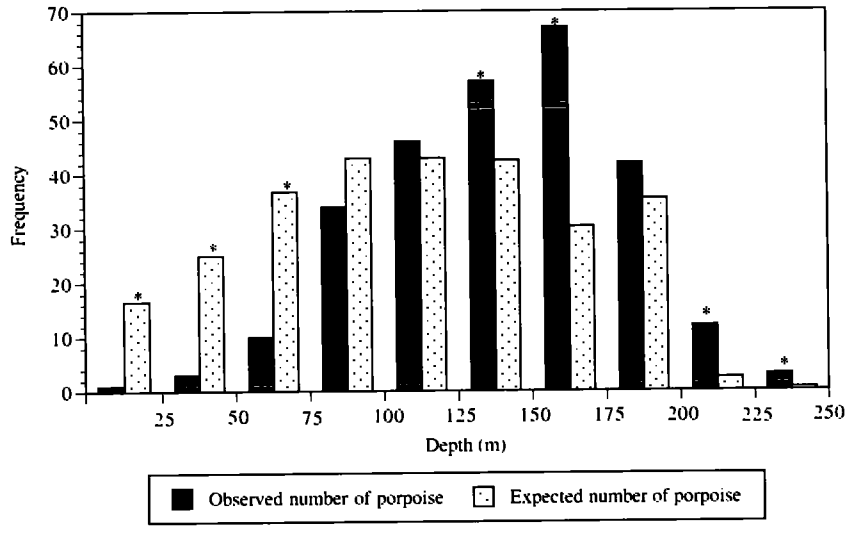


**Figure 6**

Depth distribution of 275 harbor porpoise sightings determined from random boat surveys (June to October 1992) in relation to expected distribution of harbor porpoise if they were distributed randomly with depth (as determined from depths at 584 random locations). An asterisk (*) designates a significant ($P<0.05$) difference determined with chi-square goodness-of-fit analyses.

[3] Calambokidis, J. 1991. Vessel surveys for harbor porpoise off the Washington coast. *In* H. Kajimura (ed.). Harbor porpoise interactions with Makah Salmon set net fishery in coastal Washington waters, 1988–89. National Marine Mammal Laboratory Processed Report, National Marine Mammal Laboratory, Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA 98115.

**Table 2**

Mean, standard error (SE), number of sightings, and number of harbor porpoise determined during fixed boat surveys in 1991 and 1992. In 1992, the number of harbor porpoise observed (Obs.) are presented, as are values from four randomly chosen surveys used in analysis (Anal.), comparing mean number of harbor porpoise sighted along each transect in 1991 and 1992). *n* refers to the number of transect "sides" (bow out to 90° on port or starboard) surveyed.

| | 1991 | | | | | 1992 | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | Mean | | SE | | *n* | | No. of sightings | | No. of porpoise | | |
| Transect no. | Mean | SE | *n* | No. of sightings | No. of porpoise | Obs. | Anal. | Obs. | Anal. | Obs. | Anal. | Obs. | Anal. | Obs. | Anal. | Probability |
| 1 | 2.20 | 0.80 | 5 | 11 | 18 | 2.50 | 2.00 | 0.42 | 0.41 | 8 | 4 | 20 | 8 | 31 | 13 | $P = 0.843$ |
| 2 | 1.83 | 0.48 | 6 | 11 | 16 | 1.25 | 1.25 | 0.45 | 0.63 | 8 | 4 | 10 | 5 | 22 | 17 | $P = 0.474$ |
| 3 | 1.00 | 0.38 | 7 | 7 | 13 | 0.13 | 0.25 | 0.13 | 0.25 | 8 | 4 | 1 | 1 | 1 | 1 | $P = 0.200$ |
| 5 | 2.83 | 0.54 | 6 | 17 | 29 | 2.25 | 3.00 | 0.49 | 0.58 | 8 | 4 | 18 | 12 | 25 | 18 | $P = 0.844$ |
| 6 | 0.60 | 0.40 | 5 | 3 | 6 | 0.88 | 0.50 | 0.40 | 0.29 | 8 | 4 | 7 | 2 | 12 | 3 | $P = 0.853$ |
| 7 | 1.75 | 0.63 | 4 | 7 | 10 | 1.50 | 1.00 | 0.82 | 0.41 | 8 | 4 | 12 | 9 | 26 | 19 | $P = 0.356$ |

sels underestimated true group size of harbor porpoise, missing up to 60% or more of animals (Calambokidis et al.[4]). However, these results were based on a very small sample size and the survey vessel traveled at twice the speed of our vessel. In our study, mean group size (1.91 porpoise) was only 5% different from that detected from concurrent shore-based surveys (2.01 porpoise; Raum-Suryan, 1995). We are, therefore, confident that any biases in group size estimates are small.

Accurately measuring the locations of marine mammals from vessels can be affected by the height of observers above water (Polacheck and Smith, 1989) and the use of reticle and compass binoculars (Smith, 1982; Barlow and Lee, 1994). From a low height above the water, angles are greatly affected by small deviations in reticle estimates. As radial distances to harbor porpoise decrease, however, errors in reticle estimates (sighting angles) have progressively less effect on distance calculations. The majority (78%) of our radial and perpendicular sighting distances were less than 350 m. At 350 m an error of ±0.1 reticle was equal to 50 m (the range of our data groupings which best fitted the model). Therefore, although the platform height of our survey vessel was low (2.68 m), we were able to obtain accurate sighting data by conducting surveys only during optimal sighting conditions (Beaufort ≤1), and because there was both a lack of ocean swell and the majority of sightings were less than 350 m distant.

Harbor porpoise are small, inconspicuous animals that avoid boats (Amudin and Amudin, 1974; Gaskin, 1977; Prescott and Fiorelli, 1980; Barlow, 1988). Detection of harbor porpoise before they become aware of the survey vessel is often difficult without prior knowledge of their locations. Polacheck and Thorpe (1990) observed harbor porpoise swimming away from their survey vessel a significant

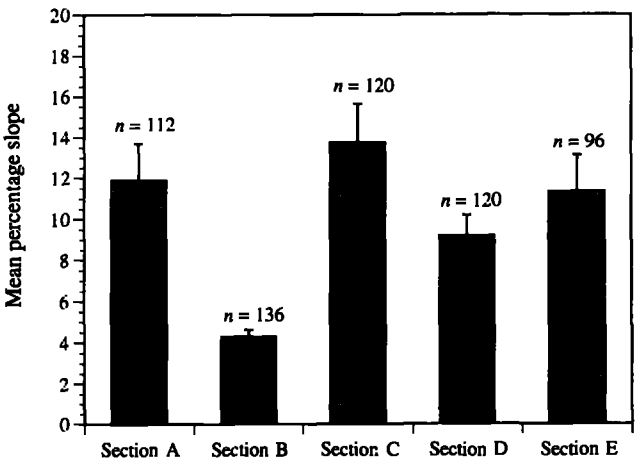


**Figure 7**

Mean percentage slope of seafloor for each section (A– E) determined from random boat surveys. Vertical lines represent standard error and "*n*" represents the number of random slope locations plotted within each section (total=584).

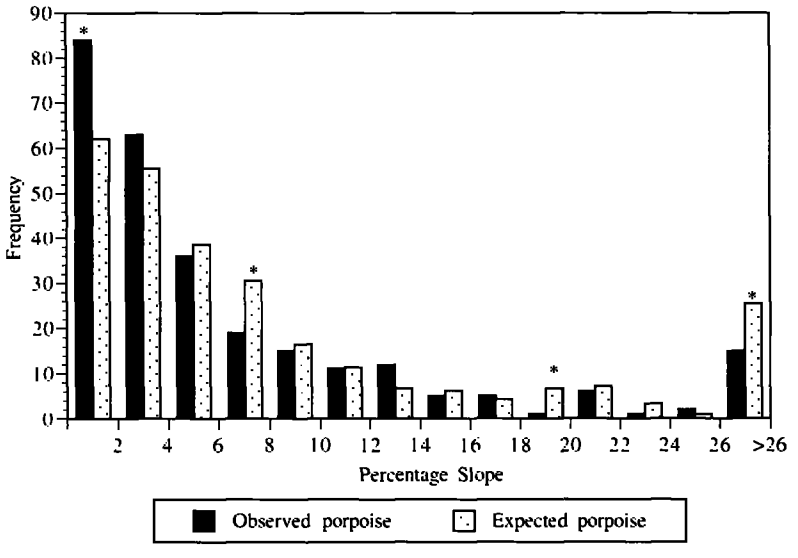


**Figure 8**

Harbor porpoise sightings (*n*=275) from random boat surveys (June–October 1992) in relation to expected distribution if porpoise were distributed randomly with slope (as determined from slopes at 584 random locations). An asterisk (*) designates a significant ($P<0.05$) difference, determined with chi-square goodness-of-fit analyses.

[4] Calambokidis, J., S. R. Melin, and D. J. Rugh. 1991. Land-based calibrations of harbor porpoise sightings from a vessel along the northern Washington coast. *In* H. Kajimura (ed.), Harbor porpoise interactions with Makah Salmon set net fishery in coastal Washington waters, 1988–89. National Marine Mammal Laboratory Processed Report. National Marine Mammal Laboratory, Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA 98115-0070.

proportion of time. Barlow (1988) reported that harbor porpoise quickly avoid a closely approaching survey vessel. Vessel avoidance by harbor porpoise may result in animals remaining undetected by observers or may affect estimates of perpendicular distance of harbor porpoise from the vessel. If the frequency of harbor porpoise sightings were greatest near the trackline and decreased with increasing perpendicular distance during this study, it appeared that most harbor porpoise were detected before potentially significant vessel avoidance occurred. If porpoise did avoid the vessel, our abundance estimates would be underestimated. Ship avoidance was likely constant throughout the survey period, however, and would not have affected results of habitat correlates.

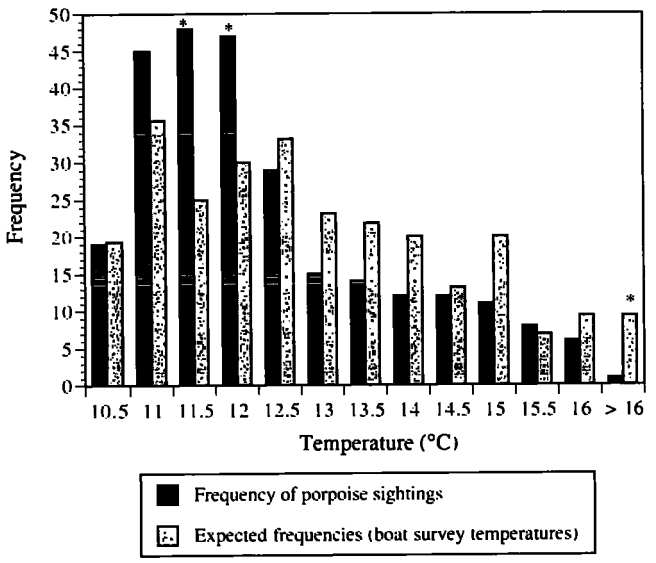


**Figure 9**

Sea surface temperatures (°C) recorded at harbor porpoise sightings ($n$=267) in relation to expected distribution of harbor porpoise if they were distributed randomly with temperature (as determined from temperatures at 427 locations along 73 random transect lines). An asterisk (*) designates a significant ($P$<0.05) difference, determined using chi-square goodness-of-fit analyses.

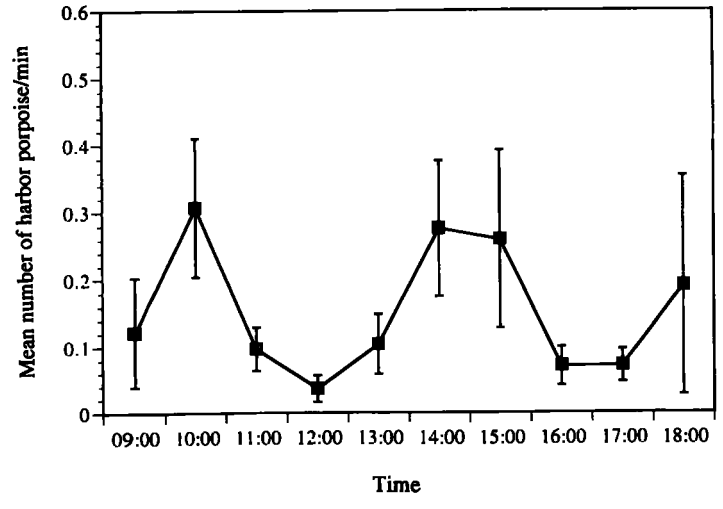


**Figure 10**

Mean number of harbor porpoise observed per minute during random boat surveys (June to October 1992) for all sections (A–E) combined. Vertical lines represent standard error.

Density estimates of harbor porpoise (1.26 porpoise/km$^2$) within the study area (237 km$^2$) were greater than densities reported by Calambokidis et al.[2] (0.42 porpoise/km$^2$) for waters off the San Juan Islands and part of the Strait of Georgia (2291 km$^2$) but were similar to density estimates of Flaherty and Stark[1] (0.85 to 1.63 porpoise/km$^2$) for the north and west San Juan Islands (1005 km$^2$). Density estimates reported by Calambokidis et al.[2] were based on an initial $g(0)$ equal to 0.324 (CV= 0.171) multiplied by a correction factor of 3.1 and yielding a $g(0)$ of one. Green et al.[5] surveyed an extensive area within the 100-m isobath off the coast of Oregon and Washington and also reported a much lower density of harbor porpoise (0.17 porpoise/km$^2$) than reported here. These differences probably result from Green et al.[5] and Calambokidis et al.[2] including regions of high and low harbor porpoise abundance in contrast to our focus on high density areas off the northern San Juan Islands.

Prey or habitat requirements often limit distribution of cetaceans to regions that may vary daily, seasonally, or yearly, depending on an individual's foraging, mating, or behavioral requirements. During this study, surveys were conducted only within the summer months (June to October) and thus may account for the relatively high density estimates of harbor porpoise within our study area. Flaherty and Stark[1] sighted harbor porpoise during all months of the year off the San Juan

[5] Green, G. A., J. J. Brueggeman, C. E. Bowlby, R. A. Grotefendt, M. L. Bonnell, and K. T. Balcomb III. 1992. Cetacean distribution and abundance off Oregon and Washington, 1989–1990. *In* J. J. Brueggeman (ed.), Final report prepared by Ebasco Environmental and Ecological Consulting, Inc. for Minerals Management Service, Pacific OCS Region. Offshore Continental Shelf (OCS) Study MMS 91-0093, 100 p.

Islands but observed more harbor porpoise in summer months (June to August) than other times of the year. Surveys of harbor porpoise throughout the year along the east and west coasts of the United States have indicated a seasonal pattern among various regions (Neave and Wright, 1968; Gaskin and Watson, 1985; Barlow, 1988; Green et al.[5]). Results of fixed transect surveys conducted in our study indicated no change in distributions of harbor porpoise between July and August 1991 and 1992. Clumped distribution of harbor porpoise along tracklines was likely associated with habitat features (harbor porpoise were sighted most often over deep water).

Among island regions, such as the Bay of Fundy, Glacier Bay, Alaska (Taylor and Dawson, 1984), and off the San Juan Islands, harbor porpoise are more often associated with deeper waters than along coastal regions of North America. Most harbor porpoise observed off the coast of California, Oregon, and Washington occurred at shallow water depths, and sightings decreased with increasing depth (Barlow, 1988; Dorfman, 1990; Calambokidis[3]; LaBarr and Ainley[6]). Incidental net entanglement of harbor porpoise within Washington waters occurred at the bottom of nets, at depths of 73 to 81 m (Scheffer and Slipp, 1948), and near the bottom or in the lower one-half of nets set from 11 to 18 m deep, indicating porpoise were foraging along the bottom or in deeper areas of the net (Gearin et al.[7]). The depth of water where harbor porpoise were sighted in this study may have been due to occurrence of prey within these areas.

The Pacific herring (*Clupea pallasi*) population in the Strait of Georgia is the largest known in Washington state, and herring are quite abundant in sections of the eastern Strait during summer, fall, and winter (Lemberg, 1978). During this study, harbor porpoise, harbor seals, and a minke whale were observed feeding on a school of Pacific herring. The dominant prey items in stomachs of harbor porpoise taken in a setnet fishery in summer off northern Washington were Pacific herring, market squid (*Loligo opalescens*), gadids, and osmerids (Gearin and Johnson[8]). Pacific herring and market squid migrate vertically within the water column, remaining close to the seafloor during the day, and approach the surface at night (Hart, 1973; Blaxter, 1985; Flaherty and Stark[1]). Characteristics of these prey items and the greater occurrence of porpoise over deep waters may indicate that harbor porpoise feed in deep water during the day. Aggregations of surface schooling fish and associated harbor porpoise were rarely (1% of surveys) observed within our study area, further indicating that harbor porpoise were likely feeding on prey in deep water.

In our study, harbor porpoise were sighted most often in shallow sloping areas with little bathymetric relief. These results contrast with those of Flaherty and Stark,[1] in which 70% of harbor porpoise sighted were found in areas with seafloor relief greater than 40%, and with those of Calambokidis,[3] who observed significantly more harbor porpoise than expected within areas of uneven bottom topography off the outer Washington coast. It is likely that slope of the seafloor does not significantly affect the distribution of harbor porpoise or their prey in our study area. We believe that harbor porpoise and their prey are associated with deeper waters in this region which, in general, has shallow slopes.

Water temperature may influence the distribution of harbor porpoise. Calambokidis[3] reported harbor porpoise sightings in water temperatures ranging from 9° to 16°C off Washington. In the Bay of Fundy, Watts and Gaskin (1985) found a negative correlation between harbor porpoise abundance and mean August SST, and Watson (1981) reported that harbor porpoise occurred in water temperatures less than 15°C in the Bay of Fundy. It is unlikely, however, that SST alone would influence harbor porpoise distribution. Most harbor porpoise entered Fish Harbor, New Brunswick, Canada, when SST was between 9° and 10°C, a period when large numbers of juvenile herring were also entering the region (Gaskin and Watson, 1985). Within the Bay of Fundy, Watts and Gaskin (1985) found herring associated with vertically mixed waters and reduced surface temperatures. This association was possibly due to increased concentrations of zooplankton, which also occurred along convergent zones (Watts and Gaskin 1985). Sea surface temperatures off the northern San Juan Islands, therefore, were possibly related to tidal currents that may be associated with concentrations of harbor porpoise prey.

[6] LaBarr, M. S., and D. G. Ainley. 1985. Depth distribution of harbor porpoise off central California: a report of cruises in April and May–June 1985. NMFS Contract No. 41 USC 252, 23 p.

[7] Gearin, P. J., M. A. Johnson, and S. Joner. 1991. Harbor porpoise interactions with the Makah Chinook Salmon Set-Net Fishery, 1988–89. *In* H. Kajimura (ed.), Harbor porpoise interactions with Makah salmon set net fishery in coastal Washington waters, 1988–89. National Marine Mammal Laboratory Processed Report. National Marine Mammal Laboratory, Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA 98115-0070.

[8] Gearin, P. J., and M. A. Johnson. 1991. Prey identified from stomachs of harbor porpoise and Chinook salmon from the 1988–89 Makah Salmon Set-Net Fishery. *In* H. Kajimura (ed.), Harbor porpoise interactions with Makah Salmon set net fishery in coastal Washington waters, 1988–89. National Marine Mammal Laboratory Processed Report. National Marine Mammal Laboratory, Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA 98115-0070.

In this study, SST was measured along tracklines and may not have represented water temperatures where harbor porpoise were sighted. Tide rips mixing water, or currents moving through the study area could have altered water temperatures by a few degrees between trackline and harbor porpoise locations. Sea surface temperature varied by 5°C from beginning to end of the 8-km tracklines. We assumed, however, less bias was introduced by collecting SST along the trackline than by continuously going off transect and potentially disturbing harbor porpoise ahead of the vessel. Because our methods were consistent over the study period, the comparison in use versus availability of SST is likely representative.

It is doubtful that time of day had a significant effect on the ability to sight harbor porpoise in our study; therefore, other environmental factors must have affected harbor porpoise distribution in relation to time of day. Occurrence of harbor porpoise appears closely associated with the strength of tidal currents. From shore-based surveys within our study area (Raum-Suryan, 1995), mean number of porpoise observed per minute was greatest two hours before each peak in the maximum flood tide, and significantly more ($P<0.05$) porpoise were observed per minute during flood than ebb tides. From June to October 1992, the majority of low tides in the northern San Juan Islands occurred in the early morning hours. The relation between the occurrence of harbor porpoise with tide and time of day indicates that porpoise movements may have been associated with concentrations of prey in flood currents and tide rips. It is possible that harbor porpoise range throughout Washington Sound but continue to return to northern San Juan Island waters as a primary foraging area.

We found a large proportion of the harbor porpoise population of Washington Sound located within our study area. Calambokidis et al.[2] estimated the population size of harbor porpoise for the San Juan Islands (2291 km$^2$) at 960 animals (corrected as in density estimate). In approximately 10% (237 km$^2$) of the area that Calambokidis et al.[2] surveyed, we estimated 30% (299 porpoise) of the harbor porpoise population. Given that our $g(0)$ was assumed to be one (thus underestimating the population size), the proportion of harbor porpoise within our study area is likely greater than 30% of the total population within the San Juan Island region. On the basis of pollutants detected in harbor porpoise tissues, porpoise along the west coast do not mix freely between California, Oregon, and Washington (Calambokidis and Barlow, 1991). In addition, Washington and California are considered repositories of genetic diversity for harbor porpoise of the Northeast Pacific (Rosel et al., 1995) and also indicate that harbor porpoise ranges may be restricted. In addition to aerial surveys conducted over Washington waters (Calambokidis et al.[2]), our study area appears to be an important site for monitoring trends in distribution and abundance of harbor porpoise in inland water of Washington.

It is not clear why harbor porpoise are not as abundant in other areas of Washington Sound as they are in our study area. The relatively low abundance outside our study area may be due to factors other than food availability, such as pollution, fishing pressure, increased boat traffic, or other environmental changes. We believe that harbor porpoise are more abundant in our study area than in other parts of Washington Sound because certain environmental conditions (deep, cool water, and strong tidal mixing) influence the distribution of harbor porpoise prey. Future monitoring studies on oceanographic conditions and prey availability associated with harbor porpoise sightings would greatly assist in determining mechanisms affecting harbor porpoise abundance and distribution in this and other areas and help in managing this genetically important stock.

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# Global phylogeography of mackerels of the genus *Scomber*

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**Abstract.**—Inter- and intraspecific genetic relationships among and within three species of mackerels of the genus *Scomber* were investigated by restriction site analysis of the whole mitochondrial (mt) DNA genome and direct sequence analysis of the mitochondrial cytochrome *b* gene. A total of 15 samples, averaging 19 individuals each, were collected from geographically isolated populations throughout the ranges of *S. scombrus* (two samples), *S. australasicus* (five samples), and *S. japonicus* (eight samples). Restriction site analysis with 12 restriction enzymes revealed substantial genetic variation within each species. Sample haplotype diversities ranged from 0.28 to 0.95, and nucleotide sequence diversities from 0.13% to 0.76%. Spatial partitioning of genetic variation was observed in each of the species. Eastern and western North Atlantic samples of *S. scombrus* exhibited significant heterogeneity in the distribution of mtDNA haplotypes, but no fixed restriction site differences were observed between samples. Similarly, no fixed restriction site differences occurred among samples of *S. japonicus* in the Atlantic Ocean, although there were significant differences in the distribution of haplotypes among samples. In contrast, samples of *S. japonicus* from within the Pacific Ocean were characterized by fixed restriction site differences. North and South Pacific samples of *S. australasicus* were highly divergent, and one of two divergent mtDNA matrilines was restricted to samples from the South Pacific. A 420-bp segment of the cytochrome *b* gene was sequenced for representatives of each of the major mtDNA lineages identified by restriction site analysis. *Scomber scombrus* differed from *S. australasicus* and *S. japonicus* by more than 11% net nucleotide sequence divergence, considerably greater than the 3.5% sequence divergence between *S. australasicus* and *S. japonicus*. Levels of interspecific genetic divergences based on restriction site data were similar in pattern, but were approximately 20% lower in magnitude when based on the cytochrome *b* sequences. Parsimony analysis and neighbor-joining of restriction site data, and parsimony analysis of cytochrome *b* sequences showed similar paraphyletic patterns in both *S. japonicus* and *S. australasicus*. Levels of divergence among samples of *S. japonicus* were similar to those between samples of *S. australasicus* and *S. japonicus*. Complete partitioning of halpotypes among some samples of *S. japonicus* that are morphologically distinct suggests that Atlantic and Indo-Pacific populations of *S. japonicus* may need to be recognized as separate species.

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Population structure is largely influenced by the biological characteristics of a species and the attributes of its environment that promote or impede gene flow. In marine fishes, dispersal of planktonic early life history stages and adult vagility can facilitate genetic exchange over great distances (Rosenblatt, 1963; Shulman and Bermingham, 1995). Features of the marine environment that limit gene flow are often equally large in scale, such as current systems, major changes in temperature or salinity, or the presence of large land masses (Sinclair, 1988). Accordingly, many genetic analyses of broadly distributed marine fishes have shown little divergence among conspecific samples from geographically distant locations.

Limited population structure has been demonstrated for a variety of marine fishes. Electrophoretic analyses of allozymes have revealed little population divergence among collections of milkfish (*Chanos chanos*) separated by up to 10,000 km (Winans, 1980), damselfish, *Stegastes fasciolatus*, sampled from throughout the 2500 km Hawaiian archipelago (Shaklee, 1984), in twelve species of tropical marine shore fishes sampled from both sides of the Pacific Barrier, a 5000-km expanse of deep ocean separating central and eastern Pacific shallow water habitats (Rosenblatt and Waples, 1986), or in five species of damselfishes collected from isolated Caribbean reefs (Lacson, 1992 ). Similarly, analyses of mitochondrial DNA have revealed little genetic differentiation among populations of five species of tropical reef fishes sampled from throughout the Caribbean (Shulman and Bermingham, 1995), or within three cosmopolitan species of tunas (Graves et al., 1984; Graves and Dizon, 1989; Scoles and Graves, 1993).

Much less information is available on the population structure of broadly distributed marine species that occur in fragmented or disjunct distributions. Recent studies of striped mullet (*Mugil cephalus*,

Crosetti et al., 1994) and bluefish (*Pomatomus saltatrix*, Goodbred and Graves, 1996) have demonstrated that significant phylogeographic population structuring can exist in discontinuously distributed marine fishes. The reduced gene flow among isolated populations of such species provide excellent opportunities for studying the effects of historical marine zoogeographical processes and observe incipient speciation.

Mackerels of the genus *Scomber*, like the striped mullet and bluefish, are ideally suited for studies of genetic population structure in cosmopolitan fishes with fragmented distributions and for comparative studies that describe genetic patterns of other more vagile scombrids (Graves et al., 1984; Graves and Dizon, 1989; Scoles and Graves, 1993). Distributional patterns of scombrids vary widely from world-wide species such as the yellowfin tuna, albacore, and skipjack tunas to supposedly wide-spread species such as the chub mackerel, *S. japonicus*, which is divided into geographically disjunct populations, to those with limited ranges such as a Spanish mackerel (*Scomberomorus munroi*) found only in the Gulf of Papua between Australia and New Guinea (Collette and Nauen, 1983). The three species of *Scomber* (*S. japonicus, S. australasicus, and S. scombrus*) occur in temperate to subtropical waters, and two (*S. japonicus* and *S. australasicus*) display antitropical distributions. Each species occurs in disjunct populations of various sizes, and their distributions overlap in several areas (Fig. 1; Collette and Nauen, 1983). The cosmopolitan chub mackerel, *S. japonicus*, occurs in coastal regions and adjacent seas of the Atlantic, Pacific, and northwest Indian oceans. The spotted chub mackerel, *S. australasicus*, is restricted to the Pacific Ocean, southeastern Indian Ocean, and the Red Sea. The Atlantic mackerel, *S. scombrus*, is restricted to the North Atlantic Ocean. The present study emphasizes *S. japonicus*, which of the three species is the most widely distributed and morphologically divergent among its isolated populations (Matsui, 1967).

## Life histories and population structures

The spawning behavior and duration of the larval stage varies among the three species of *Scomber*. *Scomber scombrus* is capable of spawning serially up to 30 times in a spawning season (Watson et al., 1992) at any time of day (Walsh and Johnstone, 1992), where *S. japonicus* spawns on average only 9 times in a season, and does so only at night (Watanabe,

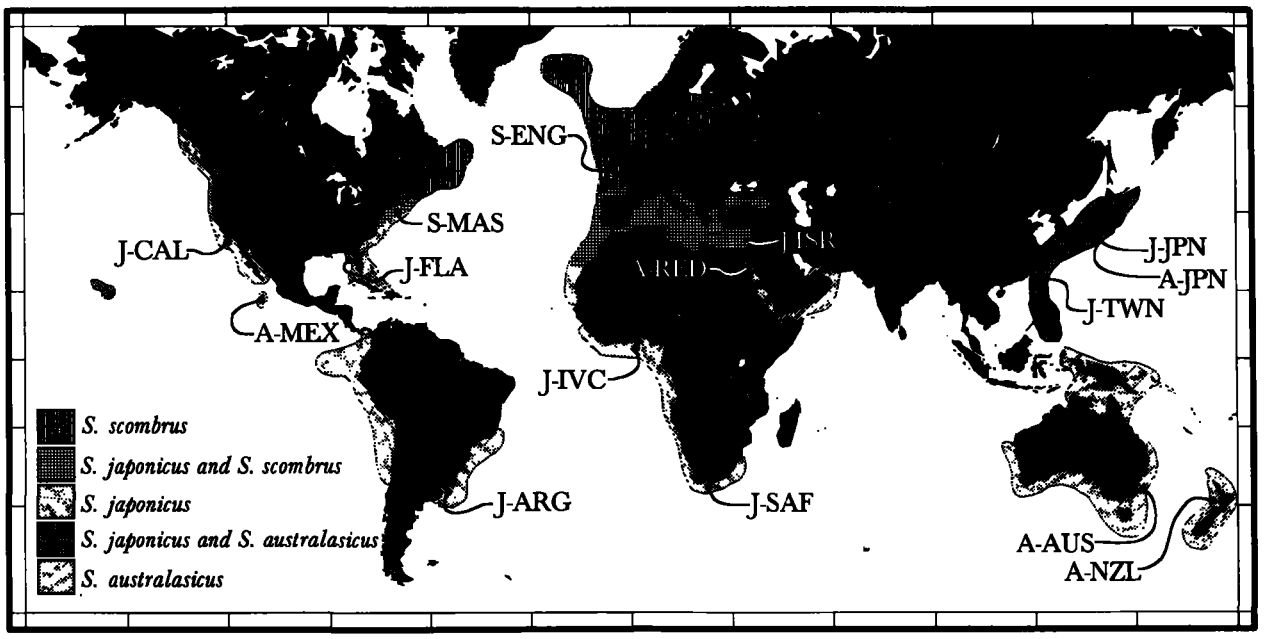



**Figure 1**

Sampling and distributions of Atlantic mackerel, *Scomber scombrus* (S-MAS and S-ENG), spotted chub mackerel, *S. australasicus* (A-RED, A-JPN, A-AUS, A-NZL, and A-MEX), and chub mackerel, *S. japonicus* (J-JPN, J-TWN, J-CAL, J-HAW, J-FLA, J-ARG, J-ISR, J-IVC, and J-SAF), according to Collette and Nauen (1983). *S. japonicus* distributions off Brazil and Namibia follow Perrotta and Aubone (1991) and Zenken and Lobov (1989), respectively.

1970). *Scomber japonicus* and *S. scombrus* have similar larval stage durations: eggs of *S. scombrus* and *S. japonicus* hatch in less than 6 d, and schooling behavior begins when larvae metamorphose (about 15 mm) which occurs at 24–9 d and 22–9 d, respectively (Hunter and Kimbrell, 1980; Ware and Lambert, 1985). Thus the duration of passive planktonic transport of the early life history stages is usually 29 d or less, but probably extends into the early juvenile stages as well. Little spawning or larval ecology data are available for *S. australasicus*, but it is expected that it has a similar early life history.

Exchange between regional populations of *S. scombrus* in the North Atlantic appears sufficient to maintain genetic homogeneity. Two spawning groups in the northwest Atlantic, the "northern contingent" in the southern Gulf of St. Lawerence, and the "southern contingent" between Cape Cod and Cape Hatteras, were identified by Sette (1950) by size composition and tagging data. However, these groups were not discriminated by meristic or growth character analysis (MacKay and Garside, 1969; Simard et al., 1992), or by allozyme analysis (Maguire et al., 1987). In the northeast Atlantic, two spawning groups, the "western stock" south and west of the British Isles, and the "North Sea stock," were identified by tagging (Hamre, 1980), but these groups were not distinguished by allozymic differences (Jamieson and Smith, 1987).

Matsui (1967) showed greater phenotypic variation in *S. japonicus* than in the other two species of *Scomber*, possibly because of its wider distribution. Populations of *S. japonicus* from the eastern and western Atlantic had nonoverlapping distributions of gill-raker counts, and other variable morphological characters of Atlantic populations were similar, including belly spots, strongly crenulated teeth, and large scales. In contrast, Pacific *S. japonicus* exhibited lightly crenulated teeth, no belly spots, and smaller scales (Matsui, 1967). Analysis of four polymorphic allozyme loci revealed no divergence among samples of *S. japonicus* from the southeast Atlantic off Namibia (Zenkin and Lobov, 1989), but heterogeneity in immunological reactivity suggested population structure off the northwest African coast (Weiss, 1980). A study of 14 polymorphic allozyme loci showed significant differences between samples from the north- and southeastern Pacific Ocean, which suggested reduced gene flow across the tropics in comparison with other similarly distributed pelagic fishes (Stepien and Rosenblatt, 1996). Differences in growth rates and morphological characters among samples within the southwest Atlantic led Perrotta (1993) to conclude that *S. japonicus* populations within the region had diverged to the level of subspecies.

To evaluate the genetic relationships among the three species of *Scomber*, and the discontinuous populations within them, we examined mitochondrial (mt) DNA restriction sites, and cytochrome *b* sequences. Analysis of mtDNA has proven useful in revealing phylogeographic structure in a variety of marine and freshwater fish species (Avise, 1992). Because mtDNA is clonally inherited, information regarding historical phylogenetic relationships is retained, hence analysis of mtDNA can render considerable information on historical relationships among populations and the mtDNA lineages they possess.

## Materials and methods

### Specimen collection

Samples of 15 to 21 individuals each of *S. scombrus*, *S. australasicus*, and *S. japonicus* were obtained from 15 locations (Table 1, Fig. 1). Specimens of *Rastrelliger kanagurta*, a species of the sister group to *Scomber* (Collette et al., 1984), were obtained from Sri Lanka. Whole fish were frozen after collection and shipped to the laboratory on dry ice.

### MtDNA preparation and analysis

MtDNA-enriched genomic DNA was isolated from 3 g of lateral red muscle, or whole young-of-year fish with digestive tracts removed (A-NZL only) according to Chapman and Powers (1984) method, modified by the omission of sucrose step gradients and the use of 1.5% sodium dodecyl sulfate for mitochondrial lysis. DNAs were digested with 10 hexameric (*Apa*I, *Bgl*I, *Bsu*36I, *Dra*I, *Pvu*II, *Sca*I, *Stu*I, *Ssp*I, *Hpa*I, *Spe*I) and 2 multi-hexameric (*Ava*I, *Hae*II) restriction endonucleases following manufacturers' (Stratagene and Gibco-BRL) instructions. DNA fragments were separated by electrophoresis in 1.0 or 1.5% agarose gels, transferred to nylon membranes by Southern transfer, and hybridized to a biotin-labeled probe as described previously (Scoles and Graves, 1993). The probe was made by separately cloning four yellowfin tuna, *Thunnus albacares*, mtDNA fragments that cover the entire mitochondrial genome in the *Pst*I site of pBluescript SK- (Stratagene). MtDNA fragments were visualized by using the BluGene Non-Radioactive Nucleic Acid Detection Kit (Gibco-BRL).

A 12-letter composite mtDNA haplotype, indicating the fragment pattern for each enzyme, was developed for each individual. Letters were assigned to restriction fragment patterns as they were encountered, beginning with 'A' for the closely related

**Table 1**

*Scomber japonicus*, *S. australasicus*, and *S. scombrus*. Sample name, size, location, haplotype diversity ($h$), and percent nucleotide sequence diversity ($\pi$).

| Sample name | Sample size ($n$) | Sample location | Haplotype diversity ($h$) | Percent nucleotide sequence diversity ($\pi$) |
|---|---|---|---|---|
| *Scomber scombrus* | | | | |
| S-MAS | 20 | Boston, Massachusetts | 0.85 | 0.29 |
| S-ENG | 20 | Plymouth, England | 0.28 | 0.07 |
| Total | 40 | | 0.58 | 0.18 |
| *Scomber australasicus* | | | | |
| A-RED | 15 | Sinai Peninsula south, Red Sea | 0.95 | 0.41 |
| A-AUS | 18 | New South Wales, Australia | 0.86 | 0.75 |
| A-NZL | 19 | Wellington, New Zealand | 0.75 | 0.77 |
| A-JPN | 21 | Tokyo, Japan | 0.81 | 0.30 |
| A-MEX | 20 | Revillagigedo Islands, Mexico | 0.59 | 0.13 |
| Total | 93 | | 0.90 | 2.18 |
| *Scomber japonicus* | | | | |
| J-FLA | 20 | Panama City, Florida | 0.93 | 0.40 |
| J-ARG | 18 | Mar del Plata, Argentina | 0.90 | 0.50 |
| J-ISR | 20 | Mediterranean coast of Israel | 0.90 | 0.38 |
| J-IVC | 20 | Abidjan, Ivory Coast | 0.91 | 0.39 |
| J-SAF | 20 | Cape Town, South Africa | 0.81 | 0.38 |
| J-TWN | 20 | Kaohsing, Taiwan | 0.86 | 0.29 |
| J-JPN | 20 | Tokyo, Japan | 0.88 | 0.35 |
| J-CAL | 20 | San Diego, California | 0.64 | 0.14 |
| Total | 158 | | 0.95 | 2.42 |
| Grand total | 291 | | | |

*S. japonicus* and *S. australasicus* group, and proceeding through the alphabet, and beginning with 'Z' and proceeding in reverse alphabetical order for *S. scombrus*. For the few *S. scombrus* restriction fragment patterns that also occurred in *S. japonicus* or *S. australasicus*, the latter species' restriction morph letter designation was used.

Estimates of nucleotide sequence divergence ($d$) among haplotypes were determined by using the approach of Nei and Li (1979) for fragment data, and Nei and Tajima (1981) and Nei and Miller (1990) for site data, with weighting based on the proportion of fragments or sites produced by each enzyme class (Nei and Tajima, 1983). Estimates of nucleon or haplotype diversity ($h$) and nucleotide sequence diversity ($\pi$) were then calculated with the program DA of the statistical package REAP (McElroy et al., 1992). Corrected nucleotide sequence divergences ($\delta$) among populations were calculated by using the protocol of Nei and Li (1979). The homogeneity of haplotype distributions among samples was evaluated by chi-square analyses using the Monte-Carlo method of Roff and Bentzen (1989) with 1000 randomizations of the data with REAP.

Restriction sites were inferred from completely additive fragment patterns, and the information for each individual was coded using a presence-or-absence matrix. Homology of restriction sites could not be assured between *S. scombrus* and the *S. australasicus-S. japonicus* group owing to the relatively large genetic divergence between the species. Restriction site data were therefore evaluated only for phylogenetic relationships within the *S. australasicus-S. japonicus* group, and an estimate of divergence between *S. scombrus* and the pooled data of *S. australasicus* and *S. japonicus* was determined by using restriction fragment data. Relationships among haplotypes were inferred by cluster analysis (unweighted pair-group method, UPGMA, Norusis, 1988). Neighbor-joining, parsimony analyses and consensus trees were generated with the PAUP* software program (test version).

## DNA amplification and sequence analysis

Individuals representative of the major *Scomber* mtDNA matrilines, identified by restriction site analysis, and of *Rastrelliger kanagurta*, were selected for DNA sequence analysis. A 418-bp region of the cytochrome *b* gene was amplified from mtDNA-enriched genomic DNA isolations by the polymerase chain reaction (PCR) with primers L15079

(5'GAGGCCTCTACTATGGCTCTTACC3') and H15497 (5'GCTAGGGTATAATTGTCTGGGTCGCC3') developed by Finnerty and Block (1992) for blue marlin (*Makaira nigricans*). Double-stranded DNA amplifications were accomplished in 100 µl of 10 mM Tris-HCl pH 8.3, 50 mM KCl, 1.5 mM $MgCl_2$, 0.001% (w/v) gelatin, 0.2 mM of each dNTP, 50 pmol of each primer, 50 ng genomic DNA, and 2.5 units *Taq* polymerase (Perkin-Elmer/Cetus). Cycling parameters were preceded by a 4-min initial denaturation at 94°C and included 38 cycles of 94°C for 1 min, 50°C for 1 min, and 72°C for 1.5 min, followed by a 5-min final extension at 72°C. Primers L15079 and H15497 would not amplify some haplotypes of *S. australasicus*. Specific primers with conserved 3' ends were designed from other sequences: CYT2A (5'TACCTTTTCATGGAAACATG3') and CYT2B (5'AAGAGGTTGGGAGAGAAGA3'). Both strands were fully sequenced by using the Sequenase kit (United States Biochemical) or the CircumVent Cycle Sequencing Kit (New England BioLabs) following the vendors' protocols.

Sequences were aligned by eye to the human mitochondrial cytochrome *b* sequence[1] (Anderson et al., 1981). Nucleotide sequence divergences ($d$) among cytochrome *b* sequences were generated with the program K of REAP. Cytochrome *b* sequences were analyzed by parsimony analysis with rooting to *Rastrelliger kanagurta* by using ALLTREES in PAUP.

## Results

MtDNA restriction site analysis of 40 *Scomber scombrus* from two locations revealed a total of 56 restriction sites, of which 16 were polymorphic, defining 13 haplotypes. Nucleotide sequence divergences among the haplotypes of *S. scombrus* ranged from $d$=0.17% to 0.86%. An average of 294 bp was surveyed, representing 1.75% of the mitochondrial genome. The average size of the *S. scombrus* mtDNA genome, determined from several restriction fragment profiles from each of the 12 restriction enzymes, was 16,784 ±213 bp (SD).

Restriction site analysis of 246 *S. japonicus* and *S. australasicus* revealed a total of 93 unique haplotypes, including information from 86 restriction sites, of which 58 were polymorphic. Among haplotypes of *S. japonicus* and *S. australasicus*, nucleotide sequence divergences ranged from $d$=0.15% to 2.9%. On average, 310 bp were surveyed per individual, representing 1.85% of the mtDNA genome. The average size of the mtDNA genome of *S. japonicus* or *S. australasicus* was estimated to be 16,781 ±195 bp (SD), not statistically different than that of *S. scombrus*.

### Genetic diversities

MtDNA restriction site analysis revealed that the genetic variability was lower in *S. scombrus* than the other two species (Table 1). S-ENG was the least variable sample in the study ($h$=0.28), consisting of four haplotypes of which three occurred only once (Table 2). Ten haplotypes were revealed in S-MAS, with three at elevated frequencies, resulting in a haplotype diversity of $h$=0.85. The overall haplotype diversity for *S. scombrus* was $h$=0.58, and nucleotide sequence diversity was $\pi$=0.18%. Three restriction enzymes, *Pvu*II, *Bgl*I, and *Bsu*36I, were invariant in *S. scombrus*, whereas the remaining nine restriction enzymes each revealed from two to five fragment patterns.

A wide range of diversities was observed among samples of *S. australasicus* ($h$=0.59–0.95) and *S. japonicus* ($h$=0.64–0.93) based on the restriction site data. Eastern Pacific samples of *S. australasicus* and *S. japonicus* from Mexico (A-MEX, $h$=0.59, $\pi$=0.13%) and California (J-CAL, $h$=0.64, $\pi$=0.14%) had lower diversities than other samples, possessing only four and six haplotypes, respectively (Tables 1 and 2). The highest haplotype diversity occurred in A-RED ($h$=0.95), with five of 10 haplotypes represented twice; the highest nucleotide sequence diversities occurred in A-NZL ($\pi$=0.77%) and A-AUS ($\pi$=0.75%) owing to the presence of two divergent mtDNA matrilines within each sample (Tables 1 and 2). With the exception of *Bgl*I in *S. australasicus*, all restriction enzymes were variable in both species, revealing two to seven fragment patterns in *S. australasicus*, and two to 15 in *S. japonicus*. The enzyme *Apa*I revealed the greatest number of variants in both species.

### Genetic divergences

Restriction fragment analysis showed *S. scombrus* to be highly divergent from *S. australasicus* and *S. japonicus*, with a net nucleotide sequence divergence of $\delta$=11.9% between *S. scombrus* and the pooled data of *S. japonicus* and *S. australasicus*. In comparison, the mean net nucleotide sequence divergence between *S. japonicus* and *S. australasicus* based on the restriction site data was only $\delta$=1.17%. Probabilities of Roff and Bentzen chi-square tests among samples that shared haplotypes are given in Table 3.

***Scomber scombrus*** Considerable intraspecific divergence was evident in *S. scombrus* from the mtDNA

[1] GenBank accession no. V00662.

## Table 2

Distributions of mtDNA haplotypes among samples of species of *Scomber*, grouped by their occurrence in phenetic cluster analysis. Letters represent fragment patterns produced by the following enzymes (left to right): *Sca*I, *Dra*I, *Stu*I, *Pvu*II, *Hae*II, *Apa*I, *Ava*I, *Ssp*I, *Bgl*I, *Hpa*I, *Spe*I, *Bsu*36I.

Western Pacific *Scomber japonicus*

| ID | Haplotype | J-TWN | J-JPN | Total |
|---|---|---|---|---|
| 1 | BAIABIAGEBAA | 4 | 5 | 9 |
| 2 | BAIABLADEBAA | 5 | 4 | 9 |
| 3 | BAIABMAGEBAA | 5 | 4 | 9 |
| 4 | BAIABJADEBAA | 2 | 1 | 3 |
| 5 | BAIABMHGEBAA | | 2 | 2 |
| 6 | BAIABJAGEBAA | | 1 | 1 |
| 7 | BAIABLAGEBAA | 1 | | 1 |
| 8 | BAIABMADEBAA | 1 | | 1 |
| 9 | BAIABMAGEBCA | | 1 | 1 |
| 10 | BAIABNAGEBAA | | 1 | 1 |
| 11 | BAIABOAEEBAA | | 1 | 1 |
| 12 | BAIABOAGEBAA | 1 | | 1 |
| 13 | BAIAGIAGEBAA | 1 | | 1 |

Eastern Pacific *Scomber japonicus*

| ID | Haplotype | J-CAL | Total |
|---|---|---|---|
| 14 | BAIABIADEAAA | 12 | 12 |
| 15 | BAIABJADEAAA | 5 | 5 |
| 16 | BAIABIADEAAB | 1 | 1 |
| 17 | BAIABIDDEAAA | 1 | 1 |
| 18 | BAIADIADEAAA | 1 | 1 |
| 19 | BAJABIADCAAA | 1 | 1 |

Atlantic *Scomber japonicus*.

| ID | Haplotype | J-FLA | J-ARG | J-SAF | J-IVC | J-ISR | Total |
|---|---|---|---|---|---|---|---|
| 20 | ABAAABAAAAAA | 1 | | 1 | 3 | 1 | 6 |
| 21 | AAAAABADAAAA | 1 | | | 1 | | 2 |
| 22 | ABAAABAHAAAA | | 3 | | | | 3 |
| 23 | ABAAABADAAAA | | | | | 2 | 2 |
| 24 | ABAAABAIAAAA | | 1 | | | | 1 |
| 25 | ABAAADAAAAAA | | | 1 | | | 1 |
| 26 | ABAAAKADAAAA | | | | | 1 | 1 |
| 27 | ABAAEBAAAAAA | | | | 1 | | 1 |
| 28 | ABAAEBADAAAA | | | | | 1 | 1 |
| 29 | ABABABAHAAAA | | 1 | | | | 1 |
| 30 | AAAAABAAAAAA | 1 | | | | | 1 |
| 31 | AAAAAAAAAAAA | 6 | 4 | | 3 | 2 | 15 |
| 32 | AABAAAAAAAAA | 4 | | | | | 4 |
| 33 | AAAAAJAAAAAA | | 2 | | | | 2 |
| 34 | AAAAAAABAAAA | | | | 1 | | 1 |
| 35 | AAAAAPAAAAAA | | 1 | | | | 1 |
| 36 | AAAAAABAABAA | | | 1 | | | 1 |
| 37 | AABAAAAABAAA | 1 | | | | | 1 |
| 38 | AABAAAACAAAA | 1 | | | | | 1 |
| 39 | ABAAAAAAAAAA | 1 | | | | | 1 |
| 40 | BAAAAJAAAAAA | | 1 | | | | 1 |
| 41 | AAGAAAADAAAA | | 4 | 9 | 5 | 6 | 24 |
| 42 | ABGAAAADAAAA | | | 1 | 2 | 3 | 6 |
| 43 | AAAAAAADAAAA | 2 | | 1 | 1 | | 4 |

*continued on next page*

**Table 2 (continued)**

Atlantic *Scomber japonicus*. (continued)

| ID | Haplotype | J-FLA | J-ARG | J-SAF | J-IVC | J-ISR | Total |
|---|---|---|---|---|---|---|---|
| 44 | AAGAAAADADAA | | | | 1 | 1 | 2 |
| 45 | AAAAAAADAEAA | | 1 | | | | 1 |
| 46 | AAAAAEADAAAA | | | 1 | | | 1 |
| 47 | AAAAAGGDAAAA | | | | | 1 | 1 |
| 48 | AABAACADAAAA | 1 | | | | | 1 |
| 49 | AACBABABAAAA | 1 | | | | | 1 |
| 50 | AAGAAAADBAAA | | | | 1 | | 1 |
| 51 | AAGAAAAEAAAA | | | 1 | | | 1 |
| 52 | AAGAAAAEABAA | | | 1 | | | 1 |
| 53 | AAGAABADAAAA | | | 1 | | | 1 |
| 54 | AAHAAAADAAAA | | | 1 | | | 1 |
| 55 | ABAAAAADAAAA | | | | | 1 | 1 |
| 56 | ABAAAAADAAAB | | | 1 | | | 1 |
| 57 | ABAAAAADBAAA | | | | 1 | | 1 |
| 58 | BAAAAAADAAAA | | | | | 1 | 1 |

Red Sea *Scomber australasicus*

| ID | Haplotype | A-RED | Total |
|---|---|---|---|
| 59 | BADAAAADDEAA | 2 | 2 |
| 60 | BADAAAADDFAA | 2 | 2 |
| 61 | BADAFAADAFAA | 2 | 2 |
| 62 | BADBAAAAAFAA | 2 | 2 |
| 63 | BADBAAADAFAA | 2 | 2 |
| 64 | AADBAAADAFAA | 1 | 1 |
| 65 | BADAAAADAEAA | 1 | 1 |
| 66 | BADBABADAFAA | 1 | 1 |
| 67 | BALBAAADAFAA | 1 | 1 |
| 68 | BALBAJADAFAA | 1 | 1 |

Unique lineage *Scomber australasicus*

| ID | Haplotype | A-NZL | A-AUS | Total |
|---|---|---|---|---|
| 69 | BCDBBAADABAA | 8 | 6 | 14 |
| 70 | BCDBBAADAAAA | | 1 | 1 |
| 71 | BCDBBAEDABAA | | 1 | 1 |
| 72 | BCDBBAFDABAA | | 1 | 1 |
| 73 | BCDBBBADABAA | 1 | | 1 |
| 74 | BCDBBGADABAA | 1 | | 1 |
| 75 | BCDBBHADABAA | | 1 | 1 |
| 76 | BCDBCAADABAA | 1 | | 1 |
| 77 | BDDBBAADABAA | | 1 | 1 |
| 78 | BDDBBAADABBA | | 1 | 1 |

Ubiquitous lineage *Scomber australasicus*

| ID | Haplotype | A-NZL | A-AUS | A-MEX | A-JPN | Total |
|---|---|---|---|---|---|---|
| 79 | BAEABACFABAA | 1 | 1 | 12 | 9 | 23 |
| 80 | BAEABACEACAA | 6 | 4 | | | 10 |
| 81 | BBEABACFABAA | | | 2 | 1 | 3 |
| 82 | BAEABACFABAA | | | 5 | | 5 |
| 83 | BAKABACFABAA | | | | 3 | 3 |
| 84 | BAEABJCFABAA | | | | 2 | 2 |

*continued on next page*

**Table 2 (continued)**

| Ubiquitous lineage *Scomber australasicus* (continued) | | | | | | |
|---|---|---|---|---|---|---|
| ID | Haplotype | A-NZL | A-AUS | A-MEX | A-JPN | Total |
| 85 | BAEABABFABAA | | | 1 | | 1 |
| 86 | BAEABACFAFAA | | | | 1 | 1 |
| 87 | BAEABSCFABAA | | | | 1 | 1 |
| 88 | BAEBBACFABAA | | | | 1 | 1 |
| 89 | BAFABACEACAA | 1 | | | | 1 |
| 90 | BBDABACFABAA | | 1 | | | 1 |
| 91 | BBEBBRCFABAA | | | | 1 | 1 |
| 92 | BEKBBACFABAA | | | | 1 | 1 |
| 93 | CAEABACFABAA | | | | 1 | 1 |

| *Scomber scombrus* | | | | |
|---|---|---|---|---|
| ID | Haplotype | S-ENG | S-MAS | Total |
| 94 | ZZZZZZZZZFZZ | 17 | 7 | 24 |
| 95 | ZZZZYZZZZFZZ | | 4 | 4 |
| 96 | ZZZZYZZZZFZZ | | 2 | 2 |
| 97 | CZYZZXZZZFZZ | | 1 | 1 |
| 98 | XZZZZZZZZFYZ | | 1 | 1 |
| 99 | ZXZZZZZZZFZZ | 1 | | 1 |
| 100 | ZYZZYZZZZFZZ | | 1 | 1 |
| 101 | ZZZZXZZZZFZZ | | 1 | 1 |
| 102 | ZZZZZVYZZFZZ | 1 | | 1 |
| 103 | ZZZZZWZZZFZZ | | 1 | 1 |
| 104 | ZZZZZZZXZFZZ | 1 | | 1 |
| 105 | ZZZZZZZYZFZZ | | 1 | 1 |
| 106 | ZZZZZZZZZYZZ | | 1 | 1 |

restriction site data. Only one *S. scombrus* haplotype (no. 94) was shared between the eastern and western North Atlantic samples, and it occurred at significantly different frequencies in each (0.35 in S-ENG, and 0.85 in S-MAS, Table 2). The distribution of haplotypes between the two samples was highly heterogeneous ($P<0.001$), although the estimate of net nucleotide sequence divergence between S-ENG and S-MAS was low ($\delta=0.011\%$), reflecting the close relationship among haplotypes (Fig. 2).

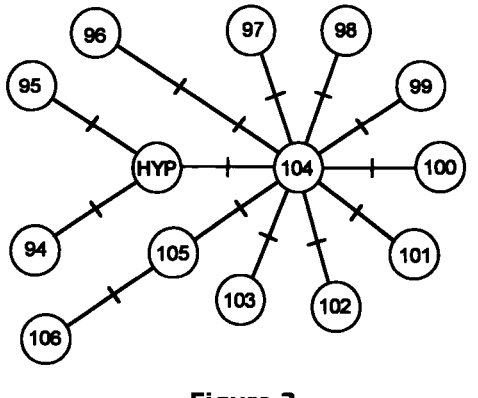



**Figure 2**

Parsimony network illustrating the relationship among mtDNA haplotypes of *Scomber scombrus*. One hypothetical haplotype (HYP) is indicated. Each dash corresponds to a single restriction-site gain or loss.

***Scomber australasicus*** Restriction site analysis of *S. australasicus* mtDNA exhibited a range of intraspecific divergences. Samples collected from Australia and New Zealand were very similar. Three haplotypes (nos. 69, 79, and 80), representing two genetically divergent matrilines, occurred at similar frequencies in each sample (Table 2), and no heterogeneity was revealed ($P=0.718$, $\delta=-0.019\%$). The two samples of *S. australasicus* from the North Pacific (A-JPN and A-MEX) revealed greater divergence, comprising twelve haplotypes, of which two were shared, and one (no. 79) occurred in a large number of individuals in both samples ($n=9$ and $n=12$, respectively). Haplotype 82 occurred in five individuals from A-MEX but was not present in the A-JPN

**Table 3**

Probabilities of significance from Roff and Bentzen's (1989) chi-square analysis with 1000 randomizations of the data of samples of Atlantic *Scomber japonicus*, Pacific *S. japonicus*, *S. australasicus*, and *S. scombrus* that shared haplotypes.

| Comparison | $\chi^2$ | Number of simulations exceeding $\chi^2$ | Probability |
|---|---|---|---|
| Atlantic *Scomber japonicus* | | | |
| J-ISR J-IVC J-SAF J-FLA J-ARG | 191.36 | 0 | <0.001** |
| J-ISR J-IVC J-SAF | 48.70 | 451 | 0.451$^{NS}$ |
| J-ARG J-IVC J-SAF | 60.84 | 28 | 0.028* |
| J-ARG J-IVC | 22.21 | 68 | 0.070$^{NS}$ |
| J-ARG J-SAF | 26.89 | 0 | 0.001** |
| J-FLA J-ARG | 28.37 | 1 | 0.001** |
| J-FLA J-ISR J-IVC | 58.40 | 16 | 0.016* |
| J-FLA J-ISR | 32.00 | 1 | 0.001** |
| J-FLA J-IVC | 24.33 | 14 | 0.014* |
| Pacific *Scomber japonicus* | | | |
| J-JPN J-TWN | 10.67 | 658 | 0.658$^{NS}$ |
| *Scomber australasicus* | | | |
| A-JPN A-MEX A-AUS A-NZL | 128.94 | 0 | <0.001** |
| A-JPN A-MEX | 17.75 | 13 | 0.013* |
| A-AUS A-NZL | 11.67 | 718 | 0.718$^{NS}$ |
| *Scomber scombrus* | | | |
| S-ENG S-MAS | 20.17 | 0 | <0.001** |

*Significantly different at $\alpha$=0.05.
**Significantly heterogeneous at $\alpha$=0.01.
$^{NS}$Not significant.

***Scomber japonicus*** Of the three species, samples of *S. japonicus* spanned the greatest geographical area, and mtDNA restriction site analysis of this species revealed the largest range of divergences. In the North Pacific, samples from Japan (J-JPN) and Taiwan (J-TWN) shared four haplotypes, three of which occurred in more than one individual in each sample (nos. 1–3, Table 2), and no significant heterogeneity was observed between the samples ($P$=0.658, $\alpha$=0.05, $\delta$=–0.010%). In contrast, a comparison of the pooled data of J-JPN and J-TWN with *S. japonicus* from the eastern North Pacific (J-CAL) revealed one fixed restriction site difference, a net nucleotide sequence divergence of $\delta$=0.30%, and genotype distributions were significantly different ($P$<0.001, $\alpha$=0.05).

Many closely related haplotypes were observed in samples of *S. japonicus* from the Atlantic and Mediterranean Sea, and several were shared among two or more sample locations (Table 2). No significant differences were observed in the distribution of haplotypes among J-ISR, J-IVC, and J-SAF, from the eastern Atlantic ($P$=0.451, $\alpha$=0.05, $\delta$=–0.003%–0.015%, Table 4), or between J-IVC and J-ARG across the Atlantic ($P$=0.07, $\alpha$=0.05, $\delta$=0.025%). All other tests of haplotype frequencies among Atlantic samples were significant ($P$<0.05).

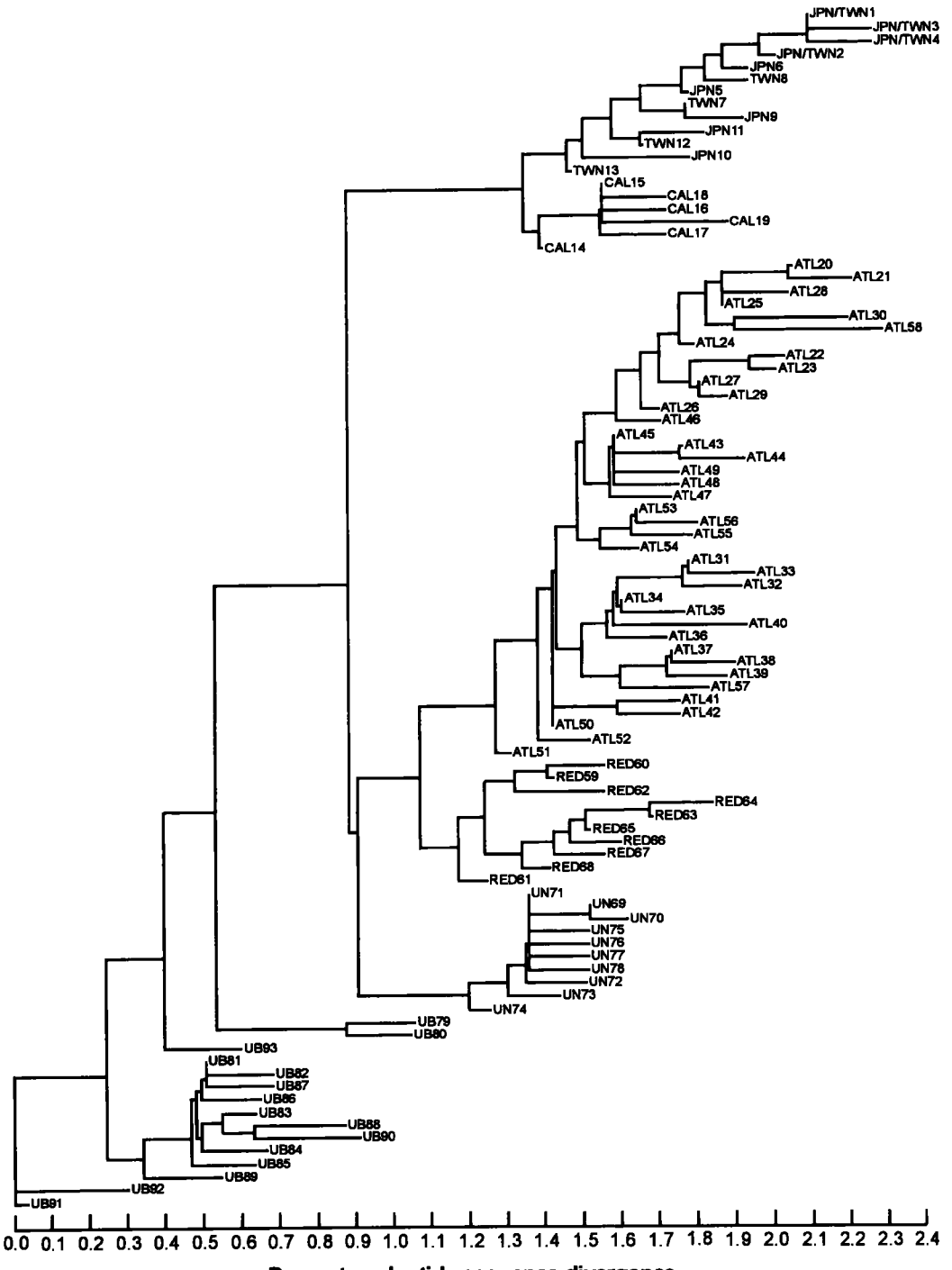
sample. Although the net nucleotide sequence divergence between A-JPN and A-MEX was small ($\delta$=0.021%), the distribution of haplotypes between the samples was significantly heterogeneous ($P$=0.013, $\alpha$=0.05). Together, the Australian and New Zealand samples of *S. australasicus* from the South Pacific were genetically distinct from the combined North Pacific samples (A-JPN and A-MEX). The mean corrected nucleotide sequence divergence between the pooled groups was high ($\delta$=0.54%), and only one haplotype was shared between the pooled South and North Pacific samples (no. 79), occurring at very different frequencies (0.05 and 0.51, respectively).

The Red Sea sample of *S. australasicus* was distinct from all other collections of this species. The mean net nucleotide sequence divergence between A-RED and the pooled data of all other *S. australasicus* was $\delta$=0.86%. The Red Sea sample was less divergent from the *S. australasicus* samples from Australia and New Zealand ($\delta$=0.51%) than were the *S. australasicus* samples from Japan and Mexico ($\delta$=1.2%)

## Phylogeographic patterns

MtDNA restriction site analysis and neighbor-joining of *S. japonicus* and *S. australasicus* mtDNA haplotypes revealed five major clusters: *S. japonicus* from the Pacific Ocean, *S. japonicus* from the Atlantic Ocean, *S. australasicus* from the Red Sea, a "ubiquitous" cluster of haplotypes of *S. australasicus* from all other samples of this species, and a "unique" cluster of only New Zealand and Australia *S. australasicus* haplotypes (Fig. 3).

Parsimony analyses were used to explore cladistic relationships among the haplotypes of *S. japonicus* and *S. australasicus* identified by mtDNA restriction site analysis. Parsimony analysis among all *Scomber* haplotypes could not be conducted because *S. scombrus* mtDNA sequences were so divergent that it was not possible to determine homologous restriction site characters among the three species. Mainly interested in patterns occurring in *S. japonicus*, we chose a root in *S. australasicus* (haplotype no. 92) on the basis of results of parsimony analyses of cytochrome *b* sequences that included *S. scombrus* and a




## Figure 3

Neighbor-joining analysis of mtDNA haplotypes of *Scomber japonicus* and *S. australasicus* identified by restriction site analysis. Branch lengths are indicated. The terminal nodes labeled ATL are Atlantic haplotypes of *S. japonicus* 20–58 from J-FLA, J-ARG, J-SAF, J-IVC, and J-ISR. Haplotypes 1–13 labeled JPN or TWN are *S. japonicus* from J-JPN and J-TWN. Haplotypes 14–9 labeled CAL are *S. japonicus* from J-CAL. Haplotypes 61–68 labeled RED are *S. australasicus* haplotypes from A-RED. Those labeled UN are "unique" haplotypes 69–78 of *S. australasicus* from A-NZL and A-AUS. Those labeled UB are "ubiquitous" haplotypes 79–93 of *S. australasicus* from A-NZL, A-AUS A-MEX, and A-JPN.

more distant outgroup, *Rastrelliger kanagurta*, and a preliminary parsimony tree drawing. Analysis of 58 informative characters yielded 1031 equally parsimonious trees. Each of these 1031 trees shared the same topology among the five major matrilines and differed only within groups, with most rearrangements occurring among Atlantic *S. japonicus* haplotypes. Branches defining the five matrilines were supported at 100% in a majority-rule consensus that illustrated the relationship of all haplotypes of *S. japonicus* and *S. australasicus* and revealed a topology that was not different from that obtained by neighbor-joining (Fig. 4).

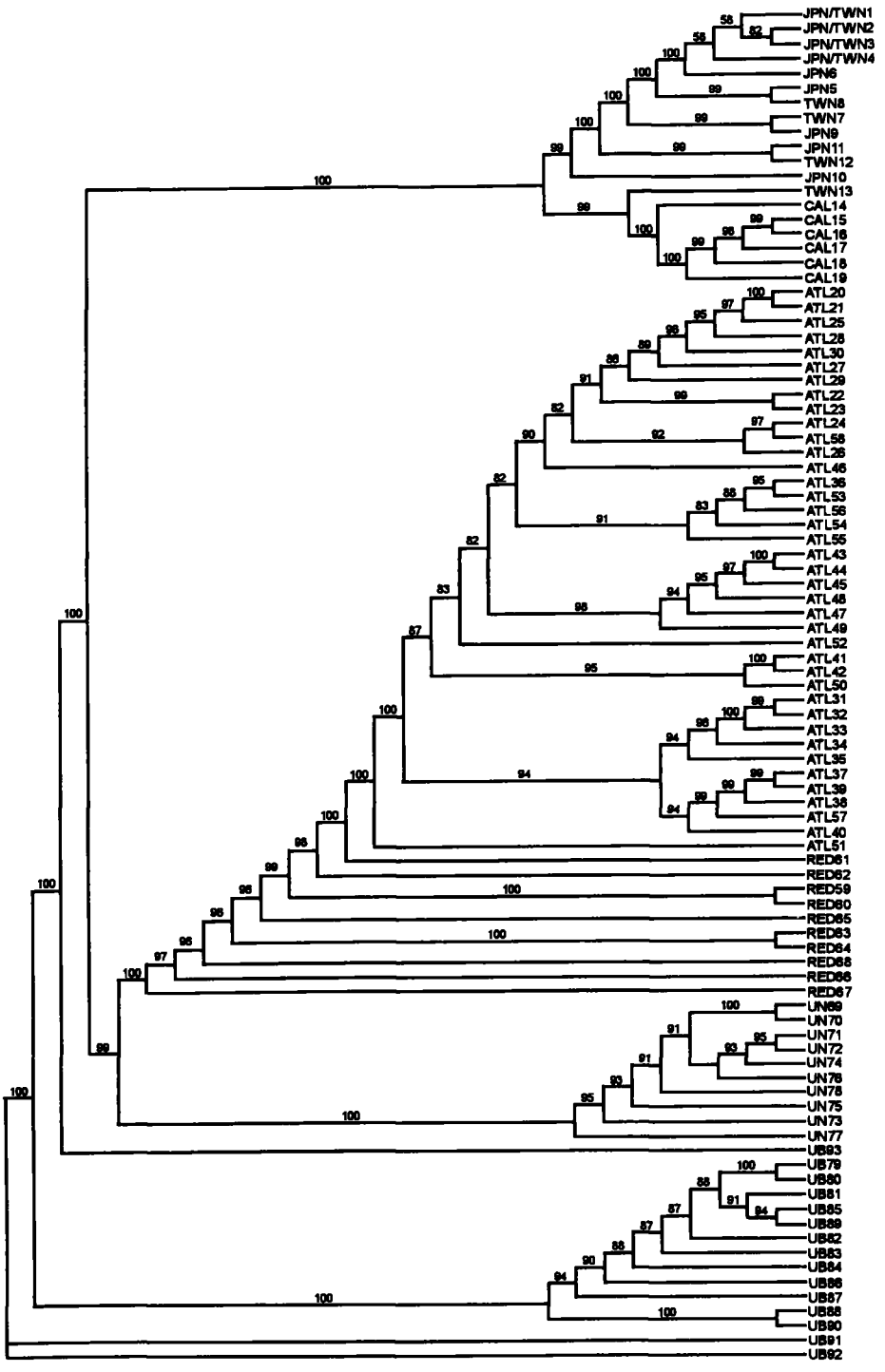
The Red Sea sample had haplotypes intermediate to *S. japonicus* and *S. australasicus*, highlighted by character state reversals. Two reversals occurred among the Red Sea *S. australasicus* and the Japan-Taiwan *S. japonicus* clades, and the unique clade of *S. australasicus*. An *Hpa*I site that is absent in eight of the 10 Red Sea haplotypes (nos. 60, 62–68), nine of the 10 unique *S. australasicus* haplotypes (nos. 69–73, 75–78), and all of the *S. japonicus* haplotypes from Japan and Taiwan, is present in all other haplotypes. A *Pvu*II site that is absent in six of the 10 Red Sea haplotypes (nos. 63–68) and all haplotypes of the unique *S. australasicus* clade is present in all other haplotypes. Consequently, corrected nucleotide sequence divergences among the Red Sea and unique *S. australasicus* haplotypes are lower than those among Red Sea and Atlantic *S. japonicus* haplotypes (Table 4). Although UPGMA cluster analysis grouped the Red Sea haplotypes with the unique *S. australasicus* haplotypes (data not shown), neighbor-joining resulted in the placement of the Red Sea sample with Atlantic *S. japonicus*, concordant with the majority-rule consensus. Neighbor-joining is favored over UPGMA because it removes the assumption that the data are ultrametric (the condition that all the taxa are equidistant from the root) (Swofford and Olsen, 1990).

Parsimony analysis of the cytochrome *b* sequences (Table 5) yielded a tree topology that was similar to the patterns observed by parsimony and neighbor-joining of mtDNA restriction site data of *S. japonicus* and *S. australasicus*. However, the analysis showed greater similarity between the unique and ubiquitous *S. australasicus* clades that were not separated by Pacific *S. japonicus*. A majority-rule consensus of two equally parsimonious trees of 86 informative characters (of 93 variable positions) of cytochrome *b* sequences showed that *S. scombrus* is the sister group to *S. japonicus* and *S. australasicus* (Fig. 5). Sequence divergences among the cytochrome *b* sequences were 1.7–3.1% in *S. australasicus*, 0.8–4.3% in *S. japonicus*, and 2.8% in *S. scombrus*. The cytochrome *b* divergences were 2.8–4.0% between haplotypes of *S. japonicus* and *S. australasicus*, and ranged from 14.6 to 17.6% between the *S. scombrus* and the *S. japonicus-S. australasicus* group. The divergence of cytochrome *b* haplotypes between *Rastrelliger kanagurta* and *S. scombrus* was 21.5% and between *Rastrelliger kanagurta* and the *S. japonicus-S. australasicus* group was 17.1–18.8%. Neighbor-joining analysis of divergences among the cytochrome *b* sequences revealed a tree that had equal topology to that in Fig. 5 (data not shown). Parsimony and neighbor-joining of mtDNA restriction site data showed a paraphyletic pattern in both *S. japonicus* and *S.*

**Table 4**

Percent net nucleotide sequence divergences (δ) among samples of *Scomber australasicus* and *Scomber japonicus* derived from mtDNA restriction site data.

| | J-FLA | J-ARG | J-ISR | J-IVC | J-SAF | J-TWN | J-JPN | J-CAL | A-RED | A-AUS | A-NZL | A-JPN | A-MEX |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| J-FLA | — | | | | | | | | | | | | |
| J-ARG | 0.042 | — | | | | | | | | | | | |
| J-ISR | 0.137 | 0.071 | — | | | | | | | | | | |
| J-IVC | 0.078 | 0.025 | –0.003 | — | | | | | | | | | |
| J-SAF | 0.165 | 0.099 | 0.007 | 0.015 | — | | | | | | | | |
| J-TWN | 1.554 | 1.472 | 1.493 | 1.522 | 1.483 | — | | | | | | | |
| J-JPN | 1.576 | 1.497 | 1.515 | 1.544 | 1.503 | –0.010 | — | | | | | | |
| J-CAL | 1.209 | 1.128 | 1.151 | 1.179 | 1.176 | 0.284 | 0.319 | — | | | | | |
| A-RED | 0.752 | 0.706 | 0.724 | 0.728 | 0.723 | 1.136 | 1.159 | 1.077 | — | | | | |
| A-AUS | 0.934 | 0.907 | 0.874 | 0.892 | 0.861 | 0.974 | 0.990 | 0.886 | 0.489 | — | | | |
| A-NZL | 0.926 | 0.909 | 0.878 | 0.894 | 0.860 | 0.991 | 1.004 | 0.872 | 0.528 | –0.019 | — | | |
| A-JPN | 1.640 | 1.599 | 1.560 | 1.579 | 1.505 | 1.523 | 1.529 | 1.533 | 1.176 | 0.554 | 0.477 | — | |
| A-MEX | 1.688 | 1.654 | 1.604 | 1.622 | 1.543 | 1.602 | 1.606 | 1.607 | 1.267 | 0.619 | 0.533 | 0.021 | — |




## Figure 4

Majority rule consensus of 1031 equally parsimonious trees of *Scomber japonicus* and *S. australasicus* mtDNA haplotypes identified by restriction site analysis. Each of the 1031 equally parsimonious trees has the same topology among the major clades, with rearrangements only within groups. Numbers at nodes indicate the percentage of times the node was supported in 1000 bootstrap replications with a heuristic search. There were 58 informative characters used to draw the tree which is 118 steps in length. The consistency index is 0.86. Terminal nodes are labeled as in Figure 3.

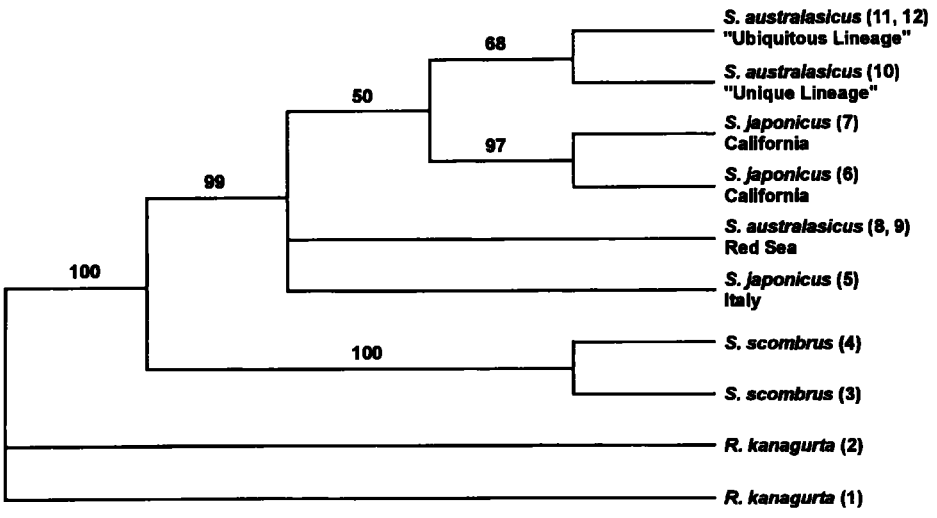



**Figure 5**

Majority rule consensus of two equally parsimonious trees drawn by using cytochrome *b* sequences of selected individuals of the major lineages chosen on the basis of results of parsimony and cluster analyses of restriction site data. The sequence numbers in parentheses correspond to the numbered sequences in Table 5. The tree is rooted to *Rastrelliger kanagurta* (sequence no. 2). Numbers at nodes indicate the percentage of times the node was supported in 1000 bootstrap replications with a heuristic search. There were 86 informative characters used to draw the tree which is 113 steps in length. The consistency index is 0.89.

*australasicus*. Parsimony analysis of cytochrome *b* sequences also revealed paraphyly in both *S. japonicus* and *S. australasicus*.

## Discussion

### Relationships at the generic level

Early studies of *Scomber* demonstrated considerable morphological divergence between species. Characterized by the presence of a swimbladder, *S. japonicus* and *S. australasicus* were once placed in the genus *Pneumatophorus*, leaving only *S. scombrus* in the genus *Scomber* (Starks, 1921). The two genera were subsequently united because many other morphological characters were shared among the three species (Fraser-Brunner, 1950; Matsui, 1967) and because the presence of a swimbladder can vary intraspecifically in the Scombridae (Collette and Gibbs, 1963).

Concordant with morphological dissimilarities between these two groups, the level of genetic divergence between *S. scombrus* and the *S. australasicus-S. japonicus* group estimated from mtDNA restriction fragment data was high (δ=11.2%). The divergence of these groups estimated from direct sequence analysis of the cytochrome *b* gene was also high (δ=16.7%). For comparison, we calculated divergences among 29 scombroid species and drew a phenetic tree (UPGMA), using the 600-bp cytochrome *b* sequences reported by Block et al. (1993).[2] The lowest intergeneric divergence in the tree was δ=3.0% between *Makaira* and *Istiophorus*, whereas the greatest was δ=31% between *Trichiurus* and *Gempylus*. The greatest divergence between species within a single genus was δ=14.6% between *Scomber japonicus* and *S. scombrus*, slightly lower than our estimate. Other interspecific divergences were δ=13.5% between *Scomberomorus cavalla* and *Scomberomorus maculatus*, 3.9% between *Sarda chiliensis* and *Sarda sarda*, 1.2–5% among five species of *Thunnus*, and 0.3–5.2% among five species of *Tetrapturus*. Although the clonal inheritance of mtDNA can result in high levels of divergence compared with estimates determined from nuclear DNA markers, the high values seen in *Scomber* suggest that a re-evaluation of generic taxonomy in *Scomber* may be in order.

### Relationships at the species level

The current taxonomy of *Scomber* is based on multiple morphological characters, including the number of interneural bones under the first dorsal fin, length of the space between the dorsal fins in rela-

[2] GenBank accession nos. L11532-L11562.

## Table 5

DNA sequences of cytochrome *b* of 12 individuals of *Scomber*, and *Rastrelliger kanagurta*, with reading frame indicated. Reported sequences of *S. japonicus* from Italy[1] and *S. scombrus*, sequences nos. 3 and 5, are from Finnerty and Block (1992). Indicated positions are relative to the full-length human mitochondrial DNA sequence[2] (Anderson et al., 1981). A '.' indicates identity to sequence number 1, and a '-' represents missing data.

| | Species | GenBank | Haplotype | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | 15085 | | | | | | | 15100 |
| 1 | *R. kanagurta* | AF032704 | Unknown | | ta | gaa | aca | tga | aac | atc | gga | gtt | g-- | | |
| 2 | *R. kanagurta* | AF032705 | Unknown | | | | | | | | | | | | |
| 3 | *S. scombrus* | L11544 | Unknown | t | g.. | ..g | ... | ... | ... | g.. | ..t | ..a | .tc | | |
| 4 | *S. scombrus* | AF032706 | S-MAS94 | | .. | ..g | ... | ... | ... | g.. | ..t | ..a | .tc | | |
| 5 | *S. japonicus* (Italy) | L11546 | Unknown | t | a.g | ..g | ... | ... | ... | ..t | ..t | ..g | .tt | | |
| 6 | *S. japonicus* | AF032707 | J-CAL15 | c | a.g | ... | ... | ... | ... | ..t | ..t | ..g | .tt | | |
| 7 | *S. japonicus* | AF032708 | J-CAL14 | | a.g | ... | ... | ... | ... | ..t | ..t | ..g | .tt | | |
| 8 | *S. australasicus* | AF032709 | A-RED62 | | .g | ..- | ... | ... | ... | ..t | --- | --- | --- | | |
| 9 | *S. australasicus* | AF032710 | A-RED60 | | | | | | | | gt | ..a | .tt | | |
| 10 | *S. australasicus* | AF032711 | A-AUS71 | c | a.g | ... | ... | ... | ... | ..t | ..t | ..a | .tt | | |
| 11 | *S. australasicus* | AF032712 | A-MEX79 | | | | | | | | ..t | ..a | .tt | | |
| 12 | *S. australasicus* | AF032712 | A-MEX81 | | | | | | | | ..t | ..a | .tt | | |

| | 15115 | | | | | | | 15130 | | | | | | 15145 | | | | | 15160 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | ctt | ctc | ctc | tta | gta | atg | ata | acc | gct | ttc | gtt | ggc | tac | gtc | ctt | ccc | tga | gga | caa | atg |
| 2 | .. | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... |
| 3 | ..c | ... | ... | c.c | ... | ... | ..g | ..t | ..c | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... |
| 4 | ..c | ... | ... | c.c | ... | ... | ..g | ..t | ..c | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... |
| 5 | ... | ... | ... | c.c | ... | ..a | ... | ... | ..a | ... | ..c | ... | ... | ... | ... | ... | ... | ..t | ... | ... |
| 6 | ... | ... | ... | c.c | ... | ..a | ... | ... | ..a | ... | ..c | ... | ... | ... | ... | ... | ... | ..c | ... | ... |
| 7 | ... | ... | ... | c.c | ... | ..a | ... | ... | ..a | ... | ..c | ... | ... | ... | ... | ... | ... | ..c | ... | ... |
| 8 | --- | --- | --- | c.c | ... | ..a | ... | ... | ..a | ... | ..c | ... | ... | ... | ... | ... | ... | ..t | ... | ... |
| 9 | ... | ... | ... | c.c | ... | ..a | ... | ... | ..a | ... | ..c | ... | ... | ... | ... | ... | ... | ..t | ... | ... |
| 10 | ... | ... | ... | c.c | ... | ..a | ... | ... | ..a | ... | ..c | ... | ... | ... | ... | ... | ... | ..c | ... | ... |
| 11 | ... | ... | ... | c.c | ... | ..a | ... | ... | ..a | ... | ..c | ... | ... | ... | ... | ... | ... | ..c | ... | ..a |
| 12 | ... | ... | ... | c.c | ... | ..a | ... | ... | ..a | ... | ..c | ... | ... | ... | ... | ... | ... | ..c | ... | ..a |

| | 15175 | | | | | | | 15190 | | | | | | 15205 | | | | | 15220 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | tcc | ttc | tga | ggt | gca | act | gtc | att | act | aac | ctc | ctt | tcc | gca | gtc | cct | tat | gta | ggc | act |
| 2 | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... |
| 3 | ... | ... | ... | ..a | ..c | ... | ... | ..c | ... | ... | ..a | ..c | ..a | ... | ..t | ..a | ..c | ... | ... | ..a |
| 4 | ... | ... | ... | ..g | ..c | ... | ... | ..c | ... | ... | ..a | ..c | ..a | ... | ..t | ..a | ..c | ... | ... | ..a |
| 5 | ... | ... | ... | ..g | ..c | ... | ... | ... | ..g | ... | ..a | ..c | ..g | ... | ... | ..a | ..c | ..t | ..t | ... |
| 6 | ... | ... | ... | ..g | ..c | ..c | ... | ... | ..a | ..t | ..a | ... | ..a | ... | ... | ..a | ..c | ..c | ..t | ... |
| 7 | ... | ... | ... | ..g | ..c | ..c | ... | ... | ..a | ..t | ..a | ... | ..g | ... | ... | ..a | ..c | ..c | ..t | ... |
| 8 | ... | ... | ... | ..a | ..c | ... | ... | ... | ..a | ... | ..a | ... | ..g | ... | ... | ..a | ..c | ..c | ..t | ... |
| 9 | ... | ... | ... | ..a | ..c | ... | ... | ... | ..a | ... | ..a | ... | ..g | ... | ... | ..a | ..c | ..c | ..t | ... |
| 10 | ... | ... | ... | ..g | ..c | ..c | ... | ... | ..a | ... | ..a | ... | ..g | ... | ... | ..a | ..c | ..c | ..t | ... |
| 11 | ... | ... | ... | ..g | ..c | ..c | ... | ... | ..a | ... | ..a | ... | ..g | ... | ... | ..a | ..c | ... | ..t | ... |
| 12 | ... | ... | ... | ..g | ..c | ..c | ... | ... | ..a | ... | ..a | ... | ..g | ... | ... | ..a | ..c | ... | ..t | ... |

| | 15235 | | | | | | | 15250 | | | | | | 15265 | | | | | 15280 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | acc | cta | gta | gaa | tga | atc | tga | ggt | ggc | ttc | tcc | gtc | gac | aat | gca | acc | ctc | act | cga | ttc |
| 2 | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... |
| 3 | ..a | ..c | ..t | ... | ... | ..t | ... | ..g | ... | ... | ..a | ..a | ... | ... | ..t | ..g | ... | ... | ..g | ... |
| 4 | ..a | ..c | ..t | ... | ... | ..t | ... | ..g | ... | ... | ..a | ..a | ... | ... | ..t | ..g | ... | ... | ..g | ... |
| 5 | ..a | ..c | ..t | ..g | ... | ... | ... | ..c | ... | ... | ..a | ..a | ... | ... | ..c | ... | ... | ..c | ... | ... |
| 6 | ... | ..c | ..t | ..g | ... | ... | ... | ..c | ... | ... | ..a | ..a | ... | ... | t.c | ... | ... | ..c | ... | ... |
| 7 | ... | ..c | ..t | ..g | ... | ... | ... | ..c | ... | ... | ..a | ..a | ... | ... | ..c | ... | ... | ..c | ... | ... |
| 8 | ..a | ..c | ..t | ..g | ... | ... | ... | ..c | ... | ... | ..a | ..a | ... | ... | ..c | ... | ... | ..c | ... | ... |
| 9 | ..a | ..c | ..t | ..g | ... | ... | ... | ..c | ... | ... | ..a | ..a | ... | ... | ..c | ... | ... | ..c | ... | ... |
| 10 | ..a | ..c | ..t | ..g | ... | ... | ..g | ..c | ... | ... | ..a | ..a | ... | ... | ..c | ... | ... | ..c | ... | ... |
| 11 | ..a | ..c | ..t | ..g | ... | ... | ... | ..c | ... | ... | ..a | ..a | ... | ... | ..c | ... | ... | ..c | ... | ... |
| 12 | ..a | ..c | ..t | ..g | ... | ... | ... | ..c | ... | ... | ..a | ..a | ... | ... | ..c | ... | ... | ..c | ... | ... |

*continued on next page*

tion to the dorsal groove length, and relative positions of the anal and dorsal fin origins (Matsui, 1967). Previous genetic data supported the specific status of *S. australasicus* and *S. japonicus*: allozyme electrophoresis revealed fixed allelic differences between *S. australasicus* and Pacific *S. japonicus* and pro-

**Table 5 (continued)**

| | 15295 | | | | | | | 15310 | | | | | 15325 | | | | | | 15340 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | ttc | gca | ttc | cat | ttc | ctt | tac | ccg | ttc | gtc | atc | gca | gca | ata | aca | atc | ctg | cac | ctt | ctc |
| 2 | ... | ... | ... | ... | ... | ... | .t. | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... |
| 3 | ... | ..c | ..t | ..c | ... | ..a | .t. | ..c | ..t | ..t | ... | tt. | ..g | gc. | g.g | g.t | ..c | ... | ..a | ..a |
| 4 | ... | ..c | ..t | ..c | ... | ..a | .t. | ..c | ..t | ..t | ... | tt. | ..g | gc. | g.g | g.t | ..c | ... | ..a | ..a |
| 5 | ..t | ..c | ... | ..c | ... | ..a | .t. | ..a | ... | ... | ... | ctg | ... | gc. | ... | ..t | ..t | ... | ..g | ..a |
| 6 | ..t | ..c | ... | ..c | ... | ..a | .t. | ..a | ... | ..t | ..t | ctg | ... | gc. | ... | ..t | ..t | ... | ..g | ..a |
| 7 | ..t | ..c | ... | ..c | ... | ..a | .t. | ..a | ... | ..t | ..t | ctg | ... | gc. | ... | ..t | ..t | ... | ..g | ..a |
| 8 | ..t | ..c | ... | ..c | ... | ..a | .t. | ..a | ... | ..t | ... | ctg | ... | gc. | ... | ..t | ..t | ... | ..g | ..a |
| 9 | ..t | ..c | ... | ..c | ... | ..a | .t. | ..a | ... | ..t | ... | ctg | ... | gc. | ... | ..t | ..t | ... | ..g | ..a |
| 10 | ..t | ..c | ... | ..c | ... | ..a | .t. | ..a | ... | ..t | ... | -t. | ..g | gc. | ... | ..t | ..t | ... | ..g | ..a |
| 11 | ..t | ..c | ... | ..c | ... | ..a | .t. | ..a | ... | ..t | ..t | ct. | ... | gc. | ... | ..t | ..t | ... | ..g | ..a |
| 12 | ..t | ..c | ... | ..c | ... | ..a | .t. | ..a | ... | ..t | ..t | ct. | ... | gc. | ... | ..t | ..t | ... | ..g | ..a |

| | 15355 | | | | | | | 15370 | | | | | 15385 | | | | | | 15400 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | ttc | cta | cat | gaa | act | gga | tca | aag | aac | cca | atg | ggc | cta | aac | tca | aat | gca | gat | aaa | atc |
| 2 | ... | ... | ... | ... | ... | ... | ... | ..c | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... |
| 3 | ... | ..t | ... | ... | ... | ..g | ... | ..c | ... | ... | ..t | ... | ... | ... | ..t | ... | ... | ..c | ... | ... |
| 4 | ... | ..t | ... | ... | ... | ..g | ... | ..c | ... | ... | ..t | ... | ... | ... | ..t | ... | ... | ..c | ... | ... |
| 5 | ... | ... | ... | ... | ..c | ..g | ... | ..c | ... | ... | ..t | ... | ... | ... | ..t | ... | ... | ..c | ... | ... |
| 6 | ... | ... | ... | ..g | ..c | ..g | ... | ..c | ... | ... | ..t | ... | ... | ... | ..c | ... | ... | ..c | ..g | ... |
| 7 | ... | ... | ... | ..g | ..c | ..g | ... | ..c | ... | ... | ..t | ... | ... | ... | ..c | ... | ... | ..c | ... | ... |
| 8 | ... | ... | ... | ... | ..c | ..g | ... | ..c | ... | ... | ..t | ... | ... | ... | ..c | ... | ... | ..c | ... | ... |
| 9 | ... | ... | ... | ... | ..c | ..g | ... | ..c | ... | ... | ..t | ... | ... | ... | ..c | ... | ... | ..c | ... | ... |
| 10 | ... | ... | ... | ... | ..c | ..g | ..g | ..c | ... | ... | ..t | ... | ... | ... | ..c | ... | ..g | ..c | ... | ... |
| 11 | ... | ... | ... | ... | ..c | ..g | ..g | ..c | ... | ... | ..t | ... | ... | ... | ..t | ... | ..g | ..c | ... | ... |
| 12 | ... | ... | ... | ... | ..c | ..g | ..g | ..c | ... | ... | ..t | ... | ... | ... | ..t | ... | ..g | ..c | ... | ... |

| | 15415 | | | | | | | 15430 | | | | | 15445 | | | | | | 15460 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | tcc | ttc | cac | ccc | tac | ttc | acc | tac | aaa | gat | gcc | cta | gga | ttt | gcc | atc | ctt | ctt | atg | gct |
| 2 | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... | ... |
| 3 | ..g | ... | ..t | ..g | ... | ..t | ..g | ..t | ... | ..c | ct. | ..c | ..c | ... | ... | g.t | ..c | ... | ..a | .gc |
| 4 | ..g | ... | ..t | ..g | ... | ..t | ..g | ..t | ... | ..c | ct. | ..c | ..c | ... | ... | g.t | ..c | ... | ..a | .gc |
| 5 | ... | ... | ... | ..a | ... | ... | ... | ... | ... | ..c | ct. | ..t | ..c | ... | ... | g.. | ..c | ..c | g.a | ..c |
| 6 | ... | ... | ... | ..a | ... | ... | ... | ... | ... | ..c | ct. | ..t | ..c | ... | ... | g.. | ..c | ..c | g.. | ..c |
| 7 | ... | ... | ... | ..a | ... | ... | ... | ... | ... | ..c | ct. | ..t | ..c | ... | ... | g.. | ..c | ..c | g.. | ..c |
| 8 | ... | ... | ... | ..a | ... | ... | ... | ... | ... | ..c | ct. | ..t | ..c | ... | ... | g.. | ..c | ..c | g.. | . |
| 9 | ... | ... | ... | ..a | ... | ... | ... | ... | ... | ..c | ct. | ..t | ..c | ... | ... | g.. | ..c | ..c | g.. | ..c |
| 10 | ... | ... | ... | ..a | ... | ... | ... | ... | ... | ..c | ct. | ..t | ..c | ... | ... | g.. | ... | ..c | g.. | ..c |
| 11 | ... | ... | ... | ..a | ... | ... | ... | ... | ... | ..c | ct. | ..t | ..c | ... | ... | g.. | ... | ..c | g.. | ..c |
| 12 | ... | ... | ... | ..a | ... | ... | ... | ... | ... | ..c | ct. | ..t | ..c | ... | ... | g.. | ... | ..c | g.. | ..c |

| | 15475 | | | | | | | 15490 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 | ctt | aaa | tcc | cta | gca | ctc | ttc | tcc | ccc | aac | ct |
| 2 | .. | | | | | | | | | | |
| 3 | ... | .cc | ... | ... | ... | ... | ... | ... | ..g | ... | . |
| 4 | ... | .cc | ... | ... | ... | ... | ... | ... | ..g | ... | . |
| 5 | ... | tcc | ..t | ... | ... | ... | . | | | | |
| 6 | ..c | tcc | ..t | ..c | ... | ... | ... | ..t | ... | ... | .. |
| 7 | ..c | tcc | ..t | ..c | ... | ... | ... | ..t | ... | ... | .. |
| 8 | | | | | | | | | | | |
| 9 | ... | tcc | .. | | | | | | | | |
| 10 | ..c | tcc | ..t | ..c | ... | ... | ... | c.t | ... | ... | .. |
| 11 | ..c | tcc | ..t | .. | | | | | | | |
| 12 | ..c | tcc | ..t | .. | | | | | | | |

[1] Block, B. 1993. Personal communication.
[2] GenBank accession no. V00662.

vided no evidence for the hybrid origin of individuals of intermediate coloration (Kijima et al., 1986).

The systematic status of geographically distant *S. japonicus* populations has been problematic because this species is characterized by considerable morphological variability. Several names have been used for the groups occurring in different areas: *S. japonicus*, western North Pacific (Houttuyn, 1782); *S. colias*, eastern Atlantic (Gmelin, 1789); *S. grex*, western North Atlantic (Mitchell, 1815); *S. diego*, eastern North Pacific (Ayres, 1857); *S. peruanus*, eastern South Pacific (Jordan and Hubbs, 1925); and *Pneumatophorus japonicus marplatensis*, western South Atlantic (López, 1955). Differences in pigmentation, tooth crenulation, scale size, and gill-raker counts on the lower first arch distinguish fish from the Pacific, western Atlantic, and eastern Atlantic. These groups were synonymized into the single species *S. japonicus* by Matsui (1967) because "[morphological] differences are smaller [between populations] than those which separate sympatric species of *Scomber* and *Rastrelliger*, and it thus seems correct to regard *S. japonicus* as a single polytypic species."

The mtDNA data did not refute the specific status of *S. japonicus* and *S. australasicus* reported by Matsui (1967). In fact, a greater divergence was found among two mtDNA lineages within *S. australasicus* than between any other pairs of samples of *S. japonicus* and *S. australasicus*. The two divergent *S. australasicus* mtDNA lineages, which differed by an average of $\delta$=1.84% according to the restriction site data, were equally represented in both South Pacific collections. A cursory allozyme analysis of 10 loci from 10 individuals of each lineage revealed no significant allelic differences in nuclear encoded genes (Scoles, 1994). The phylogenetic pattern observed in *S. australasicus* appears to be the result of postdivergence introgressive hybridization.

A similar phylogenetic pattern has been observed in other pelagic marine fishes. In blue marlin (*Makaira nigricans*), "ubiquitous" haplotypes occurring in both the Atlantic and Pacific oceans were highly divergent from other Atlantic haplotypes, forming a "unique" clade revealed by mtDNA analysis restriction fragment analysis ($n$=114, $\delta$=0.15%, Graves and McDowell, 1995) and by sequencing 612 bp of the mtDNA cytochrome *b* gene ($n$=26, $\delta$=1.6%, Finnerty and Block, 1992). Similarly, sailfish (*Istiophorus platypterus*) had Pacific and Atlantic clades that differed by $\delta$=0.27% (Graves and McDowell, 1995). The patterns in these fishes and in *S. australasicus* demonstrate that considerable mtDNA divergence can occur among haplotypes within a single sample, and suggest the limitations of basing taxonomic status only on mtDNA data.

The mtDNA data indicated the possibility of multiple taxonomic lineages within *S. japonicus*. The two major groups of *S. japonicus* (Atlantic and Pacific) are differentiated by nearly as much as are the two different lineages within *S. australasicus*. The nucleotide sequence divergence between some *S. japonicus* groups is nearly as great as between groups of *S. japonicus* and *S. australasicus* (Table 4). Unlike the two divergent *S. australasicus* lineages that were observed in single samples, the *S. japonicus* groups are geographically partitioned. The paraphyletic relationship (Figs. 3–5), geographic isolation, high level of genetic divergence (Table 4), and morphological differences among the *S. japonicus* lineages support recognition of separate species: *Scomber japonicus* Houttuyn, 1782, in the Pacific; and *Scomber colias* Gmelin, 1789, the Atlantic. This conclusion assumes that there is no significant sampling error (see Moore, 1995) and should be tested by further morphological and nuclear DNA data analyses. The Red Sea population of *Scomber*, previously considered as *S. japonicus* (Matsui, 1967), was re-examined by Baker and Collette (1998), who have assigned the Red Sea-northern Indian Ocean population to *Scomber australasicus* on the basis of morphological characters.

## Phylogeographic patterns and their origins

The distribution of haplotypes between eastern and western Atlantic samples of *S. scombrus* indicated the populations do not share a common gene pool. The close relationship among haplotypes in these samples (Fig. 2) contrasts with the finding of two divergent mtDNA matrilines ($\delta$=3.7%) in samples of capelin, *Mallotus villosus*, from eastern and western regions of the North Atlantic (Dodson et al., 1991). An intermediate level of divergence to that of *S. scombrus* and of capelin was observed between samples of bluefish (*Pomatomus saltatrix*, $\delta$=0.26%, 1 fixed difference) from the eastern and western Atlantic Ocean (Goodbred and Graves, 1996). The lower divergence in *S. scombrus* may be the result of more recent isolation or greater vagility.

Patterns of divergence in *S. japonicus* and other species in the Atlantic Ocean appear to be highly influenced by species' vagility and warm water in the tropics. Haplotype distributions were significantly different between *S. japonicus* samples from the western Atlantic Ocean (J-FLA and J-ARG), and unique haplotypes occurred within each at relatively high frequencies (10–20%). Similary, a population-genetic study of the shortfin mako shark demonstrated significantly different mtDNA haplotype frequencies between samples from the western North and South Atlantic Ocean ($\delta$=0.13%, $P$<0.001) (Heist

et al., 1996). Bluefish sampled from Brazil and the eastern U.S. coast were even more divergent (δ=1.48%) (Goodbred and Graves, 1996). But in the eastern Atlantic, no significant differentiation was seen among *S. japonicus* samples from the eastern Mediterranean Sea (J-ISR), Ivory Coast (J-IVC), and South Africa (J-SAF). Additionally, although no haplotypes were shared between bluefish samples from the Mediterranean Sea and South Africa (δ=0.35%), haplotypes in the two samples were closely related (Goodbred and Graves, 1996). In contrast, the less mobile gray mullet, *Mugil cephalis*, sampled from the Mediterranean Sea, and South Africa were highly divergent (δ=2.92) (Crosetti et al., 1994). These data suggest that fewer barriers to gene flow occur between northern and southern regions of the eastern Atlantic versus those of the western Atlantic. The tropical water of the east Atlantic occupies the smallest area of all the tropical regions, and temperate species are suspected of crossing this region by moving under the warm water mass, thereby achieving an antitropical distribution (Briggs, 1974).

It is possible that *S. japonicus* larval or adult exchange occurs between Gulf of Guinea and the northernmost extension of the southwest Atlantic *S. japonicus* population assisted by trans-Atlantic equatorial currents. These locations are separated by the most narrow region of the Atlantic Ocean. Haplotype frequencies were significantly different among all samples across the Atlantic Ocean except in one pairwise comparison of J-ARG and J-IVC. Genetic similarity between these samples may reflect recent isolation or contemporary gene flow. Eastern and western Atlantic populations of *S. japonicus* are, however, morphologically differentiated on the basis of nonoverlapping gill-raker counts (Starks, 1921; Matsui, 1967).

The sample of *S. australasicus* from the Red Sea (A-RED) had the highest estimated haplotypic diversity. No haplotypes were shared between the samples of *S. japonicus* from the Atlantic Ocean and the Red Sea, suggesting no gene flow through the Suez Canal. Fifty-two fish species are known to have made the passage, all but one from the Red Sea to the Mediterranean Sea (Golani, 1993). *Rastrelliger kanagurta*, a close relative of *Scomber*, is among those known to have invaded the Mediterranean Sea from the Red Sea (Collette, 1970). The samples of *S. japonicus* from the eastern Mediterranean Sea (J-ISR) and *S. australasicus* from the Red Sea were divergent by δ=0.72%, one fixed restriction site difference, and an additional site that was nearly fixed. These findings do not exclude the possibility of movement through the Suez Canal, which may be revealed by larger sample sizes.

Fishery data indicate that *S. japonicus* in the region of Japan and Taiwan represent separate populations with unique spawning grounds and larval retention areas (Sato, 1990). Although haplotypes in the sample from the eastern Pacific (J-CAL) were not found in other *S. japonicus* samples, haplotypes in *S. japonicus* samples from the northwest region of the Pacific Ocean (J-JPN and J-TWN) were shared at similar frequencies. The data of our study are consistent with exchange among the two western Pacific populations. Whether exchange is the result of larval drift or adult movement is indeterminable; however, movement of adult *S. australasicus* is known to occur between these regions (Chang and Wu, 1977). Greater trans-Pacific divergence than that observed in *S. japonicus* was seen in gray mullet sampled from Hawaii and the Galapagos Islands (δ=1.4%) (Crosetti et al., 1994), suggesting these population were isolated for a considerably longer period than mackerel.

The level of nucleotide sequence divergence between Atlantic and Pacific samples of *S. japonicus* was lower than expected. It has been suggested that in mammals, mitochondrial DNA evolves at rate of 2% nucleotide sequence divergence per million years (Brown et al., 1979). When this rate of divergence is applied to the 1.4% net nucleotide sequence divergence observed between Atlantic and Pacific *S. japonicus*, it appears that the two populations were isolated about 700,000 years. Such estimates of divergence are approximate at best, but if this rate of divergence is valid in *Scomber japonicus*, the observed nucleotide sequence divergence is lower than would have resulted if these populations were isolated by the uplift of the Isthmus of Panamá, 3.1–3.6 million years ago (Keigwin, 1978). Gene flow may have occurred between the two regions since the uplift of Panamá, during times of warmer climates (Avise, 1992).

Samples of *S. australasicus* between New Zealand and Australia, regions separated by nearly 2000 km of deep ocean, were genetically homogeneous. Perhaps there is a high potential for genetic exchange in *S. australasicus*, which was also indicated by comparison of *S. australasicus* samples from the northern Pacific. Although a test of homogeneity between A-JPN and A-MEX was marginally significant ($P$=0.013), the mean nucleotide sequence divergence was only 0.02%, which contrasted with the 0.30% divergence and fixed restriction site difference between samples of *S. japonicus* from the eastern and western Pacific Ocean.

The lowest genotypic and nucleotide sequence diversity in the study occurred in a sample from the Revillagigedo Islands (A-MEX) and may indicate the origin of this population by means of a founder event

from a source population in the northwest Pacific region or Hawaii. Colonization of the Revillagigedo Islands may have occurred through the migration of adults. Gene flow between other isolated populations (J-IVC and J-ARG; A-NZL and A-AUS) was also suggested by the mtDNA data and may be facilitated by the high vagility of species of *Scomber*.

Despite the genetic similarity observed among widely separated samples of *S. australasicus*, exchange in the north-south direction is restricted. Haplotypes of the unique New Zealand-Australia lineage were not observed in samples from Japan or Mexico. These data suggest that the equatorial region of the Pacific is a barrier to gene flow in *S. australasicus*, and together with the significant difference observed between western Atlantic *S. japonicus* samples, strongly emphasizes the impact of physical oceanographic conditions in shaping phylogeographic patterns. *Scomber japonicus* from the eastern North and South Pacific were also differentiated by allozyme analysis which revealed three differentiated loci of fourteen that were variable (Nei's $D$=0.033, $F_{st}$=0.20) (Stepien and Rosenblatt, 1996). These observations support the hypothesis that physical oceanographic characteristics of equatorial regions may limit gene flow in species of *Scomber*, and possibly a variety of other temperate pelagic species.

These data demonstrate that levels of heterogeneity reflect species vagilities and are shaped by physical oceanographic processes. Other studies have demonstrated that population structure in several species is generally lower between populations separated by vast ocean basins than between those separated by land masses, in some cases suggesting continued gene flow (Vawter et al., 1980; Rosenblatt and Waples, 1986; Shulman and Bermingham, 1995). But not all genetic data support a simple relationship between the degree of geographic barriers, dispersal, and genetic relatedness. In one study, five species with various life history features that limit dispersal showed no intraspecific differentiation, whereas one, *Gnatholepis thompsoni*, which had nonpelagic eggs and a long planktonic life, showed population structure across the Caribbean Sea (Shulman and Bermingham, 1995). Sinclair (1988) reviewed the effects of oceanographic characteristics on population structure and concluded that it is defined at the planktonic phase of the life history, rather than at the juvenile or adult phases, and is largely regulated by the physical environment. However, Thresher and Brothers (1985) were unable to relate larval stage duration or adult size to dispersal in several angelfish species (Pomacanthidae) and suggested that geological features are better predictors of dispersal. Clearly, the processes by which population structure emerges in marine fishes are complex. Our data support the hypothesis that oceanographic characteristics are significant in limiting dispersal in *Scomber*, especially in some equatorial regions. The exchange of adult individuals among populations appears to have a significant effect on limiting the divergence between some populations, possibly reflecting adaptations in *Scomber* for survival in the pelagic environment.

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# Population structure and stock identification of British Columbia coho salmon, *Oncorhynchus kisutch*, based on microsatellite DNA variation

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**Abstract.**—We used genetic variation at three microsatellite DNA loci to describe population structure in 34 coho salmon populations from British Columbia and to perform stock composition analysis on simulated mixed-stock fishery samples. Each microsatellite locus was highly polymorphic, with 31 alleles at *Ots*101, 20 alleles at *Ots*3, and 38 alleles at *Ots*103. Average observed heterozygosities were 86.3%, 73.3% and 74.9%, respectively. Analysis of genetic distances revealed three relatively homogeneous, geographically based groups of coho salmon populations in the following regions: the upper Skeena and Nass River watersheds, the lower Fraser River drainage, and the upper Fraser River-Thompson River watersheds. Coastal populations from the mainland of British Columbia, Vancouver Island, and the Queen Charlotte Islands formed a more heterogeneous regional stock grouping. Significantly different allele frequencies were observed among populations within regions, and allele frequencies were generally temporally stable in multiyear samples. Phylogenetic lineages within British Columbia coho salmon likely reflect geographic patterns of recolonization from at least three separate glacial refugia after the last ice age. Local spawning populations within regions may form metapopulations, but current levels of gene flow among subpopulations are apparently insufficient to prevent differentiation at neutral genetic loci. Maximum-likelihood estimates of stock composition were accurate and precise, indicating great potential for management of coho salmon at the level of metapopulations or "evolutionarily significant units" in domestic and international mixed-stock fisheries. Individual fish were identified to stock by using a discriminant analysis with a high degree of accuracy in a few regions, but more generally with approximately 50% success.

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Of the five commercially important Pacific salmon (*Oncorhynchus*) species exploited in the commercial, recreational and aboriginal fisheries of British Columbia, coho salmon is the one that has shown the largest decline in abundance in both historical (the past 100 years) and recent (the past 40 years) times (Northcote and Atagi, 1997). Coho salmon abundance has also declined dramatically in Washington State, Oregon, and California, to the extent that a number of coho salmon populations, including all of those from the upper Columbia River system, are considered extinct and others are considered endangered (Nehlsen et al., 1991; Weitkamp et al., 1995). The list of factors that may have contributed to declining coho salmon abundance is long, and includes overfishing, loss of freshwater habitat, misguided enhancement efforts, limited marine carrying capacity, and climate changes resulting in altered oceanic conditions (Fraser et al., 1982; Beamish and Bouillon, 1993; Walters, 1993; Reisenbichler, 1997).

Because coho salmon tend to spawn in small streams and rivers that are especially vulnerable to degradation through human activities, freshwater habitat degradation has been considered a major factor in declining coho abundance (Fraser et al., 1982). Similarly, coho salmon commonly are believed to be overexploited because of the mixed-stock nature of most coho salmon fisheries and the frequent bycatch of coho salmon in fisheries directed toward other species (Fraser et al., 1982). Nevertheless, the consistent long-term decline in coho abundance, which has occurred over a broad geographic range in habitats both degraded and pristine and under a range of exploitation levels (Weitkamp et al., 1995; Northcote and Atagi, 1997), indicates that changes occurring in the marine environment are also having a major negative influence on coho salmon populations. This seems especially plausible because in some regions the recent decline in coho abundance coincides with a stable number or increase in abundance of other heavily freshwater-dependent salmonids, such as sockeye salmon and stream-type chinook salmon (Northcote and Atagi, 1997). Thus, coho salmon populations may be less amenable to rebuilding through local or regional habitat improvement and harvest management than populations of other species.

The increasing conservation concerns for coho salmon have led to substantial efforts to quantify

biodiversity in the species (Bartley et al., 1992; Forbes et al., 1993; Weitkamp et al., 1995; Miller and Withler, 1997), to define the appropriate geographic scale of management to conserve the observed biodiversity (Weitkamp et al., 1995; McPhail, 1997; Small et al., 1998), and to develop stock composition methods that would enable the geographically based management required for conservation efforts (Bartley et al., 1992; Beacham et al., 1996; Miller et al., 1996; Van Doornik et al., 1996; Small et al., 1998). Coho salmon populations of California, Oregon, Washington, and southern British Columbia have been categorized into evolutionarily significant units (ESUs), that is to say, reproductively isolated populations or groups of populations that represent the important phylogenetic components of genetic variability in the species (Waples, 1991; Weitkamp et al., 1995). The use of ESUs to delineate biodiversity in Pacific salmon is concordant with an emerging model of metapopulation structure that may supersede the stock concept that has long been applied to these species. Local spawning groups of salmon are no longer viewed as independent and persistent locally adapted "stocks" (Ricker, 1972), but rather as interrelated components, or subpopulations, of a geographically based cluster of such components (the metapopulation) that share a relatively recent evolutionary history and among which gene flow still occurs (McPhail, 1997). Although adaptive differences may arise among the subpopulations of a metapopulation as the result of an appropriate balance between migration and natural selection within subpopulations, they are unlikely to persist over evolutionary time scales as subpopulations go extinct or are swamped by gene flow from adjacent subpopulations. Given this model of salmonid population structure, it is individual metapopulations (ESUs), rather than individual stocks, that managers must conserve to provide the reservoirs of genetic diversity for future evolution within the species.

In coho salmon, and other Pacific salmonids, there is accumulating evidence that the dominant influence on population structure has been the pattern of dispersal from isolated glacial refugia after the last ice age (Gharrett et al., 1987; Wood et al., 1994; Bickham et al., 1995, Miller and Withler 1997; Small et al., 1998). The distinct phylogenetic lineages that can be traced with molecular markers reveal patterns of recolonization of freshwater habitat from refugia located in the Columbia River drainage (Cascadia), the Bering Sea-Yukon River (Beringia), and coastal refugia that likely existed in British Columbia, as well as in more southern waters. For coho, chinook and sockeye salmon, many of these genetically distinct intraspecific lineages converge in British Columbia, providing us with the opportunity and challenge of conserving biodiversity *in situ*.

In this study, we examine variation among and within major river systems and coastal regions in British Columbia at three coho salmon microsatellite loci: *Ots*101, *Ots*3, and *Ots*103. Microsatellite DNA loci consist of highly variable single locus markers containing tandemly repeated arrays of noncoding 1–6 basepair core sequences (Tautz, 1989). For each locus, variation in the number of core sequences creates alleles differing in size by multiples of core-unit length. The rapid rate of mutation and high heterozygosity that characterize microsatellite loci have made them the molecular tool of choice in studies of population structure in vertebrates, including salmonid fish (Angers et al., 1995; McConnell et al., 1995; Scribner et al., 1996; Beacham et al., 1998; Small et al., 1998). In our study, we demonstrate the dual utility of microsatellite variation in defining the regionally based phylogenetic lineages of coho salmon and in accurately detecting their presence in mixed-stock fisheries for management purposes.

## Methods

### DNA samples and PCR

Adult coho salmon tissue samples were collected from 34 coho salmon populations in British Columbia (Fig. 1). Several populations were sampled in multiple years. See Miller et al., (1996) for descriptions of purified genomic DNA extractions from tissues collected up to 1993. Genomic DNA samples from 1994 and 1995 were extracted by using a chelex resin protocol (Small et al., 1998). Microsatellite alleles at three loci were polymerase chain reaction (PCR)-amplified (Sakai et al., 1985) from DNA samples by using primers for the tetranucleotide microsatellites *Ots*101 and *Ots*103 (Small et al., 1998) and the dinucleotide microsatellite, *Ots*3 (Banks[1]). Primer sequences, the PCR conditions, and size-fractionation of the PCR products are described in Small et al. (1998). PCR products from standard test fish were included on each gel to estimate the precision of allele sizing among gels.

### DNA band analysis

Gels were scanned with a Kodak charge-coupled device camera and the images were analyzed as outlined in Small et al. (1998) with BioImage Whole

[1] Banks, M. 1995. Bodega Marine Laboratory, POB 247, Bodega Bay, CA 94923. Personal commun.

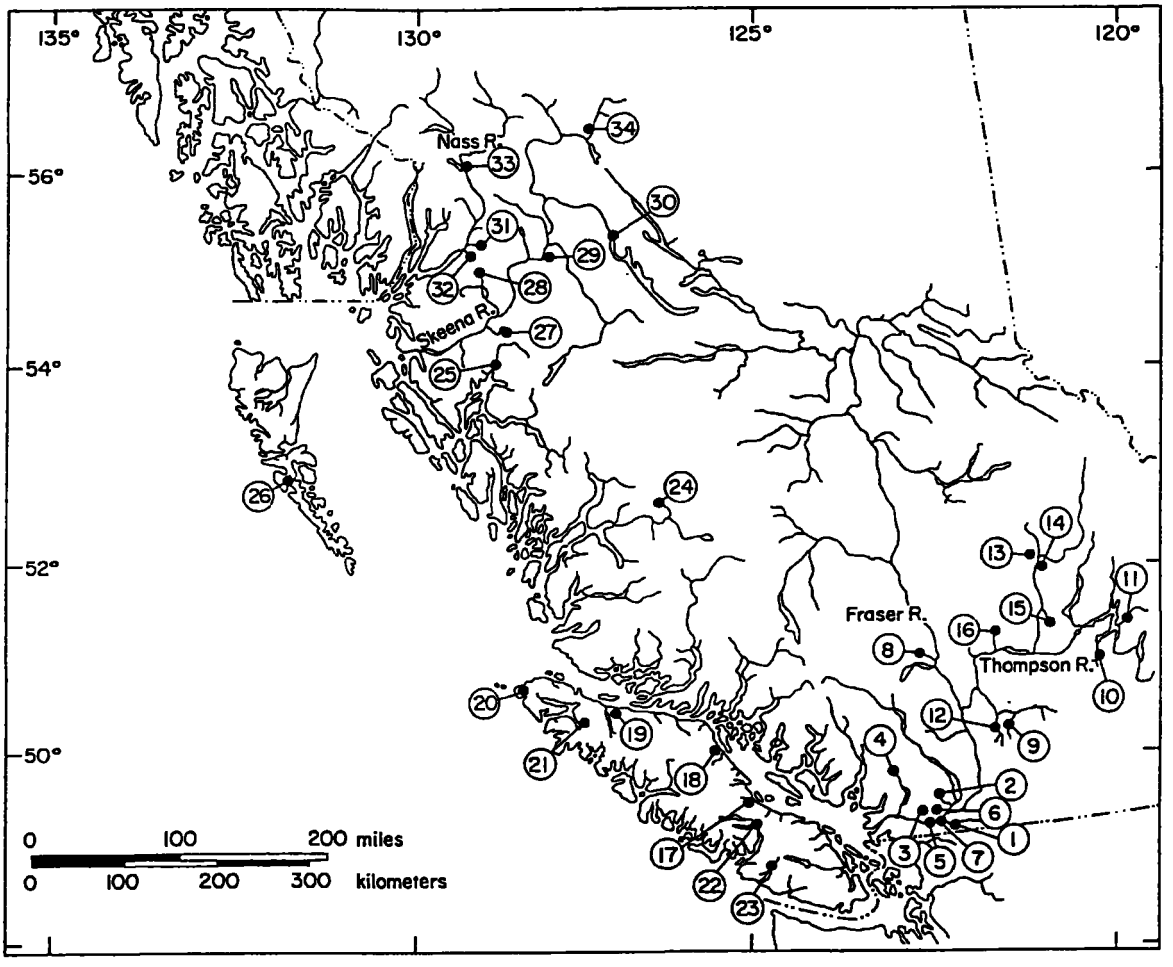


**Figure 1**

Map of British Columbia showing locations of coho salmon samples. Population numbers are placed near the waterway (region or river system name in bold type precedes population names) : **lower Fraser River** 1) Chilliwack River; 2) Chehalis River; 3) Stave River; 4) Upper Pitt River; 5) Nicomen Slough; 6) Norrish Creek; 7) Inch Creek; **upper Fraser River** 8) Bridge River; **Thompson River** 9) Coldwater River; 10) Salmon River; 11) Eagle River; 12) Spius Creek; 13) Lemieux Creek; 14) Dunn Creek; 15) Louis River; 16) Deadman River; **East Coast Vancouver Island** 17) Big Qualicum River; 18) Quinsam River; **North Coast Vancouver Island** 19) Cluxewe River; 20) Stephens Creek; 21) Waukwaas Creek; **West Coast Vancouver Island** 22) Robertson Creek; 23) Nitinat River; **Central Coast** 24) Atnarko River; 25) Kitimat River; **Queen Charlotte Island** 26) Pallant Creek; **Skeena River** 27) Clearwater River; 28) Cedar River; 29) Toboggan Creek; 30) Babine River; 34) Sustut River; **Nass River** 31) Tseax River; 32) Zolzap River; 33) Meziadin River.

Band software (Millipore Corp. Imaging systems, Ann Arbor, MI). The software estimated allele sizes to the nearest basepair with a molecular weight-size-grid created with a 20-bp DNA ladder. Alleles were identified by using a binning procedure (Gill et al., 1990; Galbraith et al., 1991). Allelic bin intervals were created from peaks in allele frequency histograms and precision estimates from standard test fish (Small et al., 1998). Bin intervals for *Ots*101 and *Ots*3 alleles are presented in Table 1 and bin intervals for *Ots*103 alleles are presented in Table 2. The mean bin width was four or more standard deviations from allele sizes of test fish. Allele size was generally four bp for *Ots*101, two bp for *Ots*3, and four bp for *Ots*103. When alleles became infrequent at the extremes of the size ranges and the precision of sizing alleles decreased, alleles were grouped into larger bins (Small et al., 1998). Thirty-one alleles were defined for *Ots*101, 20 alleles were defined for *Ots*3, and 37 alleles (as well as a null allele) were defined for *Ots*103.

## Data analysis

Linkage tests confirmed that the three loci are unlinked and pedigree analysis confirmed Mendelian

**Table 1**

Allele frequencies, observed heterozygosity (Hobs) and expected heterozygosity (Hexp) at *Ots*101 and *Ots*3 loci for coho salmon populations region with region names abbreviated as follows: Central Coast (C Coast), North Coast Vancouver Island (NCVI), West Coast Vancouver Island Populations out of Hardy-Weinberg equilibrium are indicated by * next to the observed heterozygosity. The allele number (in basepairs) is the al. (1998), Table 3. Sample sizes for *Ots*101 are given underneath the population names and for *Ots*3 are indicated by *N*.

| Alleles | **Pallant** 93 | Atnarko 87 | Kitimat 148 | **C Coast** 235 | Cluxewe 38 | Stephens 65 | Waukwaas 30 | **NCVI** 133 | Nitinat 39 | Robertson 84 | **WCVI** 123 | Quinsam 160 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Ots*101 | | | | | | | | | | | | |
| 96 | **0** | 0 | 0 | **0** | 0 | 0 | 0 | **0** | 0 | 0.065 | **0.045** | 0 |
| 100 | **0.016** | 0.034 | 0.014 | **0.021** | 0.053 | 0.031 | 0.017 | **0.034** | 0 | 0.030 | **0.021** | 0.003 |
| 104 | **0.005** | 0.011 | 0.051 | **0.036** | 0.053 | 0.077 | 0.067 | **0.068** | 0 | 0 | **0** | 0.003 |
| 108 | **0.016** | 0.011 | 0.014 | **0.013** | 0.039 | 0.031 | 0.083 | **0.045** | 0 | 0 | **0** | 0.019 |
| 112 | **0.054** | 0.011 | 0.037 | **0.028** | 0.013 | 0.008 | 0.017 | **0.011** | 0.103 | 0.036 | **0.057** | 0.072 |
| 116 | **0.022** | 0.029 | 0.064 | **0.051** | 0 | 0.023 | 0 | **0.011** | 0 | 0.071 | **0.049** | 0.051 |
| 120 | **0.065** | 0.138 | 0.081 | **0.098** | 0.092 | 0.023 | 0.017 | **0.041** | 0.051 | 0 | **0.016** | 0.081 |
| 124 | **0.141** | 0.092 | 0.088 | **0.088** | 0.171 | 0.131 | 0.101 | **0.135** | 0 | 0.042 | **0.028** | 0.084 |
| 127 | **0.091** | 0.075 | 0.057 | **0.064** | 0.066 | 0.008 | 0.051 | **0.034** | 0 | 0.054 | **0.037** | 0.097 |
| 131 | **0.124** | 0.098 | 0.095 | **0.094** | 0.145 | 0.108 | 0.101 | **0.117** | 0.141 | 0.024 | **0.061** | 0.151 |
| 135 | **0.027** | 0.006 | 0.031 | **0.021** | 0.013 | 0.038 | 0.017 | **0.026** | 0.091 | 0.071 | **0.077** | 0.019 |
| 139 | **0.081** | 0.011 | 0.031 | **0.024** | 0.013 | 0.054 | 0.067 | **0.045** | 0.051 | 0.054 | **0.053** | 0.041 |
| 143 | **0.032** | 0.011 | 0.024 | **0.019** | 0.039 | 0.069 | 0.033 | **0.053** | 0.013 | 0.083 | **0.061** | 0.063 |
| 147 | **0.011** | 0.017 | 0.041 | **0.032** | 0.079 | 0.123 | 0 | **0.083** | 0.205 | 0.149 | **0.167** | 0.022 |
| 151 | **0.022** | 0.011 | 0.010 | **0.011** | 0 | 0.054 | 0.017 | **0.030** | 0.051 | 0.054 | **0.053** | 0.009 |
| 154 | **0.011** | 0.006 | 0.027 | **0.019** | 0.039 | 0.015 | 0.017 | **0.023** | 0.013 | 0 | **0.004** | 0.003 |
| 158 | **0.011** | 0.029 | 0.047 | **0.041** | 0.013 | 0 | 0.017 | **0.008** | 0.077 | 0.012 | **0.033** | 0.019 |
| 161 | **0.027** | 0.034 | 0.027 | **0.031** | 0 | 0.008 | 0.051 | **0.015** | 0.064 | 0.125 | **0.106** | 0.041 |
| 165 | **0** | 0.069 | 0.021 | **0.038** | 0 | 0.023 | 0.051 | **0.023** | 0.026 | 0.048 | **0.041** | 0.059 |
| 169 | **0** | 0.046 | 0.047 | **0.047** | 0.053 | 0 | 0 | **0.015** | 0.038 | 0.048 | **0.045** | 0.069 |
| 173 | **0.048** | 0.040 | 0.057 | **0.051** | 0.026 | 0.008 | 0.101 | **0.034** | 0.013 | 0 | **0.004** | 0.031 |
| 177 | **0.043** | 0.057 | 0.017 | **0.031** | 0.013 | 0.046 | 0.117 | **0.053** | 0.038 | 0.012 | **0.021** | 0.022 |
| 181 | **0.038** | 0.052 | 0.041 | **0.045** | 0.039 | 0.054 | 0 | **0.038** | 0 | 0.006 | **0.004** | 0.009 |
| 185 | **0** | 0.034 | 0.037 | **0.036** | 0.026 | 0.038 | 0 | **0.026** | 0 | 0.012 | **0.008** | 0.019 |
| 189 | **0** | 0.040 | 0.021 | **0.028** | 0.013 | 0 | 0 | **0.004** | 0 | 0.006 | **0.004** | 0 |
| 193 | **0.005** | 0.006 | 0.021 | **0.015** | 0 | 0.015 | 0.017 | **0.011** | 0 | 0 | **0** | 0 |
| 197 | **0.027** | 0 | 0 | **0** | 0 | 0 | 0.017 | **0.004** | 0 | 0 | **0** | 0 |
| 201 | **0.016** | 0.011 | 0 | **0.004** | 0 | 0 | 0.017 | **0.004** | 0 | 0 | **0** | 0.009 |
| 205 | **0.032** | 0.011 | 0.003 | **0.006** | 0 | 0 | 0.017 | **0.004** | 0.013 | 0 | **0.004** | 0.003 |
| 210 | **0.016** | 0.006 | 0.003 | **0.004** | 0 | 0.015 | 0 | **0.008** | 0 | 0 | **0** | 0 |
| 215 | **0.032** | 0.011 | 0 | **0.004** | 0 | 0 | 0 | **0** | 0.013 | 0 | **0.004** | 0.003 |
| Hobs | **0.861** | *0.862 | 0.909 | **0.885** | 0.921 | 0.877 | 0.967 | **0.909** | 0.718 | 0.869 | **0.821** | 0.900 |
| Hexp | **0.935** | 0.943 | 0.946 | **0.945** | 0.921 | 0.938 | 0.933 | **0.939** | 0.897 | 0.940 | **0.927** | 0.931 |
| *Ots*3 | | | | | | | | | | | | |
| *N* | 93 | 86 | 145 | 231 | 38 | 68 | 32 | 138 | 40 | 84 | 124 | 160 |
| 66 | **0.129** | 0.052 | 0.045 | **0.048** | 0 | 0.029 | 0.109 | **0.040** | 0.013 | 0.012 | **0.012** | 0 |
| 68 | **0.005** | 0 | 0 | **0** | 0 | 0 | 0 | **0** | 0 | 0 | **0** | 0 |
| 70 | **0** | 0 | 0 | **0** | 0 | 0 | 0 | **0** | 0 | 0 | **0** | 0 |
| 72 | **0** | 0 | 0 | **0** | 0 | 0 | 0 | **0** | 0 | 0 | **0** | 0 |
| 74 | **0.011** | 0 | 0.007 | **0.004** | 0 | 0 | 0 | **0** | 0 | 0 | **0** | 0 |
| 76 | **0** | 0 | 0.003 | **0.002** | 0.013 | 0 | 0 | **0.004** | 0 | 0 | **0** | 0 |
| 78 | **0** | 0.035 | 0.003 | **0.015** | 0 | 0 | 0 | **0** | 0 | 0 | **0** | 0 |
| 82 | **0** | 0 | 0 | **0** | 0 | 0 | 0 | **0** | 0 | 0 | **0** | 0 |
| 84 | **0** | 0 | 0.014 | **0.009** | 0 | 0 | 0 | **0** | 0 | 0 | **0** | 0.025 |
| 86 | **0.027** | 0.285 | 0.124 | **0.184** | 0.079 | 0.051 | 0.063 | **0.062** | 0.112 | 0.024 | **0.052** | 0.125 |
| 88 | **0.258** | 0.215 | 0.328 | **0.286** | 0.316 | 0.191 | 0.234 | **0.236** | 0.275 | 0.179 | **0.211** | 0.281 |
| 90 | **0.071** | 0.017 | 0.003 | **0.009** | 0.013 | 0.059 | 0.047 | **0.043** | 0 | 0.221 | **0.149** | 0.034 |
| 92 | **0.011** | 0.012 | 0.066 | **0.045** | 0.092 | 0.141 | 0.078 | **0.112** | 0.151 | 0.101 | **0.117** | 0.019 |
| 94 | **0.323** | 0.251 | 0.238 | **0.242** | 0.368 | 0.419 | 0.234 | **0.362** | 0.138 | 0.292 | **0.242** | 0.338 |
| 96 | **0** | 0.017 | 0.024 | **0.022** | 0.039 | 0.007 | 0.047 | **0.025** | 0 | 0.006 | **0.004** | 0.003 |
| 98 | **0.145** | 0.116 | 0.124 | **0.121** | 0.066 | 0.051 | 0.094 | **0.065** | 0.313 | 0.161 | **0.211** | 0.166 |
| 100 | **0.016** | 0 | 0.003 | **0.002** | 0 | 0.029 | 0.016 | **0.018** | 0 | 0.006 | **0.004** | 0.006 |
| 102 | **0.005** | 0 | 0.017 | **0.011** | 0.005 | 0.078 | 0.013 | **0.033** | 0 | 0 | **0** | 0.003 |
| 104 | **0** | 0 | 0 | **0** | 0 | 0 | 0 | **0** | 0 | 0 | **0** | 0 |
| 106 | **0** | 0 | 0 | **0** | 0 | 0 | 0 | **0** | 0 | 0 | **0** | 0 |
| Hobs | **0.699** | 0.698 | *0.752 | **0.732** | 0.816 | 0.765 | 0.751 | **0.775** | 0.751 | 0.786 | **0.774** | 0.712 |
| Hexp | **0.785** | 0.790 | 0.800 | **0.809** | 0.763 | 0.765 | 0.875 | **0.789** | 0.775 | 0.798 | **0.814** | 0.762 |

from British Columbia. The weighted mean of allele frequencies for regions (in bold type) follow allele frequencies for individual populations in the (WCVI), East Coast Vancouver Island (ECVI), Skeena River (Skeena), Nass River (Nass), Thompson River (TR), and lower Fraser River (L Fr). lower limit of the allele bin. Allele frequencies for individual populations in the lower Fraser River and the Thompson River are given in Small et

| Big Qualicum 200 | **ECVI** 260 | Toboggan 164 | Cedar 47 | Babine 139 | Clear-water 48 | Sustut 36 | **Skeena** 434 | Tseax 40 | Zolzap 47 | Mexiadin 64 | **Nass** 151 | **TR** 1015 | **L Fr** 1043 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 0 | **0** | 0 | 0 | 0 | 0 | 0 | **0** | 0 | 0 | 0 | **0** | **0** | **0** |
| 0.011 | **0.007** | 0 | 0 | 0 | 0 | 0 | **0** | 0.013 | 0 | 0 | **0.004** | **0** | **0.018** |
| 0.023 | **0.014** | 0.018 | 0 | 0.029 | 0.010 | 0.028 | **0.020** | 0.013 | 0.011 | 0.063 | **0.022** | **0** | **0.009** |
| 0.025 | **0.022** | 0.015 | 0.053 | 0.068 | 0.063 | 0.056 | **0.045** | 0.025 | 0.096 | 0.078 | **0.059** | **0.001** | **0.037** |
| 0 | **0.032** | 0.003 | 0.021 | 0.004 | 0.021 | 0.042 | **0.010** | 0.025 | 0.021 | 0.031 | **0.026** | **0.001** | **0.011** |
| 0.011 | **0.028** | 0.165 | 0.149 | 0.032 | 0.042 | 0.125 | **0.104** | 0.162 | 0.138 | 0.078 | **0.114** | **0.077** | **0.034** |
| 0.085 | **0.084** | 0.186 | 0.138 | 0.273 | 0.302 | 0.181 | **0.220** | 0.151 | 0.074 | 0.172 | **0.129** | **0.015** | **0.122** |
| 0.081 | **0.082** | 0.049 | 0.138 | 0.137 | 0.031 | 0.056 | **0.084** | 0.101 | 0.096 | 0.078 | **0.088** | **0.001** | **0.082** |
| 0.081 | **0.088** | 0.003 | 0.043 | 0.011 | 0.073 | 0 | **0.017** | 0.051 | 0.011 | 0.078 | **0.037** | **0.007** | **0.112** |
| 0.131 | **0.139** | 0.076 | 0.074 | 0.007 | 0.115 | 0.014 | **0.052** | 0.025 | 0.064 | 0.023 | **0.037** | **0.071** | **0.119** |
| 0.055 | **0.039** | 0.031 | 0.085 | 0.094 | 0.011 | 0.028 | **0.054** | 0.151 | 0.117 | 0.016 | **0.088** | **0.011** | **0.121** |
| 0.063 | **0.053** | 0.006 | 0.043 | 0.011 | 0.031 | 0 | **0.014** | 0.025 | 0.021 | 0.023 | **0.022** | **0.014** | **0.073** |
| 0.025 | **0.042** | 0 | 0.053 | 0 | 0.031 | 0 | **0.009** | 0.013 | 0.021 | 0.016 | **0.011** | **0** | **0.042** |
| 0.018 | **0.019** | 0.003 | 0.043 | 0 | 0.021 | 0.028 | **0.010** | 0.075 | 0.043 | 0.031 | **0.051** | **0.002** | **0.048** |
| 0.027 | **0.019** | 0.006 | 0.011 | 0.004 | 0.031 | 0 | **0.008** | 0.013 | 0.032 | 0 | **0.015** | **0.019** | **0.027** |
| 0.035 | **0.021** | 0.006 | 0 | 0 | 0.011 | 0 | **0.003** | 0 | 0.106 | 0 | **0.037** | **0.051** | **0.021** |
| 0.013 | **0.015** | 0 | 0 | 0.004 | 0 | 0.014 | **0.002** | 0 | 0.011 | 0.008 | **0.007** | **0.011** | **0.011** |
| 0.018 | **0.028** | 0 | 0.011 | 0 | 0.042 | 0.028 | **0.008** | 0.013 | 0.021 | 0 | **0.011** | **0.081** | **0.033** |
| 0.058 | **0.058** | 0 | 0.043 | 0 | 0.021 | 0.014 | **0.008** | 0 | 0 | 0.039 | **0.015** | **0.056** | **0.011** |
| 0.045 | **0.054** | 0.031 | 0 | 0.022 | 0.011 | 0 | **0.020** | 0.050 | 0.021 | 0.016 | **0.029** | **0.159** | **0.005** |
| 0.051 | **0.041** | 0.064 | 0.021 | 0.141 | 0.063 | 0.014 | **0.075** | 0 | 0.064 | 0.055 | **0.048** | **0.111** | **0.011** |
| 0.005 | **0.013** | 0.046 | 0.011 | 0.051 | 0.021 | 0.069 | **0.041** | 0 | 0 | 0.086 | **0.040** | **0.086** | **0.005** |
| 0.005 | **0.007** | 0.031 | 0.011 | 0.018 | 0.031 | 0.111 | **0.030** | 0.013 | 0.011 | 0.047 | **0.029** | **0.091** | **0.006** |
| 0.013 | **0.015** | 0.052 | 0.032 | 0.058 | 0.052 | 0.097 | **0.055** | 0.038 | 0 | 0 | **0.011** | **0.076** | **0.009** |
| 0.013 | **0.007** | 0.119 | 0.011 | 0.029 | 0 | 0.056 | **0.060** | 0.038 | 0.011 | 0.055 | **0.040** | **0.026** | **0.013** |
| 0.027 | **0.015** | 0.082 | 0 | 0.011 | 0 | 0.042 | **0.038** | 0.025 | 0.011 | 0.008 | **0.015** | **0.017** | **0.008** |
| 0.035 | **0.019** | 0.009 | 0 | 0 | 0.021 | 0 | **0.006** | 0 | 0 | 0 | **0** | **0.006** | **0.011** |
| 0.011 | **0.011** | 0.003 | 0.011 | 0 | 0 | 0 | **0.002** | 0.013 | 0.011 | 0.016 | **0.015** | **0.007** | **0.003** |
| 0.045 | **0.026** | 0 | 0 | 0.004 | 0.011 | 0 | **0.002** | 0 | 0 | 0 | **0** | **0.001** | **0.001** |
| 0 | **0** | 0.003 | 0 | 0 | 0 | 0 | **0.001** | 0 | 0 | 0 | **0** | **0.001** | **0.001** |
| 0 | **0.001** | 0 | 0 | 0 | 0 | 0 | **0** | 0 | 0 | 0 | **0** | **0.001** | **0** |
| 0.885 | **0.889** | 0.835 | 0.809 | 0.853 | 0.813 | 0.806 | **0.822** | 0.851 | 0.883 | 0.844 | **0.821** | **0.881** | **0.874** |
| 0.935 | **0.936** | 0.902 | 0.915 | 0.871 | 0.915 | 0.892 | **0.902** | 0.925 | 0.936 | 0.718 | **0.914** | **0.915** | **0.915** |
| 191 | 351 | 161 | 48 | 139 | 47 | 37 | 432 | 39 | 46 | 52 | 137 | 1016 | 1048 |
| 0.065 | **0.036** | 0.012 | 0.021 | 0.108 | 0 | 0.068 | **0.047** | 0.013 | 0.033 | 0.048 | **0.033** | **0** | **0.034** |
| 0 | **0** | 0 | 0 | 0 | 0 | 0 | **0** | 0 | 0 | 0 | **0** | **0** | **0** |
| 0 | **0** | 0 | 0 | 0 | 0 | 0 | **0** | 0 | 0 | 0 | **0** | **0** | **0.001** |
| 0.003 | **0.001** | 0 | 0 | 0 | 0 | 0 | **0** | 0 | 0 | 0 | **0** | **0** | **0** |
| 0 | **0** | 0.003 | 0 | 0 | 0 | 0 | **0.001** | 0 | 0 | 0 | **0** | **0** | **0** |
| 0.011 | **0.006** | 0.003 | 0 | 0 | 0 | 0 | **0.001** | 0 | 0 | 0 | **0** | **0** | **0** |
| 0 | **0** | 0 | 0 | 0 | 0.011 | 0 | **0.002** | 0 | 0.022 | 0 | **0.007** | **0** | **0** |
| 0.005 | **0.003** | 0 | 0.011 | 0 | 0 | 0 | **0.002** | 0 | 0 | 0 | **0** | **0** | **0.001** |
| 0.016 | **0.021** | 0.006 | 0.031 | 0 | 0 | 0.054 | **0.010** | 0.051 | 0.011 | 0.011 | **0.022** | **0** | **0.004** |
| 0.102 | **0.113** | 0.065 | 0.229 | 0.111 | 0.128 | 0.271 | **0.132** | 0.154 | 0.272 | 0.125 | **0.182** | **0.011** | **0.082** |
| 0.209 | **0.241** | 0.181 | 0.156 | 0.227 | 0.181 | 0.054 | **0.182** | 0.103 | 0.174 | 0.163 | **0.150** | **0.125** | **0.249** |
| 0.045 | **0.041** | 0.102 | 0 | 0.065 | 0.053 | 0.041 | **0.068** | 0.077 | 0.076 | 0.067 | **0.073** | **0.078** | **0.051** |
| 0.071 | **0.047** | 0.009 | 0.021 | 0.007 | 0.011 | 0.108 | **0.019** | 0.167 | 0.011 | 0.115 | **0.095** | **0.235** | **0.114** |
| 0.262 | **0.296** | 0.363 | 0.292 | 0.223 | 0.319 | 0.203 | **0.292** | 0.218 | 0.185 | 0.115 | **0.168** | **0.444** | **0.282** |
| 0.063 | **0.036** | 0.006 | 0.011 | 0.014 | 0.021 | 0.027 | **0.013** | 0.128 | 0.033 | 0.106 | **0.088** | **0.047** | **0.028** |
| 0.136 | **0.151** | 0.127 | 0.198 | 0.108 | 0.149 | 0.054 | **0.125** | 0.038 | 0.152 | 0.154 | **0.120** | **0.026** | **0.106** |
| 0.013 | **0.011** | 0 | 0 | 0 | 0.021 | 0 | **0.002** | 0.051 | 0.011 | 0 | **0.018** | **0.006** | **0.018** |
| 0.003 | **0.003** | 0 | 0 | 0 | 0 | 0 | **0** | 0 | 0 | 0 | **0** | **0.029** | **0.031** |
| 0 | **0** | 0.051 | 0.041 | 0 | 0 | 0.014 | **0.037** | 0.011 | 0.058 | 0.032 | **0.026** | **0** | **0** |
| 0 | **0** | 0.071 | 0.068 | 0 | 0 | 0.095 | **0.064** | 0 | 0.038 | 0.064 | **0.015** | **0** | **0** |
| *0.757 | **0.735** | 0.714 | 0.792 | 0.763 | 0.723 | *0.703 | **0.728** | 0.744 | 0.696 | 0.788 | **0.729** | **0.657** | **0.772** |
| 0.848 | **0.815** | 0.801 | 0.812 | 0.849 | 0.796 | 0.865 | **0.826** | 0.850 | 0.812 | 0.885 | **0.864** | **0.722** | **0.822** |

**Table 2**

Uncorrected and corrected (bold type) allele frequencies, observed heterozygosity (Hobs) and expected heterozygosity (Hexp) at *Ots*103 locus frequencies of the populations in the region, with region names abbreviated as in Table 1. Populations out of Hardy-Weinberg equilibrium cies for individual populations in the lower Fraser River and the Thompson River are given in Table 3 of Small et al. (1998). Sample sizes

| Alleles | **Pallant** 93 | Atnarko 87 | **Kitimat** 148 | **C Coast** 235 | Cluxewe 38 | Stephens 65 | Waukwaas 30 | **NCVI** 133 | Nitinat 39 | Robertson 84 | **WCVI** 123 | Quinsam 160 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 61 | **0** | 0 | 0.007 | **0.004** | 0 | 0.037 | 0 | **0.018** | 0.105 | 0 | **0.031** | 0 |
| | **0** | **0** | **0.006** | **0.004** | **0** | **0.037** | **0** | **0.018** | **0.080** | **0** | **0.024** | **0** |
| 71 | **0** | 0 | 0 | **0** | 0.013 | 0.022 | 0 | **0.014** | 0 | 0 | **0** | 0 |
| | **0** | **0** | **0** | **0** | **0.013** | **0.022** | **0** | **0.014** | **0** | **0** | **0** | **0** |
| 75 | **0.218** | 0.039 | 0.081 | **0.064** | 0.184 | 0.265 | 0.156 | **0.217** | 0 | 0.018 | **0.012** | 0.147 |
| | **0.223** | **0.041** | **0.077** | **0.064** | **0.162** | **0.257** | **0.152** | **0.205** | **0** | **0.017** | **0.012** | **0.139** |
| 79 | **0.048** | 0.006 | 0.017 | **0.012** | 0 | 0 | 0.016 | **0.004** | 0.053 | 0.185 | **0.138** | 0.038 |
| | **0.048** | **0.006** | **0.016** | **0.012** | **0** | **0** | **0.016** | **0.004** | **0.050** | **0.161** | **0.124** | **0.035** |
| 83 | **0.021** | 0 | 0 | **0** | 0.026 | 0 | 0 | **0.007** | 0 | 0 | **0** | 0 |
| | **0.021** | **0** | **0** | **0** | **0.026** | **0** | **0** | **0.007** | **0** | **0** | **0** | **0** |
| 86 | **0.005** | 0 | 0.003 | **0.002** | 0.013 | 0.088 | 0.047 | **0.058** | 0.026 | 0.012 | **0.016** | 0 |
| | **0.005** | **0** | **0.003** | **0.002** | **0.013** | **0.089** | **0.033** | **0.053** | **0.025** | **0.011** | **0.016** | **0** |
| 90 | **0** | 0.006 | 0.003 | **0.004** | 0 | 0.007 | 0.016 | **0.007** | 0 | 0.030 | **0.020** | 0.034 |
| | **0** | **0.006** | **0.003** | **0.004** | **0** | **0.007** | **0.016** | **0.007** | **0** | **0.023** | **0.016** | **0.033** |
| 94 | **0** | 0.079 | 0.013 | **0.037** | 0.013 | 0 | 0 | **0.004** | 0.053 | 0 | **0.016** | 0.053 |
| | **0** | **0.075** | **0.013** | **0.035** | **0.013** | **0** | **0** | **0.004** | **0.039** | **0** | **0.012** | **0.051** |
| 98 | **0.005** | 0.067 | 0.010 | **0.031** | 0.026 | 0.059 | 0.031 | **0.043** | 0 | 0.024 | **0.016** | 0 |
| | **0.005** | **0.064** | **0.010** | **0.029** | **0.014** | **0.059** | **0.017** | **0.038** | **0** | **0.023** | **0.016** | **0** |
| 102 | **0.117** | 0.028 | 0.037 | **0.033** | 0.105 | 0 | 0 | **0.029** | 0.039 | 0 | **0.012** | 0.016 |
| | **0.117** | **0.028** | **0.033** | **0.031** | **0.096** | **0** | **0** | **0.026** | **0.038** | **0** | **0.012** | **0.016** |
| 106 | **0.165** | 0.017 | 0.047 | **0.035** | 0.026 | 0.051 | 0.016 | **0.036** | 0.276 | 0.042 | **0.110** | 0.003 |
| | **0.163** | **0.017** | **0.043** | **0.033** | **0.026** | **0.051** | **0.016** | **0.036** | **0.224** | **0.040** | **0.095** | **0.003** |
| 110 | **0.069** | 0.073 | 0.044 | **0.053** | 0 | 0.015 | 0.047 | **0.018** | 0.039 | 0.054 | **0.047** | 0.034 |
| | **0.063** | **0.073** | **0.037** | **0.050** | **0** | **0.015** | **0.033** | **0.015** | **0.026** | **0.037** | **0.033** | **0.029** |
| 114 | **0.027** | 0.051 | 0.034 | **0.037** | 0.013 | 0.044 | 0.125 | **0.054** | 0.026 | 0.060 | **0.043** | 0.009 |
| | **0.027** | **0.042** | **0.029** | **0.034** | **0.013** | **0.039** | **0.125** | **0.052** | **0.025** | **0.047** | **0.040** | **0.009** |
| 117 | **0.005** | 0.006 | 0.060 | **0.039** | 0 | 0.015 | 0.156 | **0.043** | 0 | 0 | **0** | 0 |
| | **0.005** | **0.006** | **0.056** | **0.037** | **0** | **0.015** | **0.124** | **0.034** | **0** | **0** | **0** | **0** |
| 121 | **0.011** | 0 | 0.013 | **0.008** | 0.079 | 0.007 | 0.047 | **0.036** | 0.053 | 0.048 | **0.047** | 0 |
| | **0.011** | **0** | **0.013** | **0.008** | **0.073** | **0.007** | **0.033** | **0.030** | **0.039** | **0.046** | **0.044** | **0** |
| 125 | **0.005** | 0.006 | 0.007 | **0.006** | 0.092 | 0.037 | 0.219 | **0.094** | 0.013 | 0.036 | **0.028** | 0.013 |
| | **0.005** | **0.006** | **0.006** | **0.006** | **0.092** | **0.037** | **0.191** | **0.087** | **0.013** | **0.034** | **0.028** | **0.010** |
| 129 | **0.011** | 0 | 0.020 | **0.012** | 0.066 | 0 | 0 | **0.018** | 0 | 0 | **0** | 0.025 |
| | **0.011** | **0** | **0.017** | **0.010** | **0.054** | **0** | **0** | **0.015** | **0** | **0** | **0** | **0.022** |
| 133 | **0.053** | 0.056 | 0.007 | **0.025** | 0 | 0 | 0 | **0** | 0 | 0 | **0** | 0.022 |
| | **0.053** | **0.052** | **0.006** | **0.023** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0.022** |
| 136 | **0.011** | 0.011 | 0.003 | **0.006** | 0 | 0 | 0 | **0** | 0.039 | 0.006 | **0.016** | 0.041 |
| | **0.011** | **0.011** | **0.003** | **0.006** | **0** | **0** | **0** | **0** | **0.038** | **0.006** | **0.016** | **0.038** |
| 140 | **0** | 0 | 0.003 | **0.002** | 0 | 0.022 | 0 | **0.011** | 0.066 | 0.006 | **0.024** | 0.056 |
| | **0** | **0** | **0.003** | **0.002** | **0** | **0.022** | **0** | **0.011** | **0.052** | **0.006** | **0.020** | **0.054** |
| 144 | **0** | 0.017 | 0.010 | **0.012** | 0 | 0.088 | 0.016 | **0.047** | 0.079 | 0 | **0.024** | 0.022 |
| | **0** | **0.017** | **0.007** | **0.010** | **0** | **0.088** | **0.016** | **0.047** | **0.064** | **0** | **0.020** | **0.022** |
| 148 | **0** | 0.034 | 0.010 | **0.019** | 0.039 | 0.066 | 0 | **0.043** | 0 | 0 | **0** | 0.019 |
| | **0** | **0.034** | **0.010** | **0.019** | **0.039** | **0.066** | **0** | **0.043** | **0** | **0** | **0** | **0.019** |
| 152 | **0** | 0.051 | 0.010 | **0.025** | 0.053 | 0 | 0 | **0.014** | 0 | 0.024 | **0.016** | 0.009 |
| | **0** | **0.039** | **0.010** | **0.019** | **0.053** | **0** | **0** | **0.014** | **0** | **0.023** | **0.016** | **0.009** |
| 156 | **0** | 0.062 | 0.040 | **0.047** | 0.053 | 0.029 | 0.016 | **0.033** | 0 | 0 | **0** | 0.025 |
| | **0** | **0.062** | **0.039** | **0.047** | **0.042** | **0.029** | **0.016** | **0.030** | **0** | **0** | **0** | **0.025** |
| 160 | **0.021** | 0.079 | 0.084 | **0.080** | 0 | 0.015 | 0 | **0.007** | 0.013 | 0 | **0.004** | 0.041 |
| | **0.021** | **0.079** | **0.071** | **0.075** | **0** | **0.015** | **0** | **0.007** | **0.013** | **0** | **0.004** | **0.036** |
| 165 | **0.021** | 0.022 | 0.101 | **0.070** | 0.105 | 0.029 | 0.016 | **0.047** | 0 | 0.006 | **0.004** | 0.159 |
| | **0.021** | **0.022** | **0.086** | **0.063** | **0.087** | **0.024** | **0.016** | **0.038** | **0** | **0.006** | **0.004** | **0.143** |
| 170 | **0.037** | 0.017 | 0.104 | **0.070** | 0.013 | 0.051 | 0.031 | **0.036** | 0.026 | 0.018 | **0.020** | 0.056 |
| | **0.037** | **0.017** | **0.096** | **0.067** | **0.013** | **0.047** | **0.031** | **0.033** | **0.025** | **0.017** | **0.020** | **0.056** |
| 175 | **0.106** | 0.028 | 0.084 | **0.062** | 0.013 | 0 | 0 | **0.004** | 0 | 0.036 | **0.024** | 0.013 |
| | **0.105** | **0.023** | **0.071** | **0.054** | **0.013** | **0** | **0** | **0.004** | **0** | **0.029** | **0.020** | **0.013** |
| 180 | **0.027** | 0.067 | 0.027 | **0.041** | 0.013 | 0 | 0 | **0.004** | 0.013 | 0 | **0.004** | 0.022 |
| | **0.027** | **0.060** | **0.026** | **0.038** | **0.013** | **0** | **0** | **0.004** | **0.013** | **0** | **0.004** | **0.022** |
| 185 | **0** | 0.028 | 0.020 | **0.023** | 0 | 0 | 0.016 | **0.004** | 0 | 0.179 | **0.118** | 0.025 |
| | **0** | **0.028** | **0.019** | **0.023** | **0** | **0** | **0.016** | **0.004** | **0** | **0.147** | **0.097** | **0.022** |
| 190 | **0** | 0.039 | 0.027 | **0.031** | 0.013 | 0.015 | 0 | **0.011** | 0.026 | 0.208 | **0.146** | 0.047 |
| | **0** | **0.039** | **0.026** | **0.031** | **0.013** | **0.015** | **0** | **0.011** | **0.025** | **0.185** | **0.132** | **0.045** |
| 200 | **0.005** | 0.028 | 0.027 | **0.027** | 0.026 | 0.015 | 0 | **0.014** | 0.013 | 0.006 | **0.008** | 0.063 |
| | **0.005** | **0.018** | **0.026** | **0.023** | **0.026** | **0.016** | **0** | **0.015** | **0.013** | **0.006** | **0.008** | **0.058** |
| 210 | **0.005** | 0.062 | 0.030 | **0.041** | 0.013 | 0.007 | 0.016 | **0.011** | 0 | 0 | **0** | 0.003 |
| | **0.005** | **0.058** | **0.029** | **0.040** | **0.013** | **0.007** | **0.016** | **0.011** | **0** | **0** | **0** | **0.003** |
| 220 | **0** | 0.011 | 0.010 | **0.010** | 0 | 0.015 | 0.016 | **0.011** | 0 | 0.006 | **0.004** | 0.003 |
| | **0** | **0.011** | **0.010** | **0.010** | **0** | **0.011** | **0.016** | **0.084** | **0** | **0.006** | **0.004** | **0.003** |
| 230 | **0** | 0.011 | 0.007 | **0.008** | 0 | 0 | 0 | **0** | 0.039 | 0 | **0.012** | 0 |
| | **0** | **0.005** | **0.006** | **0.008** | **0** | **0** | **0** | **0** | **0.026** | **0** | **0.008** | **0** |
| 250 | **0** | 0 | 0 | **0** | 0 | 0 | 0 | **0** | 0 | 0 | **0** | 0 |
| | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** |
| 270 | **0.011** | 0 | 0.003 | **0.002** | 0 | 0 | 0 | **0** | 0 | 0.006 | **0.004** | 0.003 |
| | **0.006** | **0** | **0.003** | **0.002** | **0** | **0** | **0** | **0** | **0** | **0.006** | **0.004** | **0.001** |
| **Null** | **0** | 0 | 0.032 | **0.021** | 0 | **0** | 0 | **0** | 0.050 | 0.034 | **0.039** | 0 |
| | **0.006** | **0.069** | **0.092** | **0.079** | **0.104** | **0.035** | **0.136** | **0.154** | **0.176** | **0.124** | **0.154** | **0.062** |
| Hobs | **0.856** | 0.764 | *0.779 | **0.849** | *0.697 | 0.831 | *0.625 | **0.885** | *0.632 | *0.714 | **0.705** | *0.747 |
| Hexp | **0.777** | 0.791 | 0.948 | **0.979** | 0.921 | 0.897 | 0.906 | **0.920** | 0.899 | 0.885 | **0.959** | 0.931 |

for coho salmon populations from British Columbia. The weighted means of allele frequencies for regions are in bold and follow the are indicated by * next to the observed heterozygosity. The allele number (in basepairs) is the lower limit of the allele bin. Allele frequen- are given underneath the population names.

| Big Qualicum | ECVI | Toboggan | Cedar | Babine | Clear-water | Sustut | Skeena | Tseax | Zolzap | Mexiadin | Nass | TR | L Fr |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 200 | 260 | 164 | 47 | 139 | 48 | 36 | 434 | 40 | 47 | 64 | 151 | 1015 | 1043 |
| 0 | **0** | 0.079 | 0.020 | 0.072 | 0.024 | 0 | **0.056** | 0.038 | 0.063 | 0.019 | **0.039** | **0.002** | **0.001** |
| **0** | **0** | **0.076** | **0.019** | **0.065** | **0.010** | **0** | **0.052** | **0.038** | **0.055** | **0.015** | **0.037** | **0.001** | **0.001** |
| 0 | **0** | 0 | 0 | 0.004 | 0.024 | 0 | **0.003** | 0 | 0 | 0 | **0** | **0.024** | **0.027** |
| **0** | **0** | **0** | **0** | **0.004** | **0.010** | **0** | **0.002** | **0** | **0** | **0** | **0** | **0.016** | **0.025** |
| 0.136 | **0.136** | 0.201 | 0.265 | 0.040 | 0.146 | 0.167 | **0.144** | 0.075 | 0.115 | 0.144 | **0.114** | **0.016** | **0.086** |
| **0.114** | **0.125** | **0.176** | **0.208** | **0.037** | **0.076** | **0.132** | **0.121** | **0.075** | **0.103** | **0.093** | **0.105** | **0.011** | **0.082** |
| 0.019 | **0.026** | 0.028 | 0.020 | 0.036 | 0.012 | 0 | **0.025** | 0.038 | 0.031 | 0.010 | **0.025** | **0.002** | **0.010** |
| **0.017** | **0.025** | **0.027** | **0.009** | **0.036** | **0.010** | **0** | **0.024** | **0.038** | **0.031** | **0.007** | **0.025** | **0.001** | **0.009** |
| 0 | **0** | 0.003 | 0 | 0.047 | 0.037 | 0 | **0.019** | 0 | 0 | 0 | **0** | **0.001** | **0.023** |
| **0** | **0** | **0.003** | **0** | **0.046** | **0.021** | **0** | **0.018** | **0** | **0** | **0** | **0** | **0.001** | **0.022** |
| 0.045 | **0.024** | 0.097 | 0.029 | 0.086 | 0 | 0.014 | **0.067** | 0.038 | 0.021 | 0.067 | **0.043** | **0.003** | **0.018** |
| **0.038** | **0.021** | **0.091** | **0.028** | **0.080** | **0** | **0.014** | **0.063** | **0.038** | **0.021** | **0.045** | **0.040** | **0.002** | **0.017** |
| 0.019 | **0.025** | 0.022 | 0 | 0.036 | 0.037 | 0.014 | **0.024** | 0.025 | 0.042 | 0.067 | **0.046** | **0.001** | **0.056** |
| **0.015** | **0.022** | **0.021** | **0** | **0.036** | **0.021** | **0.014** | **0.023** | **0.014** | **0.042** | **0.045** | **0.043** | **0.001** | **0.053** |
| 0.043 | **0.046** | 0 | 0 | 0 | 0.024 | 0 | **0.002** | 0 | 0 | 0 | **0** | **0.029** | **0.011** |
| **0.040** | **0.045** | **0** | **0** | **0** | **0.010** | **0** | **0.001** | **0** | **0** | **0** | **0** | **0.020** | **0.010** |
| 0.029 | **0.015** | 0 | 0 | 0.014 | 0 | 0 | **0.005** | 0.038 | 0 | 0 | **0.011** | **0.003** | **0.014** |
| **0.027** | **0.015** | **0** | **0** | **0.014** | **0** | **0** | **0.005** | **0.038** | **0** | **0** | **0.011** | **0.003** | **0.014** |
| 0 | **0.007** | 0.003 | 0.049 | 0.011 | 0.012 | 0 | **0.011** | 0.025 | 0.021 | 0 | **0.014** | **0.002** | **0.038** |
| **0** | **0.007** | **0.003** | **0.038** | **0.011** | **0.010** | **0** | **0.010** | **0.025** | **0.021** | **0** | **0.014** | **0.001** | **0.036** |
| 0.005 | **0.004** | 0.013 | 0.010 | 0.119 | 0.085 | 0.069 | **0.057** | 0.050 | 0.010 | 0.029 | **0.029** | **0.049** | **0.034** |
| **0.005** | **0.004** | **0.012** | **0.009** | **0.111** | **0.042** | **0.056** | **0.049** | **0.050** | **0.010** | **0.022** | **0.029** | **0.034** | **0.033** |
| 0.008 | **0.019** | 0.126 | 0.010 | 0.194 | 0.061 | 0.083 | **0.121** | 0.025 | 0.073 | 0.029 | **0.043** | **0.302** | **0.031** |
| **0.007** | **0.017** | **0.109** | **0.009** | **0.181** | **0.051** | **0.070** | **0.107** | **0.014** | **0.066** | **0.022** | **0.037** | **0.209** | **0.028** |
| 0.019 | **0.014** | 0.006 | 0.069 | 0.004 | 0.110 | 0.056 | **0.026** | 0.013 | 0.021 | 0.038 | **0.025** | **0.123** | **0.036** |
| **0.017** | **0.014** | **0.006** | **0.057** | **0.004** | **0.063** | **0.029** | **0.020** | **0.014** | **0.021** | **0.030** | **0.025** | **0.080** | **0.035** |
| 0.011 | **0.006** | 0.053 | 0.049 | 0 | 0 | 0 | **0.025** | 0.013 | 0.021 | 0.019 | **0.018** | **0.025** | **0.069** |
| **0.010** | **0.006** | **0.047** | **0.038** | **0** | **0** | **0** | **0.022** | **0.013** | **0.021** | **0.015** | **0.018** | **0.018** | **0.065** |
| 0.005 | **0.003** | 0.006 | 0 | 0 | 0.024 | 0 | **0.005** | 0.038 | 0.031 | 0.019 | **0.029** | **0.012** | **0.019** |
| **0.005** | **0.003** | **0.006** | **0** | **0** | **0.010** | **0** | **0.003** | **0.038** | **0.031** | **0.015** | **0.029** | **0.009** | **0.018** |
| 0.021 | **0.015** | 0 | 0 | 0 | 0.037 | 0 | **0.003** | 0.038 | 0.031 | 0 | **0.021** | **0.035** | **0.033** |
| **0.017** | **0.014** | **0** | **0** | **0** | **0.031** | **0** | **0.003** | **0.038** | **0.031** | **0** | **0.021** | **0.027** | **0.033** |
| 0.021 | **0.021** | 0 | 0 | 0.004 | 0 | 0 | **0.001** | 0 | 0 | 0 | **0** | **0.008** | **0.019** |
| **0.015** | **0.018** | **0** | **0** | **0.004** | **0** | **0** | **0.001** | **0** | **0** | **0** | **0** | **0.005** | **0.018** |
| 0.003 | **0.011** | 0 | 0 | 0 | 0 | 0 | **0** | 0 | 0 | 0 | **0** | **0** | **0.006** |
| **0.002** | **0.011** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0.006** |
| 0.045 | **0.042** | 0 | 0.010 | 0.011 | 0 | 0 | **0.005** | 0 | 0.010 | 0.010 | **0.007** | **0.002** | **0.037** |
| **0.036** | **0.037** | **0** | **0.009** | **0.011** | **0** | **0** | **0.005** | **0** | **0.010** | **0.007** | **0.007** | **0.002** | **0.036** |
| 0.024 | **0.038** | 0.003 | 0.010 | 0.004 | 0.037 | 0.014 | **0.008** | 0.038 | 0.063 | 0.087 | **0.064** | **0.001** | **0.059** |
| **0.022** | **0.036** | **0.003** | **0.009** | **0.004** | **0.031** | **0.014** | **0.008** | **0.038** | **0.066** | **0.060** | **0.062** | **0.001** | **0.056** |
| 0.016 | **0.018** | 0.016 | 0.010 | 0.011 | 0 | 0 | **0.010** | 0 | 0.042 | 0.029 | **0.025** | **0.006** | **0.058** |
| **0.013** | **0.017** | **0.015** | **0.009** | **0.007** | **0** | **0** | **0.009** | **0** | **0.042** | **0.022** | **0.025** | **0.003** | **0.056** |
| 0.008 | **0.013** | 0.006 | 0.020 | 0.004 | 0.049 | 0 | **0.010** | 0.038 | 0.010 | 0.019 | **0.021** | **0.019** | **0.039** |
| **0.007** | **0.013** | **0.006** | **0.019** | **0.004** | **0.021** | **0** | **0.008** | **0.038** | **0.011** | **0.008** | **0.018** | **0.014** | **0.037** |
| 0.051 | **0.031** | 0.022 | 0 | 0.018 | 0.049 | 0.042 | **0.022** | 0.075 | 0.021 | 0.029 | **0.039** | **0.017** | **0.038** |
| **0.041** | **0.027** | **0.021** | **0** | **0.018** | **0.031** | **0.028** | **0.020** | **0.067** | **0.022** | **0.022** | **0.037** | **0.015** | **0.037** |
| 0.106 | **0.067** | 0.035 | 0.059 | 0.061 | 0.085 | 0.153 | **0.059** | 0.038 | 0.083 | 0.058 | **0.061** | **0.004** | **0.036** |
| **0.088** | **0.060** | **0.031** | **0.056** | **0.058** | **0.042** | **0.117** | **0.052** | **0.038** | **0.077** | **0.038** | **0.056** | **0.011** | **0.036** |
| 0.061 | **0.050** | 0.041 | 0.010 | 0.036 | 0.037 | 0 | **0.031** | 0.100 | 0.031 | 0.077 | **0.068** | **0.008** | **0.026** |
| **0.044** | **0.041** | **0.037** | **0.009** | **0.036** | **0.031** | **0** | **0.030** | **0.093** | **0.031** | **0.046** | **0.061** | **0.003** | **0.025** |
| 0.056 | **0.100** | 0.009 | 0.029 | 0.004 | 0 | 0.014 | **0.009** | 0.063 | 0.021 | 0.029 | **0.036** | **0.020** | **0.035** |
| **0.044** | **0.085** | **0.009** | **0.028** | **0.004** | **0** | **0.014** | **0.009** | **0.063** | **0.021** | **0.022** | **0.036** | **0.006** | **0.033** |
| 0.053 | **0.053** | 0.003 | 0.029 | 0.025 | 0.073 | 0.042 | **0.023** | 0.025 | 0.021 | 0.019 | **0.021** | **0.065** | **0.036** |
| **0.045** | **0.051** | **0.003** | **0.028** | **0.025** | **0.042** | **0.041** | **0.021** | **0.025** | **0.021** | **0.008** | **0.018** | **0.045** | **0.035** |
| 0.056 | **0.035** | 0.025 | 0.088 | 0.004 | 0.024 | 0.069 | **0.029** | 0.038 | 0.042 | 0.010 | **0.029** | **0.008** | **0.040** |
| **0.050** | **0.034** | **0.024** | **0.076** | **0.004** | **0.020** | **0.043** | **0.025** | **0.038** | **0.042** | **0.007** | **0.029** | **0.005** | **0.040** |
| 0.043 | **0.032** | 0.031 | 0.029 | 0.018 | 0.012 | 0.056 | **0.026** | 0.038 | 0.021 | 0.048 | **0.036** | **0.007** | **0.019** |
| **0.035** | **0.029** | **0.030** | **0.028** | **0.015** | **0.010** | **0.042** | **0.024** | **0.038** | **0.021** | **0.037** | **0.036** | **0.005** | **0.019** |
| 0.005 | **0.014** | 0.035 | 0.010 | 0.029 | 0 | 0.028 | **0.025** | 0 | 0.010 | 0.058 | **0.025** | **0** | **0.019** |
| **0.005** | **0.013** | **0.034** | **0.009** | **0.029** | **0** | **0.027** | **0.025** | **0** | **0.010** | **0.045** | **0.025** | **0** | **0.018** |
| 0.061 | **0.051** | 0.085 | 0 | 0.014 | 0 | 0 | **0.035** | 0.087 | 0.073 | 0.019 | **0.057** | **0** | **0.005** |
| **0.050** | **0.048** | **0.078** | **0** | **0.014** | **0** | **0** | **0.033** | **0.071** | **0.066** | **0.015** | **0.049** | **0** | **0.005** |
| 0.027 | **0.042** | 0.022 | 0.039 | 0.018 | 0 | 0 | **0.018** | 0 | 0.042 | 0.010 | **0.018** | **0.004** | **0.004** |
| **0.023** | **0.038** | **0.021** | **0.037** | **0.018** | **0** | **0** | **0.018** | **0** | **0.042** | **0.007** | **0.018** | **0.002** | **0.004** |
| 0.003 | **0.003** | 0.025 | 0.010 | 0.05 | 0 | 0.111 | **0.035** | 0.013 | 0.031 | 0.038 | **0.029** | **0.007** | **0.005** |
| **0.002** | **0.003** | **0.024** | **0.009** | **0.048** | **0** | **0.097** | **0.033** | **0.013** | **0.031** | **0.030** | **0.029** | **0.004** | **0.005** |
| 0 | **0.001** | 0.003 | 0.010 | 0.029 | 0 | 0.069 | **0.017** | 0 | 0 | 0.019 | **0.007** | **0** | **0.002** |
| **0** | **0.001** | **0.003** | **0.009** | **0.029** | **0** | **0.068** | **0.017** | **0** | **0** | **0.015** | **0.005** | **0** | **0.002** |
| 0 | **0** | 0 | 0 | 0 | 0 | 0 | **0** | 0 | 0 | 0 | **0** | **0** | **0.001** |
| **0** | **0.003** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0.001** |
| 0.005 | **0.003** | 0 | 0.118 | 0 | 0 | 0 | **0** | 0 | 0 | 0 | **0** | **0** | **0** |
| **0.005** | **0.004** | **0** | **0.064** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** |
| 0.005 | **0.004** | 0 | 0 | 0 | 0 | 0 | **0** | 0 | 0 | 0 | **0** | **0** | **0.001** |
| **0.005** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0** | **0.001** |
| 0.060 | **0.033** | 0.030 | 0.007 | 0 | 0.163 | 0.027 | **0.041** | 0 | 0 | 0 | **0** | **0.193** | **0.007** |
| **0.153** | **0.115** | **0.080** | **0.186** | **0.052** | **0.406** | **0.197** | **0.137** | **0.066** | **0.065** | **0.300** | **0.063** | **0.444** | **0.048** |
| *0.750 | **0.764** | 0.774 | *0.588 | *0.737 | *0.390 | *0.431 | **0.721** | 0.837 | 0.802 | *0.721 | **0.836** | 0.254 | 0.875 |
| 0.945 | **0.944** | 0.915 | 0.896 | 0.921 | 0.938 | 0.919 | **0.938** | 0.950 | 0.958 | 0.942 | **0.957** | **0.086** | **0.958** |

inheritance at all three loci, although a null (nonamplifying) allele is present at *Ots*103 (Small et al., 1998). Individual samples that although amplified with both other primer sets yet produced no *Ots*103 alleles after the *Ots*103 amplification was performed three times, were scored as *Ots*103 null homozygotes. Allele frequencies at the *Ots*103 locus were then corrected according to a maximum-likelihood estimate (EM algorithm, Dempster et al., 1977) by using GENEPOP, version 1.2 (Raymond and Rousset, 1995a). Corrected frequencies were used in the genetic distance analysis. For *Ots*101 and *Ots*3, fish with a single allele were scored as homozygotes and fish with two alleles were scored as heterozygotes. Allele frequency data for individual populations in the Fraser River and Thompson River are from Small et al. (1998) and only the weighted means of total allele frequencies for these regions are presented here (Tables 1 and 2). The upper Fraser River population (Bridge River) has been grouped with the Thompson River populations in accordance with its genetic profile.

Hardy-Weinberg equilibrium (HWE) was tested with the probability test of HWE (an exact HW test, Guo and Thompson, 1992) with GENEPOP (version 1.2). *F*-statistics and their standard deviations were calculated according to Weir and Cockerham (1984) using FSTAT (Goudet, 1995). We use the notations $F_{st}$, $F_{is}$ and $F_{it}$ for Weir and Cockerham's $\theta$, $f$, and $F$, respectively. *P*-values for $\alpha = 0.05$ in all data analyses were corrected for simultaneous multiple tests (Lessios, 1992). Pairwise comparisons of populations for differences in allele distributions were conducted at all three loci with Fisher's exact tests (Raymond and Rousset, 1995b). In populations with multiple year classes, annual variability in allele frequencies was tested with 1000 simulations in a Monte Carlo analysis (Roff and Bentzen, 1989) and populations were divided into year classes for a neighbor-joining (NJ) analysis (Saitou and Nei, 1987). A NJ dendrogram illustrating genetic relationships among populations was constructed with PHYLIP 3.5c software (Felsenstein, 1993). The allele frequency matrix was resampled 500 times and Cavalli-Sforza and Edward's (1967) chord distances were estimated for population pairs. NJ dendrograms were constructed for each matrix and a consensus NJ dendrogram was generated with CONSENSE (see Felsenstein, 1993). Individual fish were classified to specific populations with a jackknife discriminant analysis (SAS Institute Inc., 1989).

## Estimation of stock composition

Microsatellite allele frequency data were examined for use in estimating stock composition in a mixed-stock fishery. We pooled low-frequency alleles in adjacent bins (so that each bin contained at least 6% of the alleles) to reduce the number of genotypes for which frequencies were estimated. This pooling resulted in 13 "analysis" bins (91 genotypes) for *Ots*101, 10 bins (65 genotypes) for *Ots*3, and 13 bins (91 genotypes) for *Ots*103 (Table 3). Genotype frequencies at *Ots*101 and *Ots*3 were estimated for each population from the allele frequencies by assuming a Hardy-Weinberg distribution of genotypes. Because genotype frequencies at the *Ots*103 locus were generally not in HWE owing to the presence of the null allele, the observed genotype frequencies were used to characterize each population for *Ots*103. Genotype frequencies at all three loci were used as input in a maximum likelihood mixed-stock fishery analysis (Fournier et al., 1984).

Two types of hypothetical mixed-stock fishery samples were simulated: single-region fishery samples composed of fish from lower Fraser River and the Thompson River coho salmon populations, and multiregion fishery samples composed of fish from populations from several regions. Populations contributing to the multiregion samples were chosen on the basis of known or inferred migration patterns. For the Fraser River fishery simulation, only populations from the lower Fraser and Thompson rivers were present in the baseline and in the mixed-stock fishery samples. In the multiregion fishery simulations, all 34 populations were used in the baseline. In all simulations, fishery samples of 200 fish were generated from specified populations in the

**Table 3**

Method of pooling low-frequency alleles for *Ots*101, *Ots*3, and *Ots*103 to reduce the number of genotypes for baseline populations in mixed-stock analyses.

| | Microsatellite allele bin numbers | | |
|---|---|---|---|
| Analysis bin no. | *Ots*101 | *Ots*3 | *Ots*103 |
| 1 | 1–7 | 1 | 1, 2, 3 |
| 2 | 8, 9 | 3–11 | 4–7 |
| 3 | 10 | 12 | 8–11 |
| 4 | 11 | 13 | 12 |
| 5 | 12 | 14 | 13 |
| 6 | 13, 14 | 15 | 14, 15 |
| 7 | 15, 16, 17 | 16 | 16–20 |
| 8 | 18, 19 | 17 | 21, 22 |
| 9 | 20, 21 | 18 | 23, 24 |
| 10 | 22 | 19 | 25, 26, 27 |
| 11 | 23, 24 | | 28,29 |
| 12 | 25, 26 | | 30–38 |
| 13 | 27–32 | | 39 |

baseline by sampling randomly, with replacement, thus simulating the randomness present in data collection. For each simulated mixed-stock fishery, stock contributions were estimated in 50 independent simulations, and means and standard deviations for the estimated contributions of each population were obtained.

## Results

### Allele frequencies and heterozygosity

Observed heterozygosity was high in all populations at *Ots*101, ranging from 0.72 for Nitinat River to 0.97 for Waukwaas River (Table 1). Heterozygosity was slightly lower at *Ots*3, ranging from 0.70 for Zolzap River to 0.82 for Cluxewe River (Table 1). At *Ots*103, observed heterozygosity varied widely among regions, ranging from 0.25 in the Thompson River (TR) to 0.89 in North Coast Vancouver Island populations (NCVI) (Table 2). For Thompson River populations, the apparently low heterozygosity values were due to high frequencies of the null allele. Of the 22 populations with data for multiple year classes, Atnarko was the only one for which allele frequencies differed significantly among year classes at all loci. Allele frequencies differed significantly among year classes in the Kitimat, Sustut, and Toboggan populations at *Ots*3, in the Kitimat River and Pallant Creek populations at *Ots*101, and in the Quinsam and Toboggan populations at *Ots*103. Year-class variation in the Fraser and Thompson River populations are reported in Small et al. (1998). Multiple samples from individual populations clustered together in NJ analyses (except for three lower Fraser River populations as noted in Small et al., 1998), indicating that allele frequency differences among year classes were less than those among populations. Thus, all fish collected from the same location in different years were pooled and treated as a single population in subsequent analyses.

### Hardy-Weinberg equilibrium

The degree of deviation from HWE varied substantially among the 3 loci (Table 1). After correction for multiple tests ($P<0.0015$), three populations (Atnarko, Deadman and Upper Pitt) deviated from HWE at *Ots*101, and three populations (Kitimat, Big Qualicum, and Sustut) were out of HWE at *Ots*3 (Table 1). In most populations, observed heterozygosity was lower than expected heterozygosity (Table 1), and this lower heterozygosity was reflected in single-locus $F_{is}$ values of 0.0435 (SD 0.009) for *Ots*101 and 0.0617 (SD 0.008) for *Ots*3 (both $P<0.005$). HWE was rejected for *Ots*103 in 25 out of 34 populations (Table 2), reflecting the presence of the null allele. The single locus $F_{is}$ value was 0.2738 (SD 0.008). Fish homozygous for the null allele were scored in most populations and corrected *Ots*103 allele frequencies were generated for all populations (Table 2).

### Population differences

In pairwise tests, all populations had significantly different allele frequencies at one or more loci, with the exception of two geographically proximate populations in the Thompson River (Lemieux River and Dunn Creek), and two sets of populations from the adjacent Skeena and Nass River systems: (Cedar River [Skeena])and Zolzap River [Nass]; and Sustut River [Skeena] and Meziadin River [Nass]). The single- and multilocus $F_{st}$ values indicated significant differentiation among populations with values of 0.040 (SD 0.006) for *Ots*101, 0.054 (SD 0.009) for *Ots*3, 0.059 (SD 0.009) for *Ots*103 (all $P<0.005$) and a multilocus value of 0.051 (SD 0.006, $P<0.005$).

### Allele frequencies

With the exception of *Ots*101 allele 96, found only in the Robertson Creek population, all alleles were present in more than one population and region. Thus, population- or region-specific alleles were generally nonexistent, but allele frequencies varied among populations and regions. At *Ots*101, lower Fraser River populations had high frequencies of smaller alleles (74% shorter than 143 bp in length) and relatively low frequencies of large alleles, whereas Thompson River populations had low frequencies of small alleles (64% longer than 161 bp). In the Thompson River populations, *Ots*3 allele 66 was absent and allele 94 was more common than in populations from other regions. *Ots*3 alleles 104 and 106 were found only in the Skeena and Nass River populations. The most striking differentiation provided by *Ots*103 was the high frequency (0.44) of the null allele in Thompson River populations. This was three times the next highest frequency (0.15) that occurred in the north and west coast Vancouver Island populations.

### Population structure

The unrooted consensus NJ dendrogram possessed three major branches that provided regional definition among coho salmon populations of British Columbia (Fig. 2). The best defined branch contained the Thompson River (and Bridge River of the upper Fraser drainage) populations, that occurred together

in all 500 trees used to construct the consensus tree. The branch containing all lower Fraser River populations was also well supported. Populations from the northern Skeena and Nass rivers were interspersed on the third branch, but only the upper Skeena and Nass populations formed a well-supported group (Fig. 2). Lower Skeena and Nass populations were more similar to a diverse central cluster of Vancouver Island and mainland coastal coho salmon populations. Within the coastal group, east coast (Big Qualicum and Quinsam), west coast (Robertson and Nitinat), and north coast (Cluxewe, Waukwaas and Stephens) Vancouver Island populations were as well distinguished from each other as they were from the more northern mainland coastal populations or the Queen Charlotte Island population of Pallant Creek.

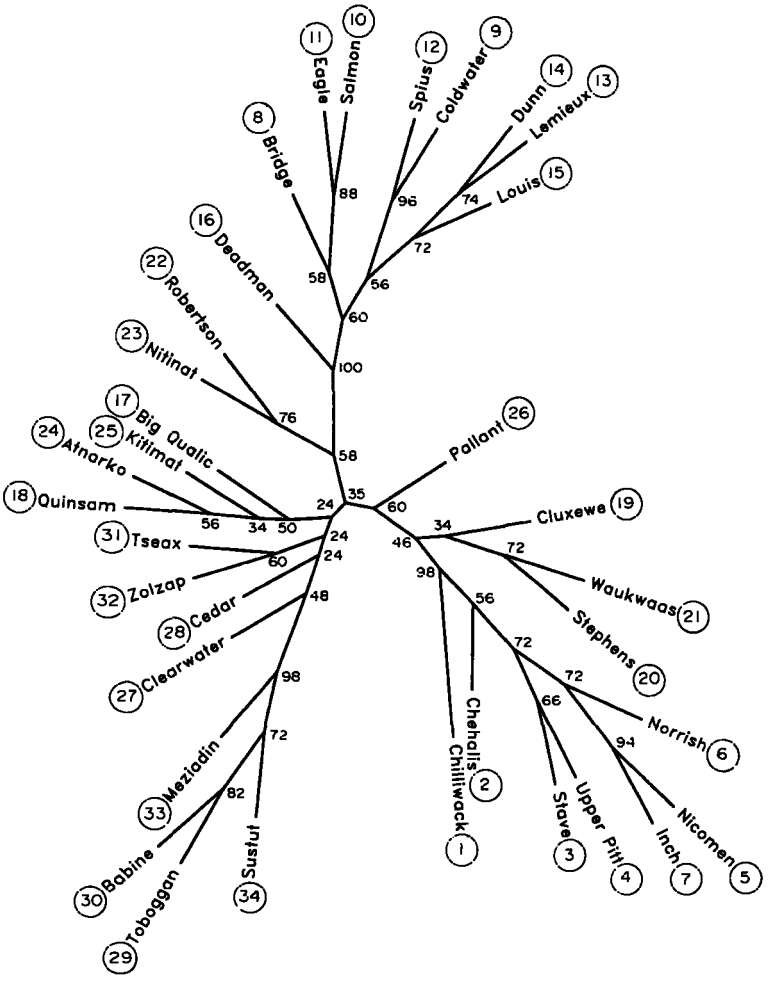


**Figure 2**

Unrooted neighbor-joining tree relating 34 British Columbia coho salmon populations. The tree was constructed from a consensus of Cavalli-Sforza and Edward's chord distances. Bootstrap values at the tree nodes were computed over 500 replications by resampling the allele frequency matrix. Bootstrap values indicate the percentage of trees in which the populations beyond the node occurred together. All names correspond to population names given in Tables 2 and 3 with the exception of Big Qualicum River which is shortened to Big Qualic. The number of the population (from Fig. 1) is next to the name.

## Estimation of stock composition

In the mixed-stock fishery simulated within the Fraser River, estimates of stock composition were accurate and precise, with an average of 2.3% of the mixture incorrectly assigned to each population (Table 4). In general, misassigned portions of the mixture were assigned to closely related populations. For instance, the 30% contribution of Coldwater River fish to the mixture was underestimated as 26.4%, but 3.1% of the mixture was assigned to the genetically similar Spius River population, although no Spius fish were included in the mixture. Fish misassigned to population were almost invariably assigned to the correct region. Less than 1% of fish were misclassified between the Thompson River and Lower Fraser regions (Table 4). Thus, within the Fraser River drainage, populations contributing to a mixed-stock sample can be identified to region and to individual population, or population group within region, with a high degree of accuracy and precision.

Accuracy and precision of stock composition estimates were also high in the simulated mixed-stock samples to which populations from different regions contributed (Table 5). Average error of individual population contributions to the mixed fishery was 1.5% (3% for populations actually contributing to the mixture), and average error of regional contributions was 2.2% (higher for regions actually contributing). In most simulations, the contributions of populations present in the mixture were underestimated because a small proportion of the mixture was allocated to baseline populations not present in the mixture. In general, misassigned fish were allocated to genetically similar populations and thus were

correctly identified to region. Regions with no populations present in the mixture were allocated less than 5% of the fish, except in the mixture composed of Vancouver Island populations (mix 1, Table 5). In that case, 10% of the fish were allocated to the lower Fraser River. The regional misclassification of Vancouver Island coho salmon as fish of lower Fraser origin in mix 1 was due largely to the allocation of 4% of the mixture to Chilliwack River, the lower Fraser population most genetically similar to the northern Vancouver Island populations (Fig. 2). Similarly, Vancouver Island and central coast fish were underestimated in mix 5, and some of them attributed to the lower Fraser rather than to other coastal island, mainland, or lower Skeena and Nass populations as might be expected from the dendrogram (Table 5; Fig. 2). Conversely, when lower Fraser coho salmon formed a high proportion of the mixture (mix 3), they were underestimated and misidentified fish tended to be attributed to Vancouver Island populations (Table 5).

In contrast, the genetic distinctiveness of Thompson River coho salmon resulted in their accurate identification in mixtures in which they were present (mixes 3 and 5) and little misrepresentation in mixtures from which they were absent (mixes 1, 2, and 4). Nass and Skeena populations were well-separated (mix 4), and contributions from lower Skeena (Cedar and Clearwater) populations were identified as well as those from the upper Skeena-Nass populations. Given the lack of separation of Skeena and Nass in the NJ dendrogram (Fig. 2), this result needs to be confirmed by more extensive sampling and further mixture analysis for populations within these two watersheds. Individual classification of Nass and Skeena fish (see below), and the lack of significant allele frequency differences between two Nass-Skeena pairs of populations, indicated that additional genetic markers may be required for accurate differentiation of Nass and Skeena coho salmon. Nevertheless, the results of these preliminary analyses indicate that a mixed-stock sample of coho salmon collected in the field can generally be resolved into its regional components by using microsatellite genetic markers.

### Identifying individuals

Accuracy of the classification of individual fish to region with discriminant analysis varied among regions (Table 6), but individual classification was generally much less accurate than was estimation of stock composition. An average of 48% of fish, ranging from 85% of Thompson to 20% of Nass individuals, was correctly classified to region. Misclassified fish were most commonly attributed to the most genetically similar region according to relationships depicted in the NJ dendrogram. The Nass and Skeena populations were interspersed in the NJ analysis (Fig. 2), and an essentially equal proportion of Nass River fish (20%) were identified as Nass and Skeena fish (Table 6). Skeena River fish were identified more accurately than Nass River fish, with 53% and 11% of the Skeena River fish classified as being of Skeena and Nass origin, respectively. If only the Fraser River populations were included in the baseline, Fraser River coho salmon were assigned to region accurately, with 93% correctly identified to either the lower Fraser River or the Thompson River (data not shown).

**Table 4**

Accuracy and precision of estimated Fraser River coho salmon population contributions in a simulated mixed-stock sample from a 16-population Fraser River baseline. A 200-fish mixture was generated with replacement from the baseline 50 times and the population composition was estimated for each mixture. The mean percentage of the mixture allocated to each population is given, followed by the standard deviation in parentheses. Regional totals are given in the rows marked TR (Thompson River) and L Fr (lower Fraser River).

| | True | Mean | SD |
|---|---|---|---|
| Coldwater | 30 | 26.4 | (4.4) |
| Salmon | 0 | 1.3 | (1.6) |
| Eagle | 20 | 15.7 | (3.4) |
| Spius | 0 | 3.1 | (3.5) |
| Lemieux | 0 | 1.0 | (1.5) |
| Dunn | 0 | 0.6 | (1.3) |
| Louis | 0 | 1.0 | (1.7) |
| Deadman | 0 | 0.5 | (0.9) |
| Bridge | 0 | 0.7 | (1.3) |
| TR | 50 | 50.2 | (1.4) |
| Chilliwack | 20 | 16.8 | (4.0) |
| Chehalis | 0 | 1.4 | (1.8) |
| Stave | 15 | 12.6 | (3.3) |
| Upper Pitt | 0 | 1.8 | (2.1) |
| Nicomen | 15 | 12.2 | (3.4) |
| Norrish | 0 | 2.9 | (2.5) |
| Inch | 0 | 2.0 | (2.4) |
| L Fr | 50 | 49.8 | (1.4) |

## Discussion

Microsatellite DNA analysis shows great promise for the elucidation of population structure in coho salmon. Very strong regional structure was apparent in the British Columbia coho salmon populations

**Table 5**

Estimated stock composition of five 200-fish mixtures of coho salmon from several regions in British Columbia using a 34-stock baseline. Each mixture was generated 50 times, and stock composition of the mixture was estimated by randomly resampling each baseline population, with replacement, to derive a new estimation of the fish mixture composition. The mean and standard deviations of 50 estimations are reported for each population. Individual population estimates are followed by the sum of contributions from a region (bold type).

| | Mix 1 | | | Mix 2 | | | Mix 3 | | | Mix 4 | | | Mix 5 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | True | Mean | SD | True | Mean | SD | True | Mean | SD | True | Mean | SD | True | Mean | SD |
| **Pallant** | **0** | **0.02** | **0.02** | **0** | **0.01** | **0.01** | **0** | **0.00** | **0.01** | **0** | **0.00** | **0.01** | **0** | **0.01** | **0.01** |
| Atnarko | 0 | 0.01 | 0.01 | 0.13 | 0.11 | 0.02 | 0 | 0.00 | 0.01 | 0 | 0.02 | 0.02 | 0 | 0.02 | 0.02 |
| Kitimat | 0 | 0.01 | 0.02 | 0.13 | 0.10 | 0.02 | 0 | 0.01 | 0.01 | 0 | 0.02 | 0.02 | 0.20 | 0.16 | 0.04 |
| **C Coast** | **0** | **0.02** | **0.02** | **0.26** | **0.21** | **0.03** | **0** | **0.01** | **0.01** | **0** | **0.04** | **0.03** | **0.20** | **0.18** | **0.04** |
| Cluxewe | 0 | 0.01 | 0.01 | 0 | 0.01 | 0.01 | 0 | 0.00 | 0.01 | 0 | 0.00 | 0.01 | 0 | 0.01 | 0.01 |
| Stephens | 0.13 | 0.10 | 0.02 | 0 | 0.00 | 0.00 | 0 | 0.01 | 0.01 | 0 | 0.01 | 0.01 | 0 | 0.01 | 0.02 |
| Waukwaas | 0.17 | 0.12 | 0.03 | 0 | 0.00 | 0.00 | 0 | 0.01 | 0.01 | 0 | 0.00 | 0.01 | 0 | 0.00 | 0.01 |
| **NCVI** | **0.30** | **0.23** | **0.03** | **0** | **0.01** | **0.01** | **0** | **0.02** | **0.02** | **0** | **0.01** | **0.01** | **0** | **0.02** | **0.02** |
| Nitinat | 0.13 | 0.10 | 0.02 | 0 | 0.00 | 0.00 | 0 | 0.00 | 0.01 | 0 | 0.00 | 0.00 | 0 | 0.00 | 0.00 |
| Robertson | 0.13 | 0.12 | 0.03 | 0 | 0.00 | 0.00 | 0.15 | 0.13 | 0.01 | 0 | 0.00 | 0.01 | 0 | 0.00 | 0.00 |
| **WCVI** | **0.26** | **0.22** | **0.03** | **0** | **0.00** | **0.01** | **0.15** | **0.13** | **0.01** | **0** | **0.00** | **0.01** | **0** | **0.00** | **0.01** |
| Quinsam | 0.17 | 0.15 | 0.05 | 0 | 0.02 | 0.03 | 0 | 0.01 | 0.01 | 0 | 0.01 | 0.01 | 0 | 0.03 | 0.04 |
| Big Qualic | 0.26 | 0.22 | 0.04 | 0.17 | 0.14 | 0.03 | 0 | 0.01 | 0.02 | 0 | 0.01 | 0.01 | 0.25 | 0.19 | 0.04 |
| **ECVI** | **0.43** | **0.37** | **0.06** | **0.17** | **0.16** | **0.04** | **0** | **0.02** | **0.02** | **0** | **0.02** | **0.02** | **0.25** | **0.22** | **0.05** |
| Toboggan | 0 | 0.00 | 0.00 | 0.26 | 0.24 | 0.03 | 0 | 0.00 | 0.00 | 0.14 | 0.15 | 0.03 | 0 | 0.01 | 0.01 |
| Cedar | 0 | 0.01 | 0.01 | 0 | 0.01 | 0.01 | 0 | 0.00 | 0.01 | 0.13 | 0.09 | 0.03 | 0.20 | 0.13 | 0.03 |
| Babine | 0 | 0.00 | 0.01 | 0.17 | 0.16 | 0.02 | 0 | 0.00 | 0.00 | 0.26 | 0.25 | 0.04 | 0 | 0.00 | 0.00 |
| Clearwater | 0 | 0.00 | 0.01 | 0 | 0.00 | 0.01 | 0 | 0.00 | 0.00 | 0.17 | 0.14 | 0.03 | 0 | 0.01 | 0.01 |
| Sustut | 0 | 0.00 | 0.00 | 0 | 0.01 | 0.01 | 0 | 0.00 | 0.00 | 0.13 | 0.10 | 0.03 | 0 | 0.00 | 0.01 |
| **Skeena** | **0** | **0.01** | **0.02** | **0.43** | **0.42** | **0.03** | **0** | **0.00** | **0.00** | **0.83** | **0.73** | **0.04** | **0.20** | **0.15** | **0.03** |
| Tseax | 0 | 0.01 | 0.01 | 0 | 0.00 | 0.01 | 0 | 0.01 | 0.01 | 0 | 0.01 | 0.01 | 0 | 0.01 | 0.01 |
| Zolzap | 0 | 0.00 | 0.01 | 0 | 0.01 | 0.01 | 0 | 0.00 | 0.01 | 0 | 0.01 | 0.01 | 0 | 0.01 | 0.01 |
| Meziadin | 0 | 0.01 | 0.01 | 0 | 0.01 | 0.01 | 0 | 0.00 | 0.00 | 0.17 | 0.13 | 0.03 | 0 | 0.01 | 0.01 |
| **Nass** | **0** | **0.02** | **0.03** | **0** | **0.02** | **0.02** | **0** | **0.01** | **0.00** | **0.17** | **0.15** | **0.03** | **0** | **0.03** | **0.02** |
| Coldwater | 0 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0 | 0.03 | 0.02 | 0 | 0.00 | 0.00 | 0 | 0.00 | 0.00 |
| Salmon | 0 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0 | 0.00 | 0.01 | 0 | 0.00 | 0.00 | 0.10 | 0.09 | 0.01 |
| Eagle | 0 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0 | 0.01 | 0.01 | 0 | 0.00 | 0.00 | 0 | 0.00 | 0.00 |
| Spius | 0 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0.20 | 0.16 | 0.03 | 0 | 0.00 | 0.00 | 0 | 0.00 | 0.00 |
| Lemieux | 0 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0 | 0.00 | 0.01 | 0 | 0.00 | 0.00 | 0 | 0.00 | 0.00 |
| Dunn | 0 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0 | 0.00 | 0.00 |
| Louis | 0 | 0.01 | 0.01 | 0 | 0.00 | 0.00 | 0 | 0.01 | 0.01 | 0 | 0.00 | 0.00 | 0 | 0.00 | 0.00 |
| Deadman | 0 | 0.01 | 0.01 | 0 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0 | 0.01 | 0.00 |
| Bridge | 0 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0 | 0.00 | 0.00 | 0 | 0.00 | 0.00 |
| **TR** | **0** | **0.02** | **0.01** | **0** | **0.01** | **0.01** | **0.20** | **0.21** | **0.01** | **0** | **0.01** | **0.01** | **0.10** | **0.10** | **0.01** |
| Chilliwack | 0 | 0.04 | 0.03 | 0 | 0.01 | 0.01 | 0.10 | 0.10 | 0.04 | 0 | 0.00 | 0.01 | 0 | 0.02 | 0.03 |
| Chehalis | 0 | 0.01 | 0.02 | 0 | 0.01 | 0.02 | 0.25 | 0.18 | 0.03 | 0 | 0.01 | 0.01 | 0 | 0.02 | 0.03 |
| Stave | 0 | 0.01 | 0.02 | 0 | 0.02 | 0.02 | 0 | 0.02 | 0.02 | 0 | 0.01 | 0.02 | 0 | 0.03 | 0.03 |
| Upper Pitt | 0 | 0.01 | 0.01 | 0 | 0.01 | 0.01 | 0 | 0.01 | 0.02 | 0 | 0.00 | 0.01 | 0.10 | 0.08 | 0.04 |
| Nicomen | 0 | 0.01 | 0.02 | 0 | 0.01 | 0.01 | 0.10 | 0.10 | 0.03 | 0 | 0.00 | 0.01 | 0 | 0.01 | 0.02 |
| Norrish | 0 | 0.01 | 0.02 | 0 | 0.01 | 0.02 | 0 | 0.02 | 0.02 | 0 | 0.01 | 0.02 | 0 | 0.03 | 0.03 |
| Inch | 0 | 0.01 | 0.01 | 0.13 | 0.09 | 0.03 | 0.20 | 0.17 | 0.03 | 0 | 0.00 | 0.01 | 0.15 | 0.11 | 0.03 |
| **L Fr** | **0** | **0.10** | **0.04** | **0.13** | **0.16** | **0.03** | **0.65** | **0.60** | **0.03** | **0** | **0.04** | **0.03** | **0.25** | **0.30** | **0.05** |

of our study on the basis of only three microsatellite loci, albeit ones selected for high levels of intra- and interpopulation polymorphism. The four major regional components of diversity in B.C. coho salmon almost certainly constitute the phylogeographic legacy of the last ice age, which ended 10–15,000 years ago. When the headwaters of the neighboring Columbia River system were in contact with the upper reaches of the Thompson-Fraser watershed, Columbia River coho salmon recolonized the Thompson and upper Fraser River (McPhail and Lindsey, 1986; Wehrhahn and Powell, 1987; Small et al., 1998). Coho salmon from the northern Bering Sea-Yukon River glacial refuge dispersed southward by

**Table 6**

Percentage of classifications of individual fish to regions for 34 populations of coho salmon from British Columbia. In this jackknife analysis the fish tested was not included in the discriminant analysis sample, which included the rest of the fish. The percentage of fish correctly classified to region is in the "correct" column and the percentage of fish from that region misclassified to other regions is read across the row. The percentage of fish from other regions misclassified to a particular region is read down the region column. *n* is the number of fish from the region.

| | | Region | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Region | *n* | Correct | Pallant | C. Coast | L. Fraser | Thompson | WCVI | ECVI | NCVI | Nass | Skeena | Total |
| Pallant | 92 | 48.91 | | 6.52 | 8.70 | 5.43 | 6.52 | 7.61 | 13.04 | 1.09 | 2.17 | 100 |
| C. Coast | 219 | 27.85 | 10.05 | | 5.94 | 6.85 | 4.11 | 17.81 | 11.42 | 7.31 | 8.68 | 100 |
| L. Fraser | 1018 | 53.73 | 4.72 | 5.89 | | 2.85 | 3.05 | 8.74 | 12.87 | 5.11 | 3.05 | 100 |
| Thompson | 798 | 84.96 | 1.13 | 2.51 | 2.63 | | 0.25 | 3.26 | 3.01 | 1.00 | 1.25 | 100 |
| WCVI | 115 | 60.00 | 6.09 | 6.09 | 11.30 | 2.61 | | 5.22 | 3.48 | 2.61 | 2.61 | 100 |
| ECVI | 338 | 44.08 | 5.03 | 10.36 | 13.61 | 2.37 | 5.03 | | 10.06 | 6.80 | 2.66 | 100 |
| NCVI | 133 | 43.61 | 4.51 | 5.26 | 18.05 | 6.02 | 1.50 | 10.53 | | 6.77 | 3.76 | 100 |
| Nass | 133 | 20.30 | 0.75 | 13.53 | 14.29 | 6.02 | 6.77 | 8.27 | 9.02 | | 21.05 | 100 |
| Skeena | 412 | 52.67 | 3.40 | 5.58 | 6.55 | 6.07 | 1.94 | 6.80 | 6.31 | 10.68 | | 100 |

sea, or traversed the shifting freshwater waterways of northern B.C., to recolonize the upper reaches of major watersheds as far south as the Nass and Skeena rivers (Lindsey and McPhail, 1986). Dispersal of coho salmon from a central B.C. coastal refuge(ia) located on the mainland or unglaciated portions of Vancouver or the Queen Charlotte Islands (or both) (Warner et al., 1982) likely established the heterogeneous mainland-coastal population group, of which lower Fraser coho salmon populations may be a distinctive offshoot.

Of the four regional components of biodiversity in B.C. coho salmon, the Thompson and upper Fraser is the most distinctive. Little introgression has apparently occurred between the lower Fraser and Thompson River coho salmon populations despite their common passage through the lower Fraser River on their return to spawning grounds for over 3,000 generations. Coho salmon populations are few and small in the Fraser River drainage above its confluence with the Thompson River, and our data show no evidence of introgression between the coho salmon of the Thompson-Fraser Rivers and the upper Skeena watersheds such as that postulated for sockeye salmon (Wood et al., 1994). However, our sampling of the Skeena watershed is limited to date, and the current analysis (in which larger, relatively infrequent, alleles have been binned) has limited power for the detection of historical gene exchange through an analysis of rare alleles.

The Skeena River watershed has been identified as the southern limit for freshwater fish and sockeye salmon that dispersed from a northern glacial refuge (Lindsey and McPhail, 1986; Wood et al., 1994; Bickham et al., 1995). Thus, it seems likely that the coho salmon populations of the upper Skeena and Nass watersheds are derived from Beringia. The genetic intermediacy of lower Skeena and Nass populations between upper Skeena-Nass and neighboring coastal populations suggests a hybrid nature for the lower river populations. The extent to which the composite nature of these populations reflects historical or current gene flow (or both) between the two founding groups, and the adaptive consequences of such introgression, has yet to be determined.

The coho populations of the lower Fraser drainage basin formed a cohesive genetic group in the NJ analysis of genetic distance in this study. This was in sharp contrast to the heterogeneity observed among other coastal mainland and island populations likely derived from one or more coastal refugia. The heterogeneity of central coast populations may reflect the existence of several coastal refugia, introgression from northern coho populations originating from Beringia that have yet to be well characterized, or simply founder effects in the establishment of individual coastal populations from a single refuge, as postulated for sockeye salmon (Wood et al., 1994). If the heterogeneity does result from an admixture of several founding groups among coastal coho populations, the lower Fraser River populations may better represent the original genetic profile of fish from a single, possibly southern, coastal refuge. Interestingly, Vancouver Island coho salmon were more frequently misclassified as lower Fraser than as central coast fish in the mixed-stock fishery simulations of our study, in spite of their apparently greater genetic similarity to central coast populations. If the

lower Fraser River populations are characteristic of coho salmon derived from a refuge located on, or to the south of, Vancouver Island, Puget Sound coho salmon populations might be expected to be of similar origin. This is consistent with the inclusion, based primarily on genetic data, of lower Fraser and southeastern Vancouver Island coho salmon populations in a Puget Sound and Strait of Georgia ESU (Weitkamp et al., 1995). Further sampling of Vancouver Island populations will be necessary to define the boundaries of the historical groups of coho salmon that likely converge there.

The geographic basis for population structure of coho salmon revealed in this study is remarkably similar to that described for sockeye salmon based on allozyme and mtDNA data (Wood et al., 1994; Bickham et al., 1995). A genetic discontinuity between chinook salmon originating from the Columbian and Beringial glacial refugia (Gharrett et al., 1987; Cronin et al., 1993) also lies in British Columbia, and dispersal from a coastal refuge(ia) can be traced in the microsatellite data for chinook salmon as well (Beacham, unpubl. data). Thus, the phylogeographic reconstruction of postglacial dispersal based on freshwater fish distributions in British Columbia (McPhail and Lindsey, 1970, 1986; Lindsey and McPhail, 1986) has proven to be taxonomically robust and also provides the foundation for the genetic architecture of anadromous Pacific salmon species.

The mixed-stock fishery analyses demonstrated the utility of microsatellite DNA variation for coho salmon stock identification. We obtained accurate and precise estimates both of population contributions in mixed-stock samples from a single drainage and of population and regional contributions in mixed-stock samples drawn from several regions. An important feature of the microsatellite data set is the strong regional structuring of the observed genetic variation, which means that contributions from populations present in a mixture sample, but not in the baseline, will be identified correctly to region. Identifying individual fish to correct populations is more difficult than estimating percentage contributions to a stock mixture, because only characteristics of individual fish are used in the classification. In general, the microsatellite loci of this study provided a similar level of accuracy in the classification of individual coho salmon to population and region as did minisatellite DNA markers (Beacham et al., 1996). Within the Fraser River drainage, identification of individual fish was more accurate with microsatellite data (correct identification of 54% of lower Fraser and 85% of upper Fraser Rive coho salmon) than with minisatellite data (correct identification of 30% and 60% of the respective groups). The identification of individual fish is an important enforcement tool, and may improve as more microsatellite loci are added to the database.

The results of this study are consistent with a depiction of population structure in coho salmon as distinct phylogenetic lines composed of geographically based metapopulations (McPhail, 1997). The more consistent regional grouping of coho salmon populations than of sockeye salmon (Wood et al., 1994) may reflect greater, or more recent, gene flow among geographically proximate coho salmon populations than among similar sockeye populations, or may reflect differences between allozyme- and microsatellite-based data sets. Moreover, the increasing power of genetic methods applied to coho salmon data, as demonstrated in this and other (Weitkamp et al., 1995; Beacham et al., 1996; Van Doornik et al., 1996; Miller et al., 1996; Miller and Withler, 1997; Small et al., 1998) studies, enable us not only to delineate regional (metapopulation) structure in coho salmon but also to identify the regional contributions of coho from different metapopulations in mixed-stock fishery harvests. Thus, the challenge for metapopulation-based coho salmon management may lie not so much in the delineation of metapopulation structure (McPhail, 1997) as in the evaluation of the biological and social costs associated with the loss, even if only temporary in historical terms, of the less productive components of metapopulation structure during periods of overall low abundance.

Additional aspects of metapopulation theory, as applied to Pacific salmonids, need to be addressed before this model of population structure will support practical management decisions. Managers need to know, at any given point in history, how the adaptive genetic diversity of a metapopulation is likely to be distributed among its subpopulations, and how many subpopulations can be lost before evolutionary potential is compromised. This depends on, among other things, which model of metapopulation structure is adopted. Are salmonid metapopulations of the "source-sink" variety in which gene flow is basically unidirectional from large source subpopulations to ephemeral sink subpopulations (Pulliam, 1988; Pulliam and Danielson 1991)? Or are salmonid metapopulations of the "balanced exchange" type, in which gene flow is bidirectional and migration rates are inversely proportional to subpopulation size (McPeek and Holt, 1992; Doncaster et al., 1997)? Current models of metapopulation structure have been more extensively investigated with respect to population dynamics (extinctions and recolonizations among subpopulations) than with respect to population and evolutionary genetics (the spatial and tem-

poral distribution of genetic diversity among subpopulations). The finding in this, and other molecular genetic studies on coho salmon (Beacham et al., 1996; Miller et al., 1996), of temporally stable allele frequency differences at neutral loci among local "stocks" (subpopulations in the metapopulation model) may indicate that there is very little effective gene flow among subpopulations (and few recolonization events in vacant habitat) on time scales of relevance to managers.

In summary, we have demonstrated that variation at microsatellite loci can be used both to define the regional and local components of coho salmon population structure in British Columbia and to identify these elements in stock composition estimation for mixed-stock fishery analysis. Molecular genetic technology will enable delineation of metapopulations or ESUs (or both) in the coho salmon of British Columbia, but management tools based on these concepts are lacking.

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# Gonadal development and associated changes in plasma reproductive steroids in English sole, *Pleuronectes vetulus*, from Puget Sound, Washington

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**Abstract.**—Gonadal development, and associated changes in reproductive parameters were investigated in adult female and male English sole *(Pleuronectes vetulus)* in Puget Sound to provide baseline data for future research on effects of contaminants on reproductive endocrine function in this species. Changes in gonadal histology, gonadosomatic index (GSI), and plasma reproductive steroids (female: 17β-estradiol [E2], testosterone [T]; male: T, 11-ketotestosterone [11KT]) were monitored throughout the spawning season. Female sole sampled July through early September were primarily regressed or previtellogenic and had low GSI and plasma steroid levels. GSI and plasma steroid levels were also low in male sole sampled during this time, but the majority had already entered spermatogenesis and, in some fish, production of mature sperm was observed. Fish sampled in October were in the early stages of vitellogenesis and spermiogenesis and showed increases in GSI and plasma steroid levels. By November, about 50% of female fish had entered vitellogenesis and about 30% of males were producing sperm. Proportions of vitellogenic females and sperm-producing males continued to increase through January, with significant numbers of spawning females and males present in February. By late March, the majority of both sexes were spent. Vitellogenic female sole had the highest plasma E2 levels, vitellogenic sole with hydrated oocytes had the highest GSI, and spawning female sole had the highest plasma T levels. Plasma T, 11KT, and GSI were highest in spawning male sole. Reproductive parameters returned to baseline levels in spawned out female and male sole. A potent maturation-inducing steroid (MIS) in many species of teleosts, 17α, 20β-dihydroxy-4-pregnen-3-one, was not detected in spawning English sole. Additional research is needed to identify the MIS in English sole and to understand better the hormonal regulation of early gonadal development in male sole.

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English sole *(Pleuronectes vetulus)* is a commercially important flatfish species indigenous to the west coast of North America. It is also a primary sentinel species for a number of environmental monitoring programs on the west coast of the United States, including the National Benthic Surveillance Project (Myers et al., 1994) and the Puget Sound Ambient Monitoring Program (PSWQA[1]). Studies suggest that female English sole are quite sensitive to environmental contaminants. For example, female sole from several sites within Puget Sound, WA, with high levels of polychlorinated biphenyls (PCBs) and polycyclic aromatic hydrocarbons (PAHs) (in sediment), exhibit various types of reproductive dysfunction, including depressed sex hormone levels, altered or inhibited reproductive development, and reduced egg and larval viability (Johnson et al., 1988, 1993; Casillas et al., 1991; Collier et al., in press).

Male English sole may also be at risk for reproductive injury. Recent studies suggest that exposure to certain chemical compounds (e.g. alkylphenols, phthalates, and some PCBs and chlorinated pesticides) can reduce testicular growth and sperm production in male teleosts (Jobling et al., 1996; Nimrod and Benson, 1996), and alterations in reproductive steroids have been reported in male fish exposed to oil and other pollutants (Truscott et al., 1992a; Idler et al., 1995). However, no comprehensive studies have been conducted on the effects of environmental contaminants on reproductive function in male English sole. Before such studies can be carried out effectively, the normal reproductive endocrine cycle of male English sole must be characterized.

The general life history of English sole is well known (Ketchen, 1947; Harry, 1959; Garrison and Miller, 1982), and its cycle of oocyte development and related changes in estradiol-17β (E2) and other plasma parameters have been described

[1] PSWQA (Puget Sound Water Quality Authority). 1995. 1994 Puget Sound update: fifth annual report of the Puget Sound Ambient Monitoring Program. Puget Sound Water Quality Authority, Olympia, WA, 122 p.

(Johnson and Casillas, 1991; Fargo and Tyler, 1994). However, no information exists on other reproductive steroids involved in oocyte development and spawning in female English sole, or on changes in reproductive parameters in male English sole during gonadal recrudescence. This study was designed to gain a better understanding of reproductive processes in both female and male English sole. This information can be used to assess the impact of environmental degradation on their reproductive development and to develop effective techniques for flatfish mariculture. It may also be useful in evaluating the reproductive status of English sole stocks that are a fisheries resource off the northwest coast of the United States.

Wild populations of female and male English sole were sampled during the 1992–93 and 1994–95 spawning cycles at two residential sites as well as at a known spawning ground in Puget Sound, Washington. Several reproductive parameters, including gonadosomatic index (GSI), histologically determined stages of gonadal development, and steroid hormones (female: plasma testosterone [T] and E2; male: T and 11-ketotestosterone [11KT]) were monitored throughout the spawning season. Additionally, 17α, 20β-dihydroxy-4-pregnen-3-one (17α, 20β-P), a potent maturation inducing steroid (MIS) in many teleosts (see review by Scott and Canario, 1987), was tested as the potential MIS in English sole.

## Materials and methods

### Chemicals

Tritium-labeled steroids were purchased from DuPont NEN (USA), and Amersham (UK). The antibodies for E2 and T were purchased from G. Niswender (Colorado State University, United States). The 11KT antibody was a gift from Y. Nagahama (Japan), and the 17α, 20β-P antibody was a gift from A. P. Scott (United Kingdom). The standards for the steroids were purchased from Steraloids, Inc. (USA).

### Collection of samples

The sampling times for fish were chosen to coincide with the period of gonadal recrudescence and spawning in English sole (Ketchen, 1947; Harry, 1959; Johnson et al., 1991). Maturing female (>200 mm total length (TL)) and male sole ( >190 mm TL) were collected from Tulalip Bay (October through January) and University Point (January through March) by otter trawl during the 1992–93 (October–March) and 1993–94 (October) spawning cycles. Additional sole were collected monthly at Pilot Point from February 1994 to December 1995. Tulalip Bay and Pilot Point (residential sites) were chosen for their large populations of English sole, and University Point was chosen because sole migrate to this area for spawning (Johnson et al., 1991; Collier et al., 1992).

Fish were kept in holding tanks aboard the research vessel for approximately one hour before sampling was carried out. The sole were weighed (to the nearest g) and measured (to the nearest mm), and blood (1 mL) was collected from the caudal vein with a heparinized syringe. Blood samples were centrifuged for 10 minutes at 800 × g, and plasma was collected and stored in triplicate bullet vials (250 µL each vial) for subsequent analysis of reproductive steroids (females: E2, T, and 17α, 20β-P; males: 11KT, and T). Immediately following blood collection, the fish were sacrificed by severing the spinal cord. The gonads were removed and weighed, and samples of gonadal tissue were collected and preserved in Dietrich's fluid (Gray, 1954) for histological examination. The abdominal contents were removed and the gutted carcass was weighed. Plasma samples were frozen and stored at –80°C until steroid analyses could be performed.

### Sample analyses

Plasma T, E2, and 11KT levels were determined by radioimmunoassay (RIA) as described by Sower and Schreck (1982), and 17α, 20β-P levels were determined by RIA as described by Scott et al. (1982). Each RIA (E2, 11KT, and T, and 17α, 20β-P) consisted of duplicates of standards (ranging from 0 to 2.0 ng/mL), samples, and quality control samples (pooled plasma from male or female English sole). Detection limits of the assays (20–80% binding range of the standard curve) were 0.006–0.3 ng/mL plasma for E2; 0.009–0.4 ng/mL for 11KT; 0.002–0.13 ng/mL for T; and 0.003–0.08 ng/mL plasma for 17α, 20β-P. For each assay, samples with steroid concentrations outside the detection limits of the assay were retested by adjusting the sample volume. All samples were corrected for dilution factor. Mean (±SE) of quality control samples were 4.4 ±0.55 ng/mL for E2 ($n$=15); 0.89 ±0.12 ng/mL for 11KT ($n$=6); and 0.29 ±0.04 ng/mL for T ($n$=16). The steroid 17α, 20β-P was not detected in quality control samples.

Gonadal tissues collected for histological examination were embedded in paraffin, sectioned, stained with Harris hematoxylin and eosin-phloxine (Luna, 1968) and examined by light microscopy. Ovarian developmental stage (Table 1) was classified accord-

**Table 1**

Classification scheme for female ovarian developmental stages, modified from histological criteria outlined in Johnson et al. (1991).

| Stage | Features |
|---|---|
| Regressed | Primary and secondary oocytes |
| Previtellogenic | Vacuolated secondary oocytes with clear peripheral vacuoles; zonal radiata present |
| Vitellogenic | Yolked oocytes present |
| Vitellogenic with hydrated oocytes | Yolked globules coalescing; hydrated oocytes present, no postovulatory follicles (POFs) |
| Spawning | Hydrated oocytes with POFs |
| Spawned out | Many POFs visible, yolked oocytes undergoing resorption, and inflammatory infiltrate, beta or gamma atretic follicles or macrophage aggregates (or both) generally present |

ing to the criteria modified from Johnson et al. (1991). Testicular developmental stage was classified as modified from Billard (1992). GSI was calculated by using the formula GSI = (gonad weight (g) /gutted weight (g)) × 100.

### Statistical analysis

Mean (±SE) GSI and plasma reproductive steroid levels were calculated by month and gonadal maturation stage. Analysis of variance (ANOVA) and subsequent multiple comparison testing by Fisher's protected least significant difference (PLSD) test (95% CI), were used to test for changes in these factors during the reproductive cycle (Dowdy and Wearden, 1991). The data was normalized by log transformation prior to statistical comparisons.

## Results

### Classification of testis

The testicular developmental stages for male English sole are shown in Figure 1, A–F. The testis consists of tubules of reproductive cells in various stages of development. Testicular development is categorized into six stages: regressed (Fig. 1A), early recrudescence (Fig. 1B), late recrudescence (Fig. 1C), early spermiogenesis (Fig. 1D), spawning (Fig. 1E), and spawned out (Fig. 1F). Each stage is characterized as follows: in the regressed stage, tubules contain only spermatogonia; in early recrudescence, primary and secondary spermatocytes begin to appear; in the late recrudescent stage spermatogonia, spermatocytes (primary and secondary), and spermatids are evident, but no spermatozoa; in early spermiogenesis primarily spermatocytes (primary and secondary), spermatids, and early sperm production are evident; in the spawning stage predominately mature sperm fill the tubular space and sperm ducts; in the spawned-out testis, the tubular space and sperm ducts are largely empty and few sperm remain.

### Size at sexual maturation

The size of English sole captured in this study ranged from 212 to 455 mm for females and from 195 to 345 mm total length for males. Histological analyses of the gonads showed that a majority of the female sole <260 mm TL were immature (regressed–previtellogenic), and failed to reach vitellogenesis (Table 2). Male sole <230 mm reached spermatogenesis but most did not fully mature and spawn (Table 3). Female sole <260 mm were excluded from further statistical analyses, but no size limit was used for male sole.

### Proportions of fish undergoing gonadal maturation and spawning

**Female** Figure 2 shows the proportion of female sole at different ovarian developmental stages by month. Even among adult sole (>260 mm), regressed females were found all year, and the mean proportion of the regressed animals each month was 24% (±11%, SD). Developing females were found as early as July; 14% of the female sole sampled in July were vitellogenic. The proportion of vitellogenic sole generally increased until January (78%), then decreased in the following months; by March only 11% of the sole sampled were vitellogenic. Spawned out females were found as early as October (1%), and the proportion increased through March (31%).

**Male** Figure 3 shows the proportion of male sole at different testicular developmental stages categorized by month of capture. Animals collected in July consisted of regressed males (12%) and early developing males (25% each were at early and late recrudescence), and males in early spermiogenesis (38%). Spawning males were found as early as October (16%), and the proportion generally increased until February (91%). By March, 41% were spawning and 36% were spawned out. Unlike females, in which a certain proportion of fish did not develop during the reproductive cycle, almost all males collected did

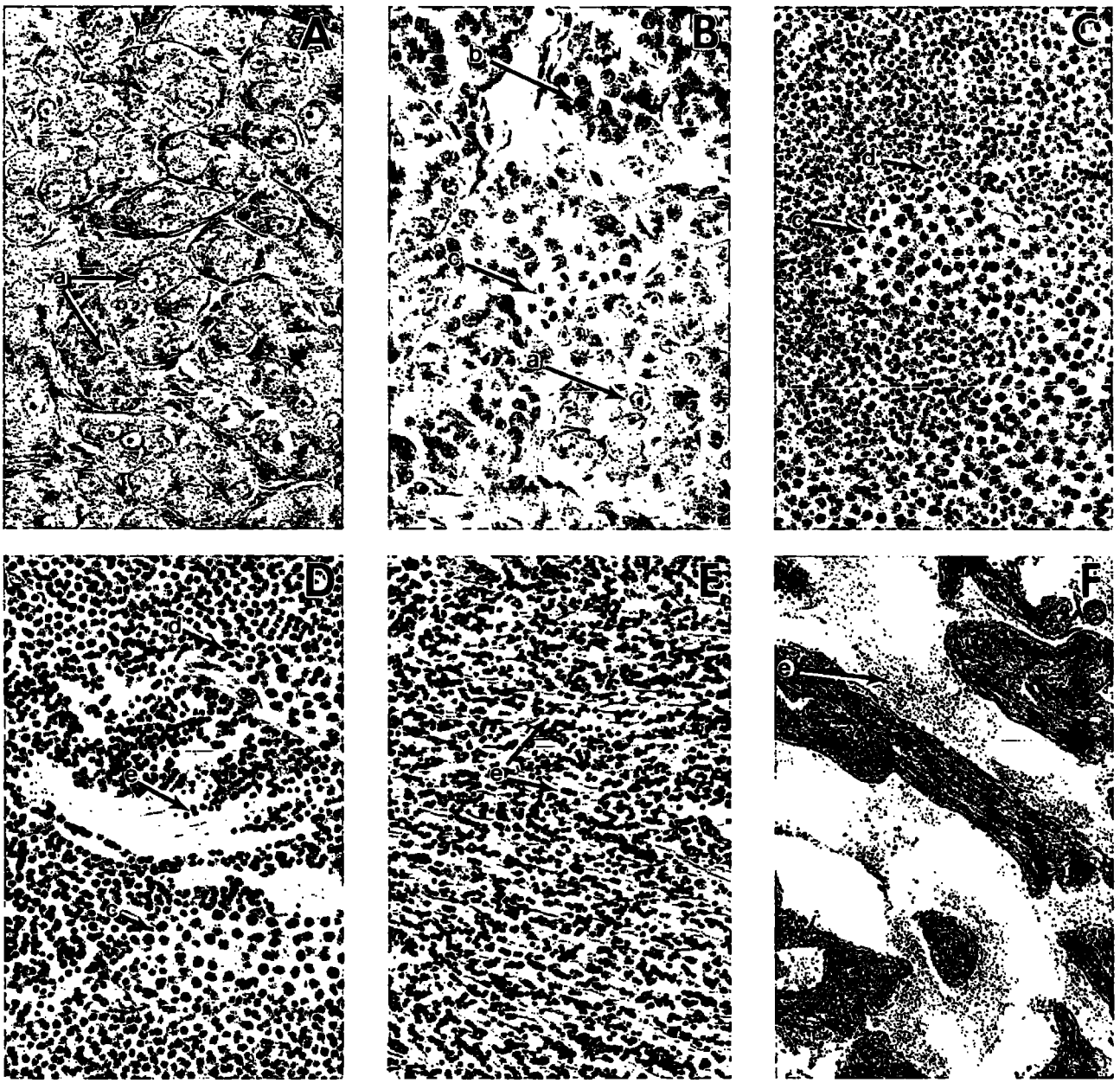


**Figure 1**

Micrographs of testicular developmental stages in male English sole: (**A**) regressed (510×), (**B**) early recrudescence (560×), (**C**) late recrudescence (560×), (**D**) early spermiogenesis (560×), (**E**) spawning (540×), and (**F**) spawned out (180×). a=spermatogonia, b=primary spermatocytes, c=secondary spermatocytes, d=spermatids, and e=spermatozoa.

enter spermiogenesis. However, only a small proportion of males <230 mm were actually producing sperm, and none in this size range were collected on the spawning ground. The smallest male caught at University Point measured 238 mm, suggesting that males <230 mm may not migrate to the spawning ground (University Point) (Table 3).

## Changes in reproductive parameters during gonadal recrudescence

**Female** Figure 4, A and B, shows reproductive parameters in female sole at each developmental stage. Generally, the immature (regressed and previtellogenic) sole had low GSI (1.4 ±0.1, $n$=85), and low

**Table 2**

Length maturation relationship in female English sole collected during months of gonadal recrudescence, October–March. Numbers represent percentage of the animals in the length class at each ovarian stage.

| Length (mm) | Regressed | Previtellogenic | Vitellogenic | Vitellogenic with hydrated oocytes | Spawning | Spawned out | *n* |
|---|---|---|---|---|---|---|---|
| <220 | 50 | 50 | | | | | 2 |
| 221–230 | 100 | | | | | | 1 |
| 231–240 | 100 | | | | | | 11 |
| 241–250 | 78 | 11 | 11 | | | | 9 |
| 251–260 | 69 | 15 | 15 | | | | 13 |
| 261–270 | 31 | 23 | 31 | 7.7 | | 7.7 | 13 |
| 271–280 | 32 | 16 | 37 | | | 16 | 19 |
| 281–290 | 44 | 11 | 44 | | | | 18 |
| 291–300 | 25.7 | 23 | 40 | 2.9 | | 8.6 | 35 |
| 301–310 | 34 | 13 | 44 | | 3.1 | 6.3 | 32 |
| 311–320 | 33 | 12 | 45 | | 3 | 6.1 | 33 |
| >320 | 26.9 | 16 | 47 | 2.9 | 7 | 11 | 172 |

plasma reproductive steroid concentrations (E2: 650 ±110 pg/mL plasma, $n$=66; T: 80 ±12 pg/mL plasma, $n$=66). Increases in GSI and reproductive steroids were observed in animals at the previtellogenic stage, and peak levels of GSI (20.0 ±4.8, $n$=9) and plasma E2 levels (7000 ±4700, $n$=4) were found in vitellogenic sole with hydrated oocytes, whereas peak plasma T levels (2300 ±620, $n$=9) were found in spawning females. All reproductive parameters were reduced in spawned out sole (GSI: 2.8 ±0.5, $n$=31; E2: 280 ±70, $n$=21; T: 90 ±50, $n$=21). 17α, 20β-P was not detected in female sole.

Figure 5, A–C, shows the mean levels of reproductive parameters in female sole at each month of collection. The sole sampled in July had low GSI (2.14 ±0.45, $n$=23) and plasma reproductive steroid levels (E2: 710 ±160, $n$=26; T: 100±30, $n$=27), which remained low until the onset of vitellogenesis (September–October for the majority of fish). The highest GSI (12.0 ±2.9, $n$=10) and plasma steroid levels (E2: 12000 ±5000, $n$=3; T: 2400 ±1200, $n$=4) were observed in January. By March, GSI and plasma reproductive steroid levels were reduced to levels comparable to those found in sole sampled in July. In general, fish from Tulalip Bay and Pilot Point had similar levels of reproductive parameters, which were lower than levels in fish from the University Point. The fish at University Point were either in final maturation or were actively spawning, whereas fish from Tulalip Bay and Pilot Point were migrating to spawning areas to undergo final maturation.

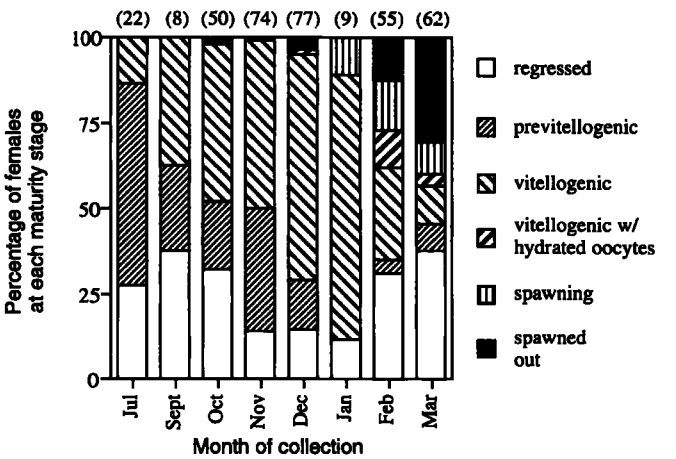


**Figure 2**

Percentage of female English sole at each stage of ovarian development by collection month. Numbers in parentheses represent animals sampled each month and histologically analyzed for ovarian stages.

**Male** Figure 6, A and B, shows the reproductive parameters in male sole at each developmental stage. The changes in reproductive parameters were similar to those observed in female sole. Generally, GSI (0.60 ±0.08, $n$=6) and plasma steroid levels (11KT: 1900 ±920 pg/mL plasma, $n$=4; T: 160 ±60 pg/mL plasma, $n$=4) were low in regressed animals. Increases in GSI and reproductive steroids were observed in animals at the early recrudescence stage and peaked in spawning fish (GSI: 1.6 ±0.1, $n$=91; 11KT: 5300 ±610, $n$=57; T: 830 ±130, $n$=64). Repro-

**Table 3**

Length maturation relationship in male English sole collected during months of gonadal recrudescence, October–March. Numbers represent percentage of the animals in the length class at each testicular stage.

| Length (mm) | Regressed | Early recrudescence | Late recrudescence | Early spermiogenesis | Spawning | Spawned out | *n* |
|---|---|---|---|---|---|---|---|
| <220 | | | | 85 | 15 | | 13 |
| 221–230 | 6.7 | 13 | 6.7 | 60 | 13 | | 15 |
| 231–240 | 13 | 6.7 | 13 | 33 | 27 | 6.7 | 15 |
| 241–250 | | 6.7 | 3.3 | 27 | 60 | 3.3 | 30 |
| 251–260 | 5.6 | 5.6 | 0 | 47 | 39 | 2.8 | 36 |
| 261–270 | | 2.9 | 2.9 | 49 | 40 | 5.7 | 35 |
| 271–280 | | 4.8 | | 43 | 48 | 4.8 | 21 |
| 281–290 | | 6.7 | | 40 | 53 | | 15 |
| 291–300 | | | | 36 | 64 | | 14 |
| 301–310 | | | | 38 | 50 | 13 | 8 |
| 311–320 | | | | 25 | 50 | 25 | 4 |
| >320 | 10 | | 10 | 10 | 70 | | 10 |

ductive parameters were reduced in spawned out fish (GSI: 0.8 ±0.1, $n$=8; 11KT: 83 ±5, $n$=8; T: 24 ±7, $n$=7), and plasma steroid levels in spawned out fish were significantly lower than levels observed in fish at other stages of testicular development.

Figure 7, A–C, shows the mean levels of reproductive parameters in male sole at each month of collection. GSI in sole sampled during July was low (0.89 ±0.18, $n$=6), increased to a peak in January (2.6 ±0.7, $n$=4), and returned to baseline levels in sole sampled in March (0.8 ±0.8, $n$=22). Plasma steroid levels were low in sole sampled in July (11KT: 890 ±140, $n$=13; T: 120 ±30, $n$=12) even though a few fish expressed milt. The levels increased to a peak in February (11KT: 13000 ±2800, $n$=6; T: 1800 ±340, $n$=14), and decreased in March (11KT: 1300 ±950, $n$=18; T: 400 ±310, $n$=15). Highest levels of plasma T and 11KT were found in fish from University Point where fish had migrated to spawn. A few fish with comparable levels of 11KT were found in March from the residential site at Tulalip Bay.

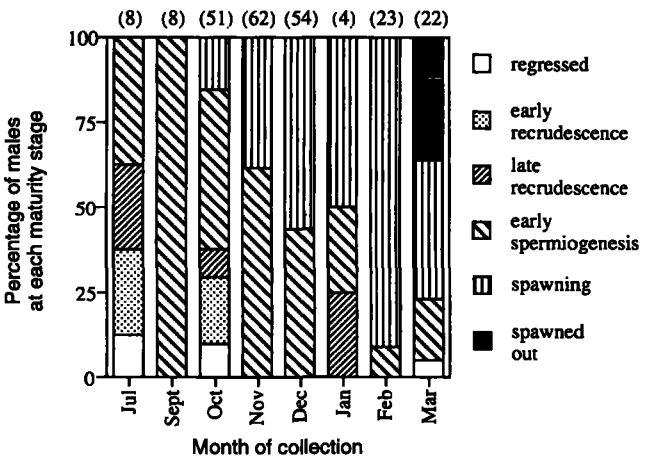


**Figure 3**

Percentage of male English sole at each stage of testicular development by collection month. Numbers in parentheses represent animals sampled each month and histologically analyzed for testicular stages.

## Discussion

Typical size-at-maturity for English sole is 260 and 210 mm TL for female and male sole, respectively (Garrison and Miller, 1982). Histological analyses of gonads collected in our study showed the smallest group of vitellogenic females to be 240–249 mm TL, but generally fish less than 260 mm TL were immature. Also, among females >260 mm, which were presumably old enough to undergo sexual maturation, approximately 24% were found in the regressed stage even during the peak of the reproductive season. This finding is consistent with findings by Johnson et al. (1988), in which the percentage of vitellogenic females at reference areas during peak recrudescence was about 80%. In contrast, males at much smaller length (i.e. 195 mm) were maturing, but no spawned out males were found at sizes <230 mm, suggesting that males <230 mm may not migrate to the spawning area. Although fish age was not determined in this study, length-at-age relationships determined for Puget Sound English sole (Myers et al., 1993) showed

that females at 260 mm were three years of age, and males at 195 mm were two years of age. Other studies have shown that females first mature at three years of age, whereas males mature at two years of age (Smith, 1936; Harry, 1959).

The pattern and timing of ovarian development observed in our study were similar to previous reports on English sole (Garrison and Miller, 1982; Kruse and Tyler, 1983; Johnson et al., 1991; Fargo and Tyler, 1994). Gonadal recrudescence in Puget Sound English sole began in early fall (September–October), vitellogenesis and spermiogenesis peaked in early winter (December–January), and spawning took place during late winter months (February and March). However, our findings suggest that small proportions of animals did enter vitellogenesis early; vitellogenic sole were found as early as July, whereas spawned out sole were found as early as October. In an earlier study that investigated oocyte development in female English sole (Johnson et al., 1991), the earliest spawning females were found in January. This discrepancy may be due to the fact that the number of fish collected in early fall in the first study (Johnson et al., 1991) was small compared with the present study; therefore, early spawning females may not have been observed. Nevertheless, changes in reproductive parameters (GSI, and plasma sex steroids) were similar to those described by Johnson et al. (1991) and to the reproductive endocrine cycles described for other species of female flatfish (e.g. Liu et al., 1991; Methven and Crim, 1991; Harmin et al., 1995). Generally, regressed fish had low values for the various reproductive parameters. The onset of vitellogenesis was accompanied by an increase in GSI and plasma sex steroid levels. After spawning, these levels declined to levels similar to those observed in regressed animals. Reproductive parameters at the two residential sites (Pilot Point and Tulalip Bay) were similar and supported the findings of Laroche and Richardson (1979) who observed no apparent latitudinal trend in the time of spawning in sole from the Oregon coast. Reproductive parameters in fish from University Point, however, were higher because a majority of sole at this site were undergoing final maturation or spawning (Johnson et al., 1991).

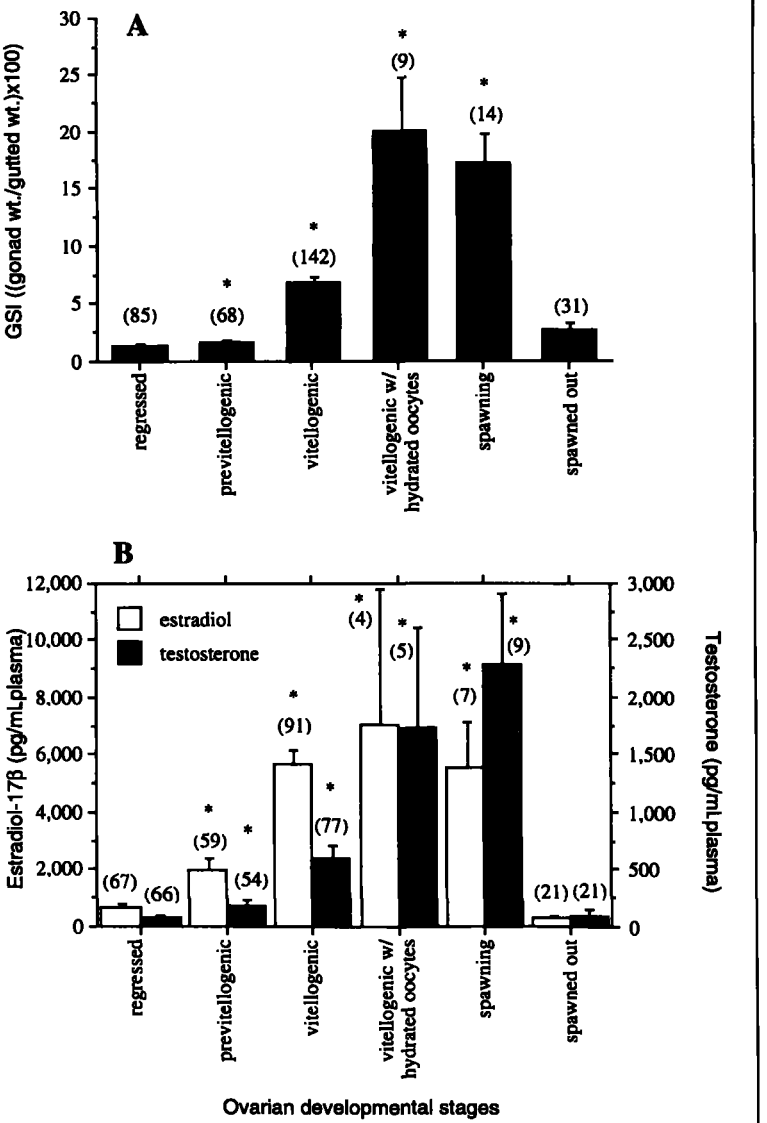


**Figure 4**

Mean ±SE of (**A**) gonadosomatic index (GSI), and (**B**) plasma steroid concentrations in female English sole at each stage of oocyte development. * denotes significantly higher levels than levels observed in regressed and spawned out fish (ANOVA, Fisher's PLSD, 95% CI). Numbers in parentheses represent animals at each ovarian developmental stage.

It is well established that E2 stimulates the liver to produce vitellogenin (Ng and Idler, 1983), and in this study, as in Johnson et al. (1991), vitellogenesis in female English sole coincided with a rise in plasma E2 concentrations. Plasma concentrations of T, a biosynthetic precursor to E2 (Kagawa et al., 1982), changed in parallel with the plasma E2 concentrations, although plasma T levels were lower than plasma E2 levels at all stages of gonadal development. Higher plasma T levels were observed in

vitellogenic sole compared with regressed sole, and highest plasma T concentrations were observed in spawning sole. Similar observations have been made in winter flounder *(Pleuronectes americanus)*, where concentrations of T have been correlated with oocyte stages characterized by germinal vesicle migration (Truscott et al., 1992b). In salmonids, estrogens and androgens such as T appear to play an important role in regulating production of pituitary GTH-II (Xiong et al., 1993, 1994), which stimulates the production of progestins, steroids involved in inducing final maturation (Swanson, 1991). This would be consistent with the high concentrations of T observed in spawning female English sole and winter flounder.

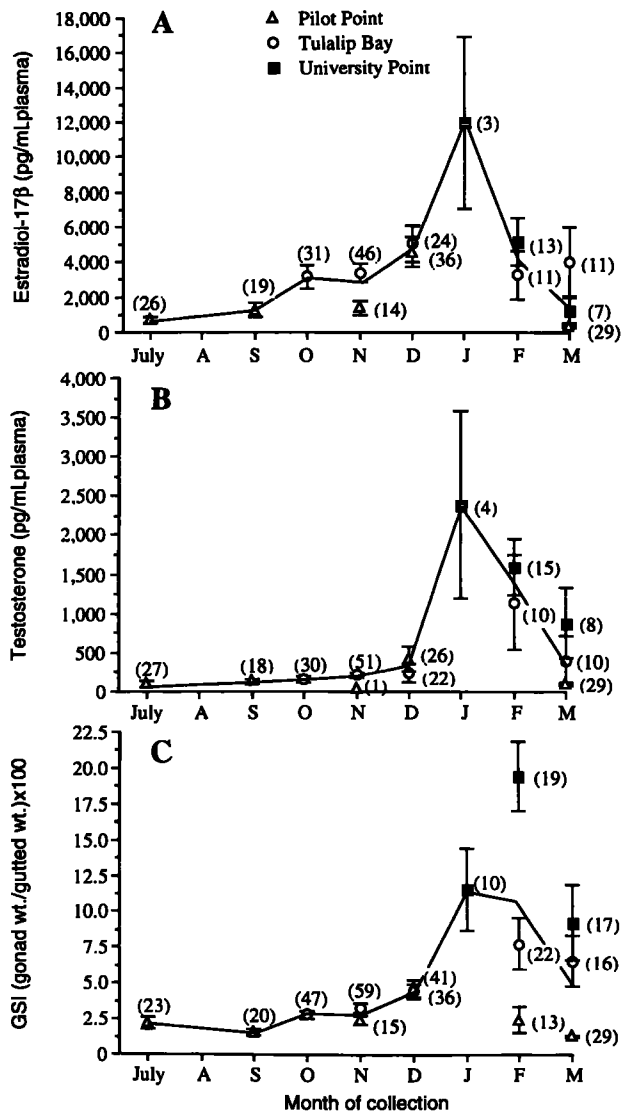


**Figure 5**

Mean ±SE of (**A**) gonadosomatic index (GSI), (**B**) plasma estradiol 17-β (E2) concentrations, and (**C**) plasma testosterone (T) concentrations in female sole from Tulalip Bay, Pilot Point, and University Point at each month of fish collection. Line represents mean levels at each month of fish collection. Numbers in parentheses represent animals sampled each month at each site.

In male teleosts, 11KT is known to be important in stimulating spermatogenesis, whereas T is known to be important in feedback effects on the pituitary (Borg, 1994). T is a biosynthetic precursor to 11KT (Ozon, 1972). As with E2 in female sole, the levels of T and 11KT covaried in male sole; 11KT levels were significantly higher than T levels at all stages of gonadal development. Similar relations between T and 11KT concentrations have been observed in other flatfish species, such as Pacific halibut *(Hippoglossus stenolepis)* (Liu et al., 1991) and winter flounder (Harmin et al., 1995). These results are consistent with the role of 11-oxygenated androgens as the dominant regulatory androgens in male teleosts, stimulating secondary sexual characters, reproductive behavior, and spermatogenesis (Borg, 1994).

In male winter flounder (Harmin et al., 1995) and plaice (Wingfield and Grimm, 1977), reproductive parameters (GSI, plasma 11KT and T concentrations) increased with the onset of seasonal testicular recrudescence, reached a peak in prespawning and spawning males, then decreased in spawned out males. However, in most male teleosts that have been studied, the levels of plasma 11KT and T peak during the prespawning period rather than during the spawning period (Borg, 1994). For example, the levels of plasma 11KT and T in Atlantic halibut *(Hippoglossus hippoglossus)* peaked briefly in sperm-producing fish, then declined during the spawning period (Methven and Crim, 1991). The reproductive parameters measured in male English sole were similar to the patterns observed in winter flounder and plaice, where steroid concentrations remained high during the peak spawning period.

Interestingly, the reproductive steroid levels observed in spawned out male English sole were significantly lower than levels observed in regressed males that were collected in summer and early fall. A pattern somewhat like this was also observed in male winter flounder and Atlantic halibut. In both male winter flounder (Harmin et al., 1995) and Atlantic halibut (Methven and Crim, 1991), the plasma steroid levels were low in spent males but began to increase about two months after the peak spawning period. Although this study did not measure reproductive parameters in the months immediately following the peak spawning period (i.e. April through June), similar changes

in plasma steroid levels may have occurred in male English sole and would account for the significant difference in plasma steroid levels between spent and regressed males.

A few male English sole sampled in July expressed milt even though reproductive steroid levels were low. Release of milt was also observed in winter flounder (Harmin et al., 1995) and Atlantic halibut (Methven et al., 1991) a few months earlier than vitellogenesis in females. Moreover, in winter flounder (Harmin et al., 1995), milt remained expressible a few months after the spawning season even though steroid levels were low during this time. Histological analyses of English sole testis showed that initiation of spermiogenesis does begin in July in a substantial proportion of sole, in spite of their low plasma steroid concentrations. This phenomenon has also been observed in other male fish, but the mechanism accounting for it is not entirely clear. Borg (1994) suggests that concentrations of T and 11KT in the testis itself may be quite high in early spermatogenesis, sufficient to stimulate spermiogenesis even when plasma concentrations of T and 11KT are low. The early production of mature sperm may be typical of most northern latitude, temperate zone teleosts in which fully developed spermatozoa are formed before winter and stored for discharge in spring (Lofts, 1987).

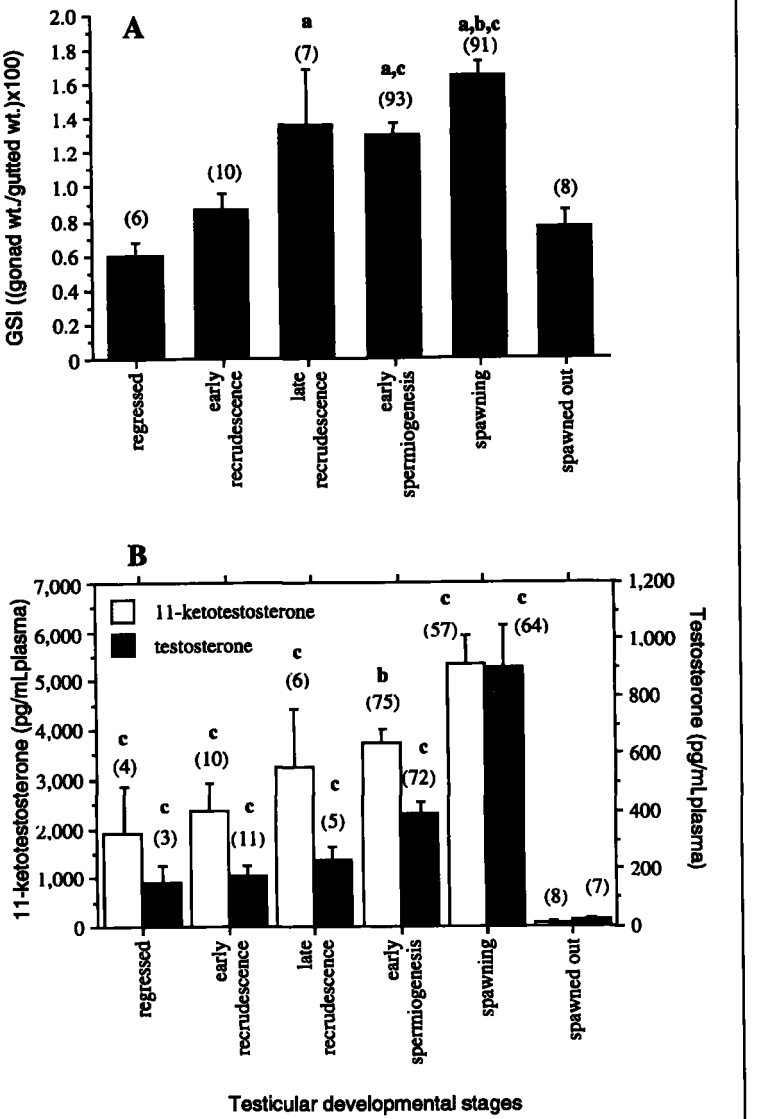


**Figure 6**

Mean ±SE of (**A**) gonadosomatic index (GSI) and (**B**) plasma steroid concentrations in male English sole at each stage of testicular development. "a" denotes significantly higher levels than levels observed in regressed fish; "b" denotes significantly higher levels than levels observed in early recrudescence fish; and "c" denotes significantly higher levels than levels observed in spawned out fish (ANOVA, Fisher's PLSD, 95% CI). Numbers in parentheses represent animals at each testicular developmental stage.

It is unclear which steroid induces final oocyte maturation in English sole. In all teleosts which have been studied, final maturation is triggered by a surge in plasma concentrations of a maturational gonadotropin (GTH-II). GTH-II stimulates gonadal production of progesterones and related compounds, the C21 steroids, which induce final oocyte maturation and production of sperm (Swanson, 1991). In most teleosts, 17α, 20β-P is believed to be a potent MIS (Scott and Canario, 1987, 1992; Inbaraj et al., 1995). However, in flatfish species that have been studied, low or nondetectable levels of 17α, 20β-P were found (Howell and Scott, 1989; Truscott et al., 1992b; Mugnier et al., 1995). Similarly, 17α, 20β-P was not detected in spawning English sole, and in some flatfish species, other steroids have been suggested as the MIS. For example, in winter flounder 17β-hydroxy-5β-androstan-3-one and T were correlated with oocyte stages characterized by germinal vesicle migration (Truscott et al., 1992b), whereas in turbot *(Scophthalmus maximus L.)* 17α, 21β,21-trihydroxy-4-pregnene-3-one-20 has been shown to induce final maturation (Mugnier et al., 1995). Recent studies also suggest that in plaice *(Pleuronectes platessa)* and Dover sole *(Solea solea)* 17α, 20β-P actually does induce final maturation but is metabolized before it can be detected in

the bloodstream with conventional RIAs (Scott and Canario, 1992; Inbaraj et al., 1995). Clearly, additional research is needed in this aspect of English sole reproductive biology.

In summary, the reproductive endocrine cycle in female and male English sole from two residential sites and a spawning site in Puget Sound, WA, was characterized by measuring reproductive steroid concentrations and correlating them with collection time and histological assessment of gonadal stage. This study provides the first description of the reproductive endocrine cycle in male English sole and can be used as a baseline tool in evaluating the effects of contaminants on reproductive endocrine function in male English sole, or in individuals used in mariculture.

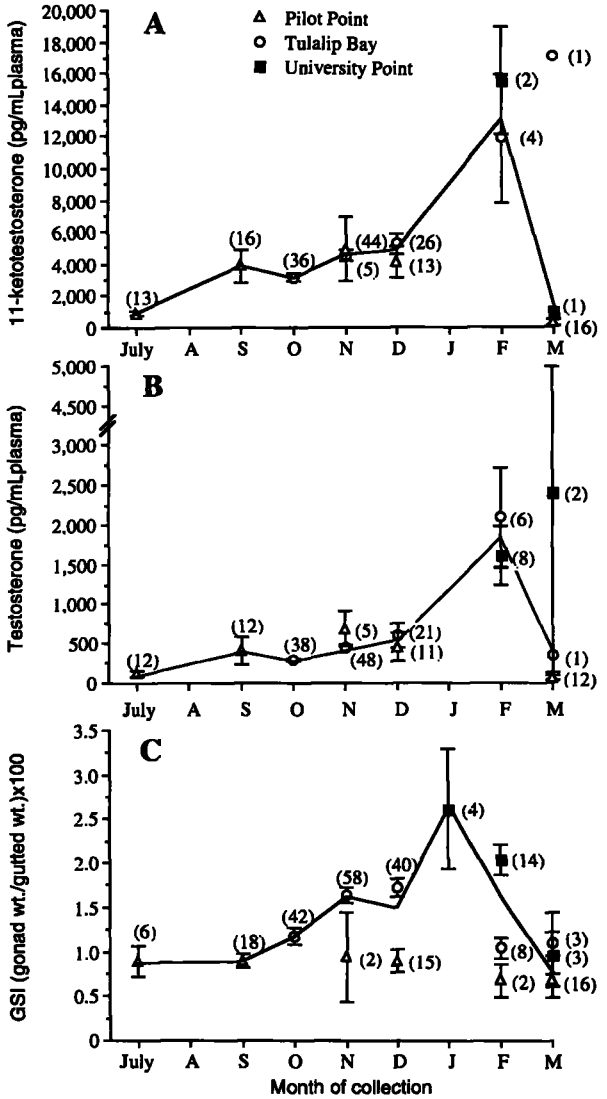


**Figure 7**

Mean ± SE of (**A**) gonadosomatic index (GSI), (**B**) plasma 11-ketotestosterone (11KT) concentrations, and (**C**) plasma testosterone (T) concentrations in male sole from Tulalip Bay, Pilot Point, and University Point at each month of fish collection. Line represents mean levels at each month of fish collection. Numbers in parentheses represent animals sampled each month at each site.

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# Parasitism of the golden king crab, *Lithodes aequispinus*, by two species of snailfish, genus *Careproctus*

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**Abstract.**—Along the continental slope of the eastern Bering Sea, two species of *Careproctus* snailfishes deposit eggs within the branchial chambers of the commercially important golden king crab (*Lithodes aequispinus*). The larger of the two species is the pink snailfish (*C. furcellus*); the smaller species is an undescribed species referred to as the red snailfish. According to 1982 trawl survey data, incidence of snailfish eggs and larvae within crab branchial chambers increases with carapace length (CL) and is greater for male than female crabs. A logistic model fitted to the incidence data predicts that a 140-mm-CL male will have an incidence of 0.52, approximately 1.9 times greater than the incidence for a 100-mm male. Incidence for a 100-mm-CL male is approximately 1.9 times greater than that for a female of equal size. On the basis of developmental stages of embryos carried by female golden king crab and the developmental stages of snailfish embryos within a female's branchial chambers, snailfish appear to deposit eggs preferentially in crabs that are early in their molt cycle. The presence of the egg masses results in gill compression, localized necrosis of gill tissue and, in extreme cases, total loss of gill tissue on one side of the body. For crabs of commercial size, the presence of eggs and larvae increases mortality within the holds of fishing vessels by 35%. The current incidence of eggs and larvae in commercial sized males, however, is so low that the effect on the commercial fishery is considered to be small.

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Fish. Bull. 96:871–884 (1998).

Liparid snailfish in the genus *Careproctus* extrude eggs through an anteriorly positioned ovipositor into the branchial chambers of large lithodid crabs. This relationship was first described, independently, by Rass (1950) and Vinogradov (1950) for *C. sinensis* and *Paralithodes camtschatica* in the northwest Pacific. Subsequent studies, however, have shown that additional species both within *Paralithodes* as well as within three other lithodid genera (*Lithodes, Lopholithodes* and *Paralomis*), also serve as hosts to various *Careproctus* species and that the association appears to be widespread according to reports from the North and South Pacific and South Atlantic (Hunter, 1969; Parrish, 1972; Peden and Corbett, 1973; Anderson and Cailliet, 1974; Balbontin et al., 1979; Melville-Smith and Louw, 1987; and Love and Shirley, 1993).

The advantages that snailfish gain by placing their eggs within an enclosed, constantly aerated space have been recognized since the association between *Careproctus* and lithodid crabs was discovered (Rass, 1950). The disadvantages to the crab, however, remain equivocal, with reports of no obvious damage (Hunter, 1969; Parrish, 1972), minor gill compression by the egg mass (Anderson and Cailliet, 1974; Melville-Smith and Louw 1987), and gill bleeding (Love and Shirley, 1993). Knowledge of the disadvantages is important because most affected lithodid species support commercial fisheries.

In this paper, we report on the deposition of egg masses by two species of *Careproctus* into the branchial chambers of the golden king crab (*Lithodes aequispinus*), a large, commercially harvested lithodid occurring along the continental slope of the North Pacific (Somerton and Otto, 1986). The identity of the two *Careproctus* species is uncertain because the taxonomy of the family Liparididae is problematic and incomplete (Allen and Smith, 1988). The larger species (Fig. 1), henceforth called the pink snailfish, is certainly within the *C. melanurus* group of morphologically similar species (Allen and Smith, 1988) and is likely to be *C. furcellus* which has been observed throughout the Bering Sea and Aleutian Islands (Kido, 1988). The smaller species (Fig. 1), henceforth called the red snailfish, is tentatively identified as a member of the *C. mederi* group described by Kido (1988), who re-

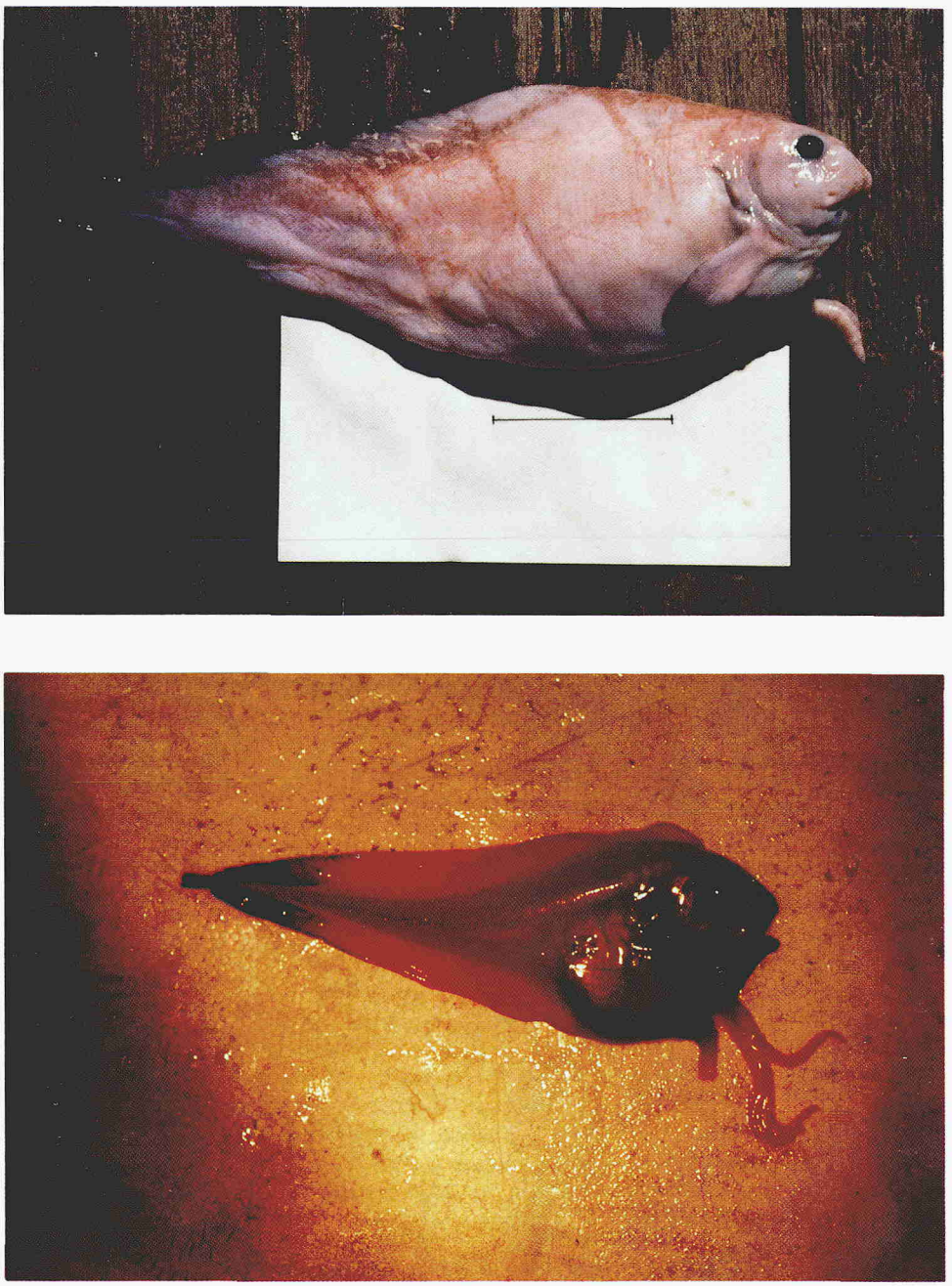

**Figure 1**

(Upper) pink snailfish (*Careproctus furcellus*); (lower) red snailfish (*C.* species). Both specimens are ripe females with their ovipositors extended. Note that the red snailfish has extremely long lobes on the pectoral fins that, in the picture, have been positioned in front of the body for clarity.

ferred to it as *Careproctus* species B.[1] Here we first examine the characteristics of this association, then consider how *Careproctus* snailfish choose their host crabs and what the consequences may be to the crabs.

[1] Stein, D. 1996. National Marine Fisheries Service, 1315 East-West Hwy., Silver Springs, MD, 20910. Personal commun.

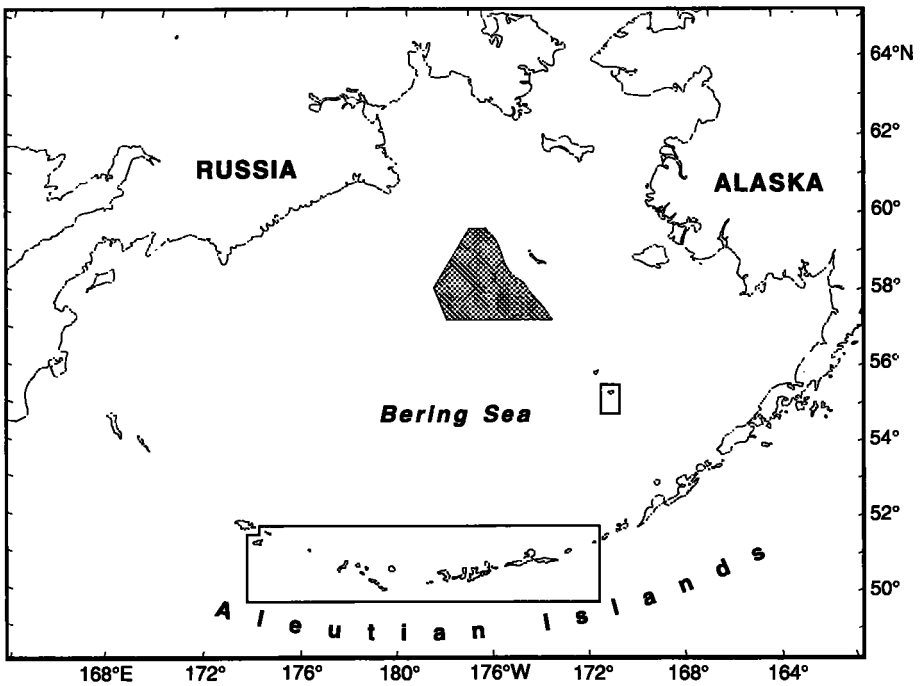


**Figure 2**

Collecting sites for the 1982 trawl survey (shaded area) and the 1996 commercial catch sampling areas in the Bering Sea and Aleutian Islands (unshaded areas).

## Materials and methods

Golden king crab were sampled 11 July–25 August 1982 aboard the FV *Rujin Maru no. 8* while it was conducting a bottom trawl survey of the benthic resources along the continental slope of the eastern Bering Sea (Fig. 2). All golden king crab were first sorted to sex, then measured for carapace length (CL) from the base of the eye to the posterior midline of the carapace. Females were evaluated for maturity, on the basis of relative width of their abdomens, and if mature, their pleopods were examined to determine whether they were carrying uneyed embryos, eyed embryos, or remnants of recently hatched embryos (egg cases and funiculi), or whether they were bare.

During this sampling, the senior author discovered that many of the crabs contained *Careproctus*-like egg masses or larvae within their branchial chambers. Further inspection of the egg masses and larvae revealed that there appeared to be two distinct types, one with egg diameters or larvae lengths considerably larger than the other. Several species of *Careproctus* were also captured in the trawls but two species, pink and red snailfish, predominated. Gentle pressure applied to the abdomens of some individuals of both species resulted in eggs being extruded through the ovipositor (Fig. 1) or milt being extruded out the genital papilla (Stein, 1980). The eggs of pink snailfish were visibly larger than those of red snailfish and the egg sizes of both species clearly matched the egg sizes found within the crabs. Consequently, starting on 27 July, 48 consecutive trawl hauls were sampled as follows for *Careproctus* spp. and their eggs and larvae.

All golden king crabs were examined for the presence of *Careproctus* egg masses or larvae clusters by removing their carapaces. Each mass was evaluated to type (uneyed embryos, eyed embryos, or larvae) and species (large eggs and larvae were assigned to pink snailfish; small eggs and larvae were assigned to red snailfish), and for location (i.e. which side of the crab it was obtained). Snailfish were first sorted to species, then externally sexed, if possible, by the presence of either an ovipositor or a genital papilla. Snailfish were then gently squeezed about the abdomen and classified as ripe if either eggs or milt were extruded. Thus, the sex could be either known or unknown and, if known, the individual could be either ripe or unripe.

The 1996 incidence of snailfish eggs and larvae within golden king crab were assessed by Alaska Department of Fish and Game at-sea observers and port samplers during the golden king crab fishing season in the Aleutian Islands and eastern Bering Sea. Female and small (<135 mm-CL) male golden

king crab, which are not retained by the fishery, were sampled aboard commercial vessels by occasionally collecting all individuals from one randomly chosen trap. Sampled crabs were first measured for carapace length, then examined for the presence of snailfish eggs and larvae, without regard to species, by removing their carapaces. Legal-size male crab were sampled from the commercial catches when they were landed at the processing plant. Catches were first separated into groups of live and dead crabs, then counted and subsampled by examining up to 100 individuals from each group for the presence of snailfish eggs. Port samples were collected for crabs caught either in the Bering Sea (three landings) or the Aleutian Islands (six landings; Fig. 2), but at-sea samples were collected only in the Aleutian Islands.

Thirteen golden king crabs found, during commercial sampling, to contain snailfish eggs or larvae were frozen whole, with the eggs or larvae left in place for later processing. Eighteen of 23 egg and larvae samples were nonhatched egg masses that were placed in water overnight to fully rehydrate, then weighed to the nearest 1 mg. Displacement volume of the egg masses (mL) was measured in a graduated cylinder. Egg masses were then teased apart and the total number of eggs counted. Diameters of approximately 200 eggs randomly chosen from each egg mass were measured to the nearest 0.03 mm with an optical micrometer. Volumes of the gills on both the affected and unaffected side of the crab were measured by displacement after they were excised with a scalpel at their bases. Volume of the empty branchial chamber on one side of the crab was then measured by securing the carapace in its proper place on the crab and then injecting Polycel insulating foam into the branchial cavity through a small hole. After any excess was removed, the volumes of the foam casts were then measured by displacement to the nearest milliliter. The 23 egg and larvae samples were then subjected to restriction fragment length polymorphism (RFLP) analysis (Dowling et al., 1996) by using six restriction enzymes to determine species identity.[2] Species identification patterns were established by using the RFLP analysis on six *Careproctus rastrinus*, eight *C. furcellus*, and one *C. cypselurus* collected in crab pots during commercial sampling.

The incidence (e.g. probability of occurrence) of snailfish eggs and larvae as a function of several predictor variables was described with a generalized linear model, with a logit link function and a binomial variance function (Venables and Ripley, 1994). For each crab, model inputs included a binary response variable (presence or absence of eggs or larvae). For the 1982 survey data, predictors included two continuous variables (carapace length and depth) and a discrete variable (sex). For the 1996 port sampling data, predictors included two discrete variables (area and whether the crab was alive or dead). Model selection was accomplished iteratively by first testing the significance of each interaction term with a likelihood ratio test, then by discarding the least significant term. This process was then repeated on each main effect and any associated interaction terms.

Differences in the depth distributions of male and female crab and of spawning and nonspawning snailfish were tested by first calculating a Cramer-von Mises statistic from catch-per-tow and depth data, then by determining the significance of the statistic with randomization (Syrjala, 1996).

Association between the developmental stage of eggs carried by a female golden king crab and the developmental stage of snailfish eggs within a crab's branchial chambers was tested with a Spearman's rank order correlation coefficient. Because king crabs extrude eggs onto their pleopods soon after molting (Powell and Nickerson, 1965; Sloan, 1985), the stage of embryonic development is a crude measure of the relative time since molting. Positive correlation between the developmental stages of crab and snailfish embryos would indicate that snailfish preferentially choose newly molted crabs as hosts. To simplify interpretation, 3 of 26 females were not used because they contained more than a single egg mass or larvae cluster. Embryonic developmental stages for snailfish (uneyed, eyed, and larval) and crabs (uneyed, eyed, and hatched) were considered as ordered variables and were assigned numeric codes (i.e. 1, 2, 3). Mature female crabs without any obvious egg remnants attached to the pleopods were grouped with females carrying hatched eggs because egg remnants may have been missed in the macroscopic examination performed at-sea.

The mortality rate of male crabs in the holding tanks of commercial vessels was estimated separately for crabs with and without snailfish eggs and larvae on the basis of 1996 port sampling data for commercial crab landings. For each landing, the total number of live crabs that were infested was estimated by multiplying the number of live crabs landed by the infested proportion in the catch subsample. The total number of infested dead crabs was estimated similarly. The mortality rate of infested and uninfested crabs was then estimated as the number dying divided by the total in each category. Average mortality rate was then estimated as the mean over all landings.

[2] Lopez, A. 1996. Marine Molecular Biological Laboratory, University of Washington, Seattle, WA. Personal commun.

## Results

### Depth distributions of golden king crabs and snailfish

The 48 hauls sampled on the 1982 survey were randomly distributed between 192 and 900 m. Over this range, golden king crab catch-per-tow (Fig. 3) and carapace length (Fig. 4) declined with increasing depth. Male and female crab occurred at significantly different depths (randomization test, $P$=0.005), with the median depth of males (203 m) being less than that of females (336 m).

Pink snailfish abundance declined with depth; most of the population occurred at depths <450 m (Fig. 5). Conversely, red snailfish abundance increased with depth; most of the population occurred at depths >450 m. (Fig. 5). Red snailfish was approximately six times more abundant, averaged over the entire survey area, than pink snailfish (mean catch per haul: red snailfish=4.57, pink snailfish=0.75, total number of both species=226). As a result, red snailfish were predominate at depths as shallow as 350 m. The proportion of the individuals that were ripe (both sexes combined) did not differ significantly between species (chi-square test, df=1, $P$=0.341). Ripe pink snailfish (both sexes combined) were found at significantly shallower depths than unripe individuals (randomization test, $P$<0.001), but ripe and unripe red snailfish did not differ in depth ($P$=0.255).

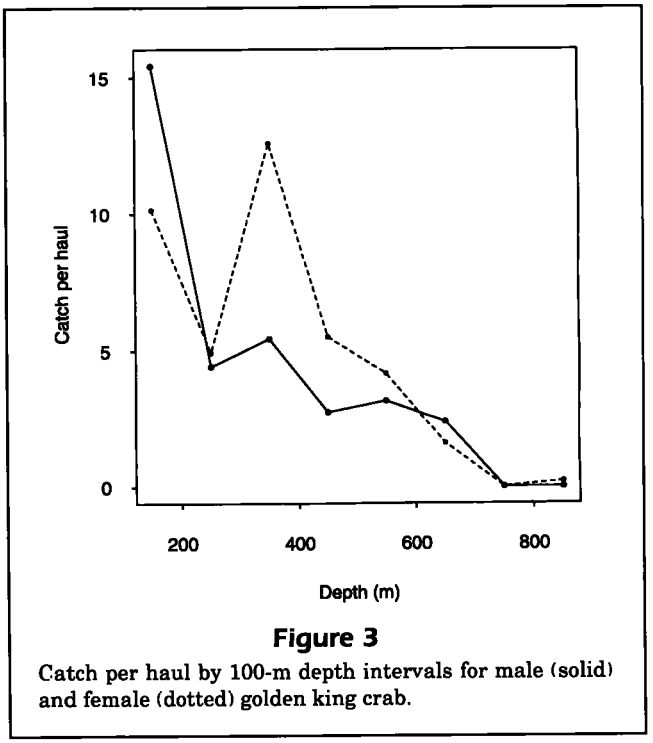


**Figure 3**

Catch per haul by 100-m depth intervals for male (solid) and female (dotted) golden king crab.

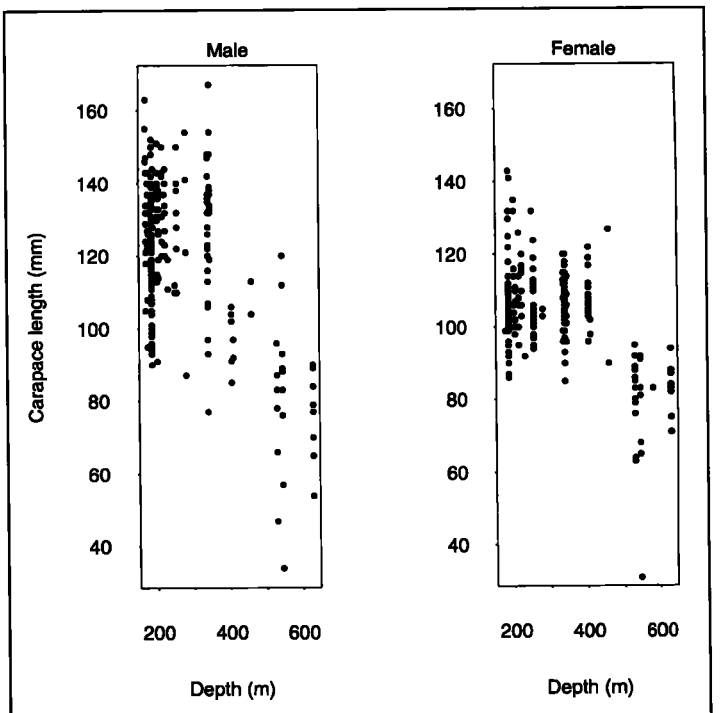


**Figure 4**

Carapace length of all crabs captured as a function of depth for male (left) and female (right) golden king crab.

### *Careproctus* eggs and larvae

Snailfish eggs are self adhesive and form compact masses that are often shaped like casts of the interior of the branchial chambers (Fig. 6). After hatching, larvae remain grouped together within the crab, thus allowing multiple batches of larvae to be easily distinguished. Of the 515 golden king crab examined on the 1982 survey, 97 contained 128 egg masses or larvae clusters. Twenty-three of the crabs had more than one egg mass or larval cluster (16 had 2, 6 had 3, and 1 had 4 egg masses or larvae clusters). The abundance of multiple occurrences relative to single occurrences did not differ between snailfish species (chi-square test, df=1, $P$= 0.111), indicating that the two species were equally likely to deposit eggs in previously infested crabs. Combined over both species, the number of egg masses found within infested crabs increased with carapace length (linear regression, $n$=94, $P$=0.049), indicating that large crabs tended to have more multiple occurrences. In three cases of multiple occurrences, eggs or larvae of both snailfish species were present. The relative abun-

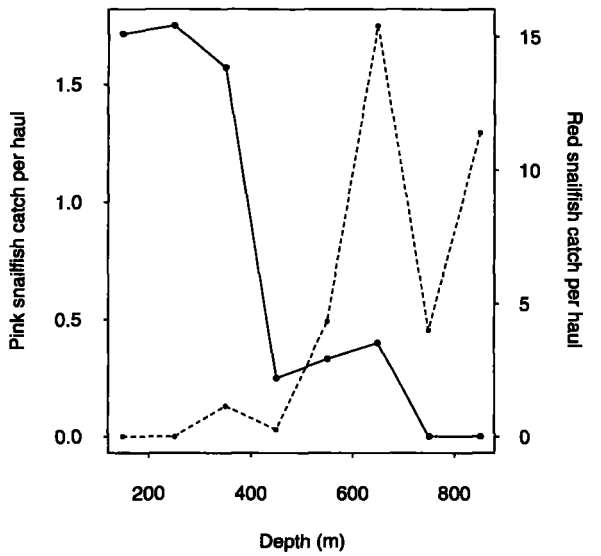


**Figure 5**

Catch per haul by 100-m depth intervals for pink snailfish (solid) and red snailfish (dotted).

dance of the three developmental stages (uneyed eggs, eyed eggs, and larvae) did not differ between snailfish species (chi square test, $P$=0.163), indicating that the timing of the egg deposition events and subsequent embryonic and larval developmental rates were about the same for both species. Summed over both species, the relative abundance of uneyed and eyed embryos was about equal, whereas the abundance of larvae was less than 20% that of either embryonic stage (Table 1).

Mean egg diameter was 4.83 mm (SD=0.29, eggs=4207, egg masses=18) and mean egg number was 688 (SD=84.0, egg masses=15). By comparison, the mean diameter of eggs taken from the ovarian lumen of a single pink snailfish was 4.9 mm (SD=0.124, $n$=208) and the total number of eggs was 790 with a displacement volume of 48.2 mL. Based on this specimen, mean egg volume was 0.061 mL (SD=0.017) and mean egg mass was 0.064 gm (SD=0.020).

Volume of single egg masses increased asymptotically with branchial volume (Fig. 7), indicating that up to some crab sizes, egg mass volume is limited by the available space in the branchial chambers. Up to 65% of the available volume within the branchial chambers (i.e. branchial volume – gill volume) was filled by a single egg mass.

**Table 1**

Incidence of *Careproctus* egg masses and larval clusters by species and stage of development.

| | Uneyed embryos | Eyed embryos | Larvae | Total |
|---|---|---|---|---|
| Red snailfish | 36 | 45 | 6 | 87 |
| Pink snailfish | 24 | 14 | 3 | 41 |
| Total | 60 | 59 | 9 | 128 |

## Incidence of snailfish eggs and larvae in golden king crab

Before developing a statistical model describing the 1982 incidence of snailfish eggs and larvae as a function of crab sex, carapace length, and sampling depth, we performed statistical tests to determine whether the two snailfish species could be combined in the analysis. Incidence of pink and red snailfish eggs did not differ by sex of host (chi-square test, df=1, $P$=0.28), nor by size of host ($t$-test, df=128, $P$=0.58), but incidence did differ by depth. Pink snailfish occurrences declined with increasing depth until none were encountered at depths >400 m (Fig. 8). In contrast to this, red snailfish masses increased in abundance with depth until reaching a peak at between 300–400 m, then declined until none were encountered at depths >600 m. Despite the difference in depth distribution for each species, the species were combined to simplify analysis. Because the combined incidence of eggs and larvae increased with depth to a peak at 250 m, then subsequently declined (Fig. 8), the depth effect in the model included a quadratic term. The best fit of a logistic model to the combined incidence data indicated that sex ($P$<0.001), length ($P$=0.003), and depth ($P$<0.001) were all highly significant (Table 2). The fitted model predicts 1) incidence increases with size (Fig. 9), 2) incidence is greater for males than females (Fig. 9), and 3) incidence is greater at middepth (i.e. significant quadratic depth effect, Table 2).

The best fit of a logistic model to the 1996 incidence in commercial males indicated that area ($P$<0.001) and whether the crabs were landed dead or alive ($P$=0.046) were both significant (Table 2). Incidence in the Bering Sea was over three times greater than in the Aleutian Islands. Incidence in dead crabs was 1.9 times greater than in live crabs in the Bering Sea and 1.6 times greater in the Aleutian Islands (Table 3). Incidences in live commercial males from the Aleutian Islands were 2.5 times greater than in sublegal males and 12.5 times greater than in females (Table 3). Incidence in 1996 of live commercial males in the Bering Sea was less than 20% of the incidence in 1982 commercial size males

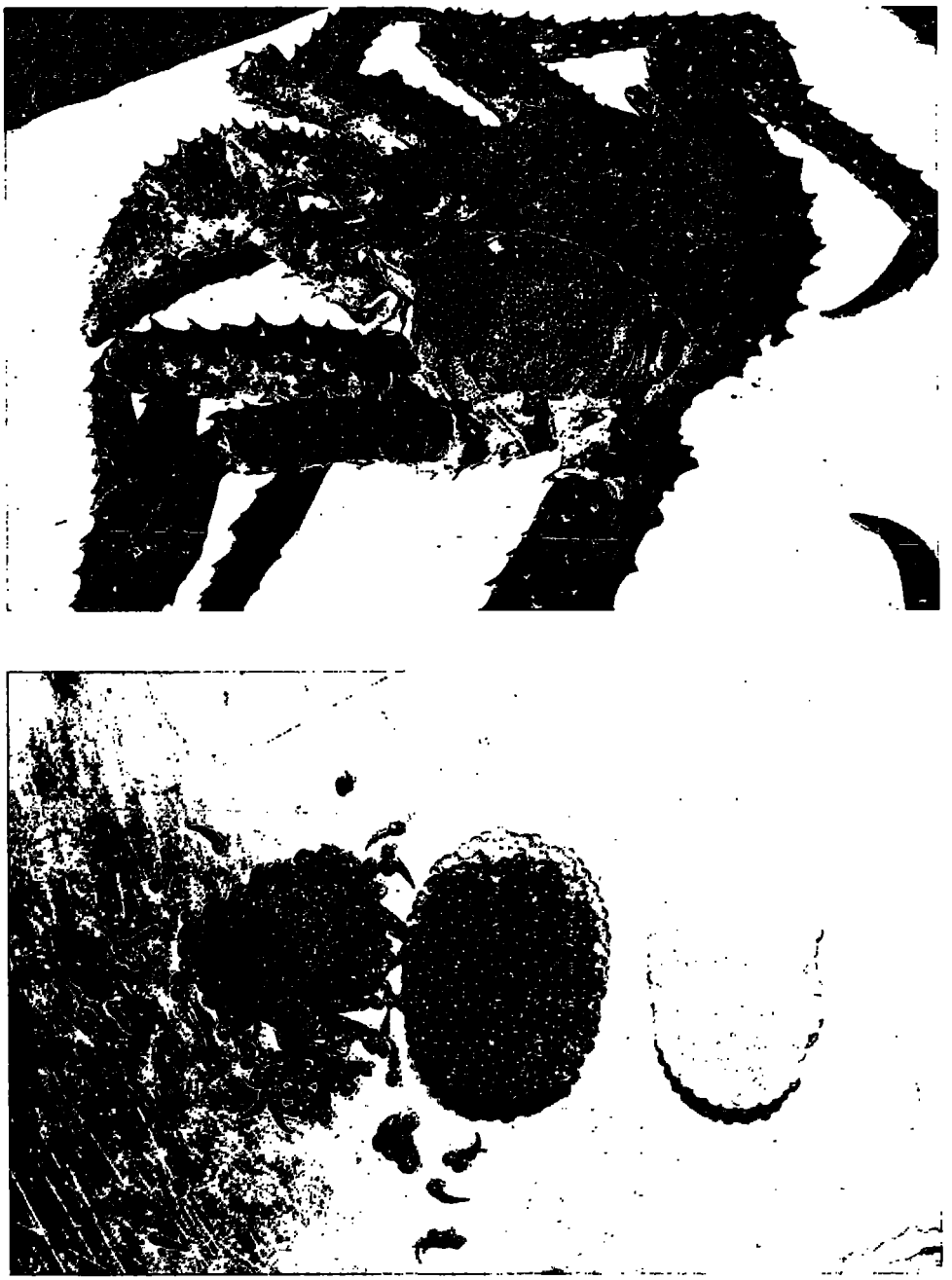

**Figure 6**

(Upper) A male golden king crab with part of the carapace cut away to show two *Careproctus* egg masses in different stages of development. (Lower) An early uneyed egg mass (right), a late uneyed egg mass (center), and a larvae cluster (left) taken from a single golden king crab.

(CL>135 mm; Table 3). The probability of a male dying in the holding tank of a commercial vessel was 0.035 if the crab contained snailfish eggs and larvae and 0.025 if the branchial chambers were empty, indicating that snailfish infestion increases the holding mortality of crabs.

## Association between crab and snailfish embryonic development stages

Mature female golden king crab carried snailfish embryos in all three stages of development (uneyed, eyed, and larval) only when they themselves were

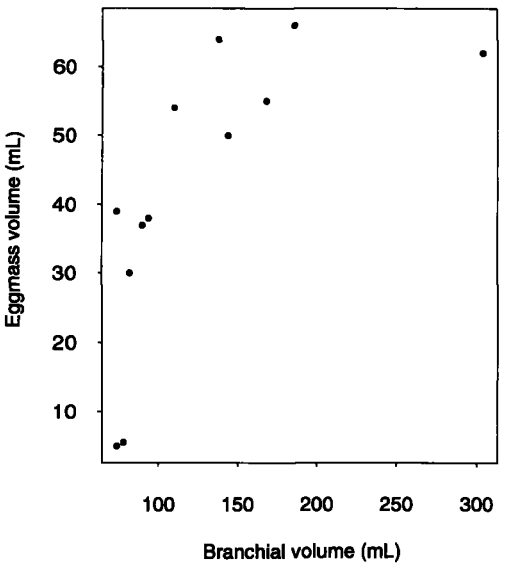


**Figure 7**

Volume of single egg masses as a function of the volume of the branchial chambers of the host crab.

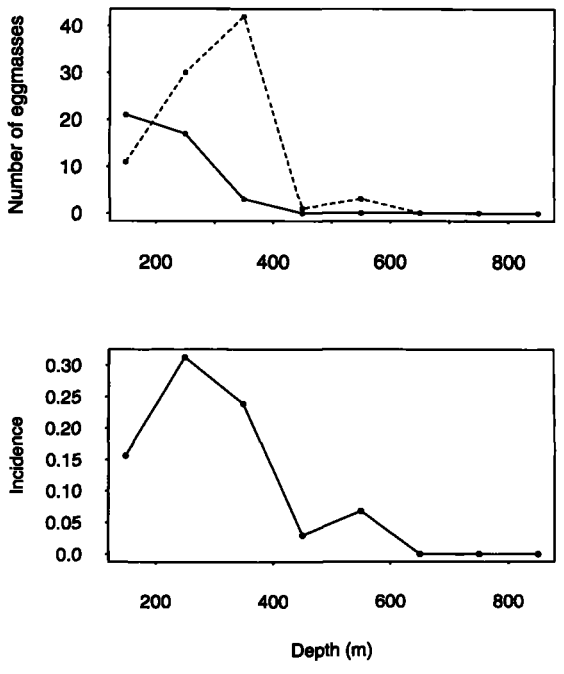


**Figure 8**

Number of egg masses by 100-m depth intervals for pink snailfish (solid line) and red snailfish (dotted line, upper). Incidence, or proportion of all crabs having snailfish eggs or larvae of either species, by 100-m depth interval (lower).

**Table 2**

Summary statistics of the fitted logistic models.

**Model 1 (1982 survey data)**

logit( incidence) = intercept + sex + length + depth + depth$^2$ + sex*depth + sex × depth$^2$

| Coefficient | Value |
|---|---|
| Intercept | –8.6724639 |
| Sex | –2.2823274 |
| Length | 0.0261672 |
| Depth | 0.0310400 |
| Depth$^2$ | –0.0000432 |
| Sex × depth | 0.0187658 |
| Sex × depth$^2$ | –0.0000512 |

Significance tests of main effects

| Effect | Likelihood ratio | df | Probability |
|---|---|---|---|
| Length | 8.87 | 1 | 0.003 |
| Sex | 25.02 | 3 | <0.001 |
| Depth | 20.92 | 4 | <0.001 |

**Model 2 (1996 port sampling of commercial catch)**

logit( incidence) = intercept + area + dead or alive

| Coefficient | Value |
|---|---|
| Intercept | –2.744489 |
| Area | –0.667367 |
| Dead or alive | –0.300833 |

Significance tests of main effects

| Effect | Likelihood ratio | df | Probability |
|---|---|---|---|
| Area | 22.39 | 1 | <0.001 |
| Dead or alive | 3.96 | 1 | 0.046 |

carrying uneyed embryos (Table 4). As crab embryos became more developed, so too did the snailfish embryos. Thus, crabs with eyed embryos were not found with uneyed snailfish embryos, and crabs with hatched embryos were not found with uneyed or eyed snailfish embryos. Considering the three development stages of both species as an ordered random variable, the crab developmental stages were highly correlated (rho=0.68, $P$=0.005) with the snailfish developmental stages.

## Genetic determination of species identity

All 14 of the fish samples, but only 10 of the 23 egg and larvae samples, collected by commercial fishery observers were sufficiently well preserved to allow

**Table 3**

Incidence of snailfish (*Careproctus* spp.) egg clusters within golden king crab (*Lithodes aequispinus*). Included are the total landed catch in numbers of live and dead crab, number of crab in each category examined, and the number with egg masses.

| Sampling type | Area | Condition | Catch | Crabs examined | Crabs with fish eggs | Percent infested |
|---|---|---|---|---|---|---|
| Incidence in male crabs >135 mm CL | | | | | | |
| 1996 port | Bering Sea | live | 12788 | 302 | 25 | 8.3 |
| | | dead | 351 | 44 | 7 | 15.9 |
| | Aleutian Is. | live | 46206 | 603 | 15 | 2.5 |
| | | dead | 1508 | 343 | 14 | 4.1 |
| 1982 survey | Bering Sea | live | | 55 | 24 | 43.6 |
| Incidence in female crabs and male crabs ≤135 mm CL | | | | | | |
| 1996 at-sea | Aleutian Is. | male | | 1641 | 12 | 0.7 |
| | | female | | 1631 | 4 | 0.2 |
| 1982 survey | Bering Sea | male | | 183 | 44 | 24.0 |
| | | female | | 274 | 26 | 9.5 |

DNA amplification. *Careproctus furcellus*, *C. rastrinus*, and *C. cypselurus* fish samples could be readily distinguished in the RFLP analysis. Of the 10 usable egg and larvae samples, two were identified as *C. furcellus* and eight clearly differed from all of the fish samples.

## Effect of the egg masses on gill function

The presence of egg masses within the branchial chamber of a crab was associated with three distinct pathological conditions of the gills. First, egg masses compressed the gills so strongly that a distinct impression of the egg mass was left on the gill surface (Fig. 10, upper, p. 880). Second, gills on the infested side of a golden king crab were often darker in color than those on the opposing side (Fig 10, lower, p. 880). Third, gills on the infested side often had areas of blackened, necrotic tissue (Fig. 10, p. 881). Several gills with necrotic tissue were examined microscopically after standard histological preparation.[3] A stage-wise progression of tissue damage was evident, beginning as small lesions with hemocyte encapsulations. As the lesions increased in size, they were more likely to be melanized, indicating a chronic condition, and often occluded one or more gill lamellae. Small (occluding one or more lamellae) to medium size (occluding the gill stem) lesions typically possessed new cuticle and normal respiratory epithelium underneath the affected area, indicating that the gill tissue would be regenerated during the next molt. In extreme cases, all of the gills on the affected side of the body were reduced to blackened stubs (Fig. 10, p. 881).

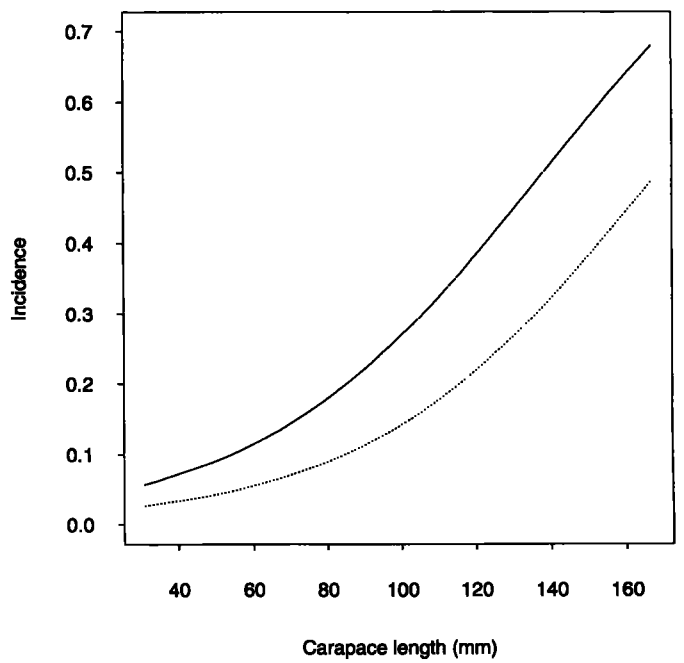


**Figure 9**

Incidence of *Careproctus* eggs and larvae, predicted by the generalized linear model, for male (solid line) and female (dotted line) golden king crab as a function of carapace length.

[3] Morado, F. 1996. Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA. Personal commun.

**Figure 10**

Pathological conditions associated with the presence of a snailfish egg mass in the branchial chamber of a golden king crab. Compression of the left gills and impression of individual eggs on the gill surface (upper). Blackened necrotic tissue on the right gills (lower). Complete loss of left gills (facing page). The fifth pereiopods, which act as gill cleaning appendages, are shown in their folded state at the posterior junction of the carapace and abdomen (lower).

## Discussion

The branchial chambers of golden king crab provide *Careproctus* embryos and larvae with a well aerated environment and protection from predators. This advantage would be jeopardized if they were ejected prematurely by crab molting. To minimize the risk of this happening, snailfish must either have the

**Figure 10 (continued)**

ability to choose host crabs that are early in their molt cycle or that have embryonic and larval residence times that are short in relation to the intermolt period of the crab. Evidence that snailfish have both attributes is provided by the association that we found between the embryonic developmental stages of crabs and those of the snailfish found within the crabs.

Preference for newly molted crabs is indicated by the observed presence of young (uneyed) snailfish embryos in female golden king crab carrying uneyed embryos but not in those carrying eyed embryos or remnants of hatched larvae (Table 4), because king crabs deposit their eggs soon after molting. Snailfish may locate newly molted crabs olfactorally, by detecting minute traces of molting hormones in the same way that some male crabs locate premolt females (Ryan, 1966).

A relatively short embryonic and larval residence time, compared with the intermolt period of the crab, is indicated by the presence of late snailfish developmental stages (eyed embryos and larvae) in newly molted (uneyed) female golden king crab (Table 4). The length of the embryonic periods for pink and red snailfish are unknown, but the large size of the eggs and low temperatures of the water in which they incubate (average bottom temperature on the 1982 survey was 3.8°C) indicate that the embryonic periods are probably quite long. Incubation times are

**Table 4**

Number of female golden king crab observed categorized by the development stage of their own embryos and the snailfish embryos within their branchial chambers.

| | Snailfish stages | | |
|---|---|---|---|
| Crab stages | Uneyed | Eyed | Larvae |
| Uneyed | 9 | 4 | 1 |
| Eyed | 0 | 1 | 0 |
| Hatched | 0 | 0 | 3 |

greater in colder water and for fish with larger eggs (Pauley and Pullin, 1988), but there are no studies applicable to a large egg-producing deep slope species such as *Careproctus*. If chinook salmon (*Oncorhynchus tshawytscha*) are used as an approximate model for a relatively large egg, cold water species, then 4.5 months would be required for hatching at 3.8°C. (Alderdice and Velsen, 1978). Although this rate of embryonic development may be long for a fish, it is considerably shorter than that of golden king crab which perhaps exceeds 1 year (Somerton and Otto, 1986).

If snailfish can preferentially choose newly molted crabs as hosts, then their spawning season must occur at the same time as the molting season of the

crab. However, the variety of snailfish embryonic stages that occurred during the 1982 sampling (Table 1), coupled with the probable slow developmental rate, indicates that pink and red snailfish have either a protracted spawning season, or perhaps lack spawning seasonality. Previous studies of snailfish reproduction have reported that aseasonal spawning was typical of abyssal and slope snailfishes, although *C. malanurus*, a close relative to pink snailfish, has a seasonal peak in spawning off Oregon (Stein, 1980). The likelihood for preferential selection of early molt-stage crabs is not necessarily diminished by aseasonal spawning in red and pink snailfish because golden king crab also have aseasonal reproduction and molting (Somerton and Otto, 1986).

The incidence of snailfish eggs and larvae was greater in male than in female crabs and increased with crab size in both the 1982 survey (Table 2; Fig. 9) and the 1996 commercial sampling (Table 3). The preference for male crabs as hosts over females is quite pronounced. For example, at the median 1982 sampling depth, a 100-mm male is 1.9 times more likely to contain eggs and larvae than an equal-size female (Fig. 9). As in our study, male *Lithodes tropicalis* had a higher incidence of snailfish eggs than females (Melville-Smith and Louw, 1986), but the apparent sex selection was attributed to size selection and to a large sexual dimorphism in crab size. In our case, we believe sex itself is important in host choice because sex was a significant predictor of incidence even when size and depth effects were included in the model. Such sex selection may not be universal, however, because a previous study of *L. aequispinus* reported that incidence was higher in females (Love and Shirley, 1993). Why a preference for males should occur is not obvious. One possible explanation, based on aquarium observations (Love and Shirley, 1993), is that female golden king crab aggressively defend the embryos attached to their pleopods. Perhaps this aggressiveness can discourage the attempts of a snailfish to extrude her eggs into the branchial chambers of the crab.

The apparent preference for large crabs is also quite pronounced. For example, at the median 1982 sampling depth, a 140-mm-CL male is 1.9 times more likely to contain snailfish eggs or larvae than a 100-mm-CL male (Fig. 9). The apparent preference of snailfish for large crabs is likely due to two distinct attributes associated with size in lithodid crabs. First, large king crabs molt less frequently than small king crabs. Although the molting frequency of golden king crabs is unknown, for male red king crabs (*Paralithodes camtschaticus*), molting frequency diminishes continuously with increasing age (McCaughran and Powell, 1977). Since a lower molt frequency would result in a lower probability of premature release of eggs and larvae, it is an advantageous feature for a perspective host to have. Second, larger crabs have larger branchial chambers to contain snailfish eggs. In our case, egg mass volume increased with branchial volume (Fig. 10), indicating that the size of an egg mass is limited by the size of the branchial chamber. This increase, however, diminished with crab size, indicating that in large crabs the size of an egg mass may be determined more by snailfish fecundity than by the availability of space. It is not clear what effect the space limitation would have on the searching behavior of snailfish. If a female snailfish is capable of partitioning a batch of ripe eggs among several spawning events, then she might be able to reduce the problem of space limitation by depositing eggs in several crabs. If instead female snailfish must deposit their entire batch in one spawning event, then considerably more searching would be required to find a crab with sufficient volume. To help provide some indication of whether a female partitions a batch of eggs, we measured egg batch volume for a single 40-cm pink snailfish, considering only eggs that were free in the ovarian lumen. Because the measured volume (48 mL) is about equal to the median volume of the egg masses found in crabs (Fig. 7), it is possible that a female spawns an entire batch in one event. If this is true, then a female would have to determine, perhaps by probing with her ovipositor, whether a prospective host has sufficient branchial volume for her batch of eggs.

Besides size and sex, other aspects of crab host choice by snailfish have been postulated. Melville-Smith and Louw (1987) suggested that *Careproctus* might preferentially choose only one side of host *L. tropicalus* to deposit egg masses. In our case, neither pink snailfish nor red snailfish chose one side of the crab over the other (binomial test, red snailfish, $P$=0.39, pink snailfish, $P$=0.76). Love and Shirley (1993) and Melville-Smith and Louw (1987) suggested, after finding no crabs with egg and larvae masses in both branchial chambers, that snailfish are inhibited from depositing egg masses in the unaffected branchial chamber of previously infested crabs, presumably to reduce host mortality. In our case, this feature was not true because of 23 crabs that had at least two egg or larvae masses, 13 had masses on both sides.

Because large crabs occur in shallower waters than small crabs and males occur in shallower waters than females, the preferred hosts of both snailfish species occur in the shallower portion of the 1982 depth range. Pink snailfish occur at approximately the same depths as their preferred hosts, but red

snailfish live in deeper waters and must migrate into shallower water to find suitable hosts. For red snailfish, a spawning migration is apparent by the shallower peak in the depth distribution of its egg masses (350 m; Fig. 8) compared with the depth distribution of the fish themselves (650 m; Fig. 5). For pink snailfish, by comparison, the depth distributions of the egg masses and fish nearly coincide. If the spawning migration is undertaken only by ripe fish, then a difference in depth distribution between ripe and unripe fish would be expected for red snailfish but not for pink snailfish. We are unable to account for our observation that the expected shift in depth distribution was found for pink snailfish but not red snailfish.

One shortcoming of the 1982 sampling of snailfish eggs and larvae is that the species identification was based on an apparent species difference in egg and larvae size. Although larvae were collected in an attempt to establish identification by linking larval characteristics to adult fish, the larvae were poorly ossified and their identities could not be determined.[1] In a second attempt at species identification, we subjected the eggs and larvae collected in the 1996 sampling to RFLP analysis. On this basis, it was possible to establish that pink snailfish do deposit eggs in golden king crab. Unfortunately, we had no red snailfish tissue available to establish an identification pattern for the RFLP analysis because red snailfish were not captured during the 1996 sampling (the commercial crab fishery does not extend into sufficiently deep water). Therefore, it was not possible to determine if the 8 of 10 specimens not matching any of the three sampled *Careproctus* species were, as we suspect, red snailfish.

Damage to the gills from the presence of egg masses may result from two causes. First, gill compression could be strong enough to restrict blood flow, resulting in localized necrosis. Second, egg masses could interfere with the functioning of the fifth pereiopod (Fig. 10), which is covered with setae and functions as a gill-cleaning appendage (Pohle, 1989). Experiments with other lithodid crabs have demonstrated that gill fouling similar to the discoloration observed in golden king crab could be experimentally produced either by restricting the movement of the fifth pereiopod or removing the setae from this appendage. The fouling is due not only to the accumulation of detritus on the gill surface, but also the accumulation of a host of organisms that feed on the detritus or directly on the gill tissue itself (Pohle, 1989). In golden king crabs, the degeneration of the gill tissue can proceed to the point that all of the gill tissue on the infested side is missing (Fig 10). In cases of small to medium lesions, it was clear from histological examinations that gill regeneration would occur at the next molt, but crabs with extreme cases of gill degeneration were not examined histologically and it is not known whether gill regeneration would occur. However, in at least one case, a newly molted golden king crab was encountered with no gills on one side of the body. Perhaps, this crab was an extreme case of gill damage which did not regenerate. Gill damage not only influences a crab's respiration but also its capability for ion exchange. Lithodid crabs that died as the result of the restriction of their cleaning appendages displayed considerable abdominal swelling which is indicative of ion imbalance (Pohle, 1989).

The 35% higher mortality of infested male crabs, compared with uninfested crabs, within the live tanks of commercial vessels (Table 4) indicates that the presence of egg masses hinders the ability of crabs to withstand the stress of capture and confinement. The impact on the fishery, however, depends on the incidence of snailfish eggs and larvae as well as the additional mortality they induce. In the case of the 1996 incidence in the Bering Sea (8.5%, Table 3, corrected for deadloss), for example, live-tank mortality increased by only 0.08%. Even at the higher incidence found in 1982 (44%), additional live-tank mortality would have been only 0.40%. Although the mortality that is induced on wild crabs is unknown, it appears that the impact of snailfish parasitism on the golden king crab fishery is small.

## Acknowledgments

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# Settlement and recruitment of queen conch, *Strombus gigas*, in seagrass meadows: associations with habitat and micropredators

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**Abstract.**—A suction dredge survey was conducted in the Bahamas in a tidal flow field system which contained a nursery ground for the economically significant gastropod *Strombus gigas* (queen conch). Settlement of larval conch within the system was associated with the specific location of the nursery and positively correlated with subsequent recruitment to the juvenile population (<45 mm shell length). Settlement was relatively independent of habitat features including depth, sediment characteristics, and macrophytes. Conversely, densities of micropredators (small crabs, shrimp, and predaceous gastropods) capable of consuming early postsettlement conch were often correlated with habitat features such as seagrass shoot density, seagrass detritus, and organic content of the sediment. The density of small xanthid crabs (mode=1.5 mm carapace width) was positively correlated with density of live postsettlement conch (mean ≤4/m$^2$), suggesting that conch settle in predator-prone areas or that the crabs respond numerically to small conch (or both). Densities of xanthids were very high (to >200/m$^2$), and the crabs probably represent an important source of mortality for small conch in the primary nursery ground. Shells of dead conch indicated that molluscan and asteroid predators probably caused most of the predatory mortality on young conch that settled outside the nursery. Because critical settlement and recruitment habitats for queen conch are associated with particular hydrographic conditions, these habitats cannot be identified or predicted simply by mapping obvious features such as seagrass cover, depth, or sediment type. An understanding of dynamic processes, such as larval transport and retention, selective settlement mechanisms, and trophic ecology, will be required to identify critical nursery habitats.

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Distribution of marine species with planktonic larvae is a function of both pre- and postsettlement processes. Location of reproductive sources, physical and oceanographic processes, duration and survivorship of larval stages, and larval behavior combine to determine settlement location, whereas predation, suitable habitat, and the behavior of early juveniles affect the number of individuals that survive to represent juvenile recruitment (Keough and Downes, 1982; Luckenbach, 1984; Connell, 1985). Experiments conducted in the laboratory with a large variety of species have shown that settlement in the field is probably a nonrandom process for the majority of marine invertebrates, and settlement behavior is usually assumed to place juveniles in habitats most suitable for growth or survival (or both) (Hadfield and Scheuer, 1985; Butman and Grassle, 1992; Grassle et al., 1992; Davis and Stoner, 1994; Stoner et al., 1996a).

Despite an abundance of data and experiments on settlement, relatively little is known about the relative importance of settlement rate and postsettlement predation in controlling local recruitment of most species to juvenile stages (Osman and Whitlatch, 1995). Because early postsettlement juveniles of many benthic species, especially those associated with soft sediments, are difficult to survey, quantitative data related to recruitment often depend upon observations of the smallest juveniles that can be detected easily. The result is a relatively poor understanding of the crucial period between settlement and first detection in the benthos (Keough and Downes, 1982; Luckenbach, 1984).

Queen conch (*Strombus gigas*) is a large gastropod that has great economic significance throughout the Caribbean and adjacent regions (Appeldoorn, 1994). Despite the wealth of information now available for conch larvae (Davis, 1994; Stoner and Davis, 1997), juveniles in year class 1 (e.g. Marshall, 1992; Iversen et al., 1987; Appeldoorn, 1994), and adults (Appeldoorn, 1988; Stoner and Sandt, 1992), little is known about larval settlement and the early postsettlement stage. Newly settled queen conch (<10 mm) are cryptic, often buried (Iversen et al., 1989; Sandt and Stoner, 1993), and are readily preyed upon by micropredators such as xanthid

crabs and certain polychaetes (Ray-Culp et al., 1997). Queen conch <50 mm shell length have rarely been encountered in the field (Iversen et al., 1994; Ray and Stoner, 1995; Iversen and Jory, 1997), and the only density data extant for these small conch were collected by Sandt and Stoner (1993) near Lee Stocking Island, Bahamas. However, queen conch settle at a large size (1.2 mm), compared with many other mollusks, and even the smallest juvenile, unless crushed completely, leaves an identifiable shell record of its settlement in the sediment (our study). This record can be used to examine the settlement-recruitment relationship and spatial variation in settlement.

Our study had three primary objectives. First, we conducted an extensive dredge survey for newly settled queen conch in and around a well-studied nursery area in the central Bahamas during the summer recruitment season in 1992. The survey was designed to test the hypothesis that the long-term distribution pattern of year-class 1 and 2 conch was associated with settlement pattern. The sum of live and dead individuals was used as an index of settlement at each sampling station, and the number of surviving (live) conch served as an index of recruitment. Through this survey, we gathered the first quantitative data on the distribution of queen conch <45 mm shell length (1.5–44 mm). Second, we used observations of shell damage sustained by dead individuals to determine the primary predatory forms on newly settled queen conch. We also examined spatial variation in predation type. Third, we examined the effects of environmental characteristics, such as depth, sediments, macrophytes, older conspecifics, and distribution of potential predators, on the observed distribution of newly settled queen conch.

## Study area

The Exuma Cays are an important source of queen conch for a large fishery in the Bahamas; the island chain is 250 km long, bordered to the east by the Exuma Sound, and to the west by the Great Bahama Bank. Water exchange occurs through numerous tidal inlets separating the islands, creating extensive tidal flow fields on the shallow bank. Nurseries of juvenile conch (1- and 2-yr-old, 70–150 mm SL) are located primarily on the bank side of the Exuma Cays near these inlets and are typically associated with seagrass meadows (2–4 m deep) that are flushed with clear, oligotrophic water from the Sound during flood tide (Stoner et al., 1996b).

We elected to survey postlarval conch in a tidal flow field located west of Lee Stocking Island and south of Norman's Pond Cay because the conch nursery near Shark Rock (Fig. 1) is well studied. Prior to sampling, five years of data had been collected on the distribution and abundance of 1- and 2-year-old juvenile conch, and environmental characteristics such as seagrass biomass, depth, and tidal currents had been mapped (Jones, 1996; Stoner et al., 1996b). Drogue studies have shown that, on flood tide, water from the Sound enters the inlet north of Lee Stocking Island, passes close to Shark Rock, and flows west of the nursery for a distance that is dependent on wind conditions and tidal phase (e.g. spring, neap) (Stoner et al., 1994). Tidal currents, which reach 100 cm/s at midtide, flow between sand bars in an S-shaped pattern following the bank bathymetry (Fig. 1B). The middle of the tidal channel is ~3 m deep and vegetated primarily with the seagrass *Thalassia testudinum*. Depth and seagrass density gradually decrease from midchannel to bare sand on both sides of the channel. Tidal range is ~1 m.

Annual surveys conducted between 1988 and 1992 showed that aggregations of juvenile queen conch always grazed within a 2-km long section of the tidal flow field close to Shark Rock (Fig. 1) and, at any given time, occupied only portions of the suitable habitat available (Stoner et al., 1996b). Stations for this study were established with reference to long-term distribution of conch in this area (Stoner and Waite, 1990; Stoner and Ray, 1993; Ray and Stoner, 1994) and to represent both down-channel and across-channel dimensions of the flow field. One line of stations was established in midchannel down the flow field from Adderly Cay (A) to Cook's Cay (F) with an attempt to locate all of the stations in similar depth and moderate seagrass shoot density. Stations A and F were each located ~4 km from the geographic center of the traditional nursery ground (Fig. 1), and stations B and E were located ~250 m outside the northeastern and southwestern ends of the nursery, respectively. Stations C3 and D3 were each established ~500 m from the geographic center of the nursery (Fig. 1C).

To represent the across-flow field dimension, five more stations were selected along two transects that lay perpendicular to the main axis of the tidal current at stations C3 and D3, as well as across the seagrass gradient. *Thalassia testudinum* density ranged from 4 to 704 shoots/$m^2$ and from 0.5 to 178 g dry wt/$m^2$ across this gradient in 1991 (Ray and Stoner, 1994) (Fig. 1C). Three stations were established along the D transect in addition to D3, increasing in macrophyte cover from bare sand at D1 to high seagrass and detrital biomass at D4. Along transect C, two stations were established in addition to C3, ranging from sand to moderate seagrass shoot density and macrophyte biomass. There were no areas of high seagrass biomass present near transect C and,

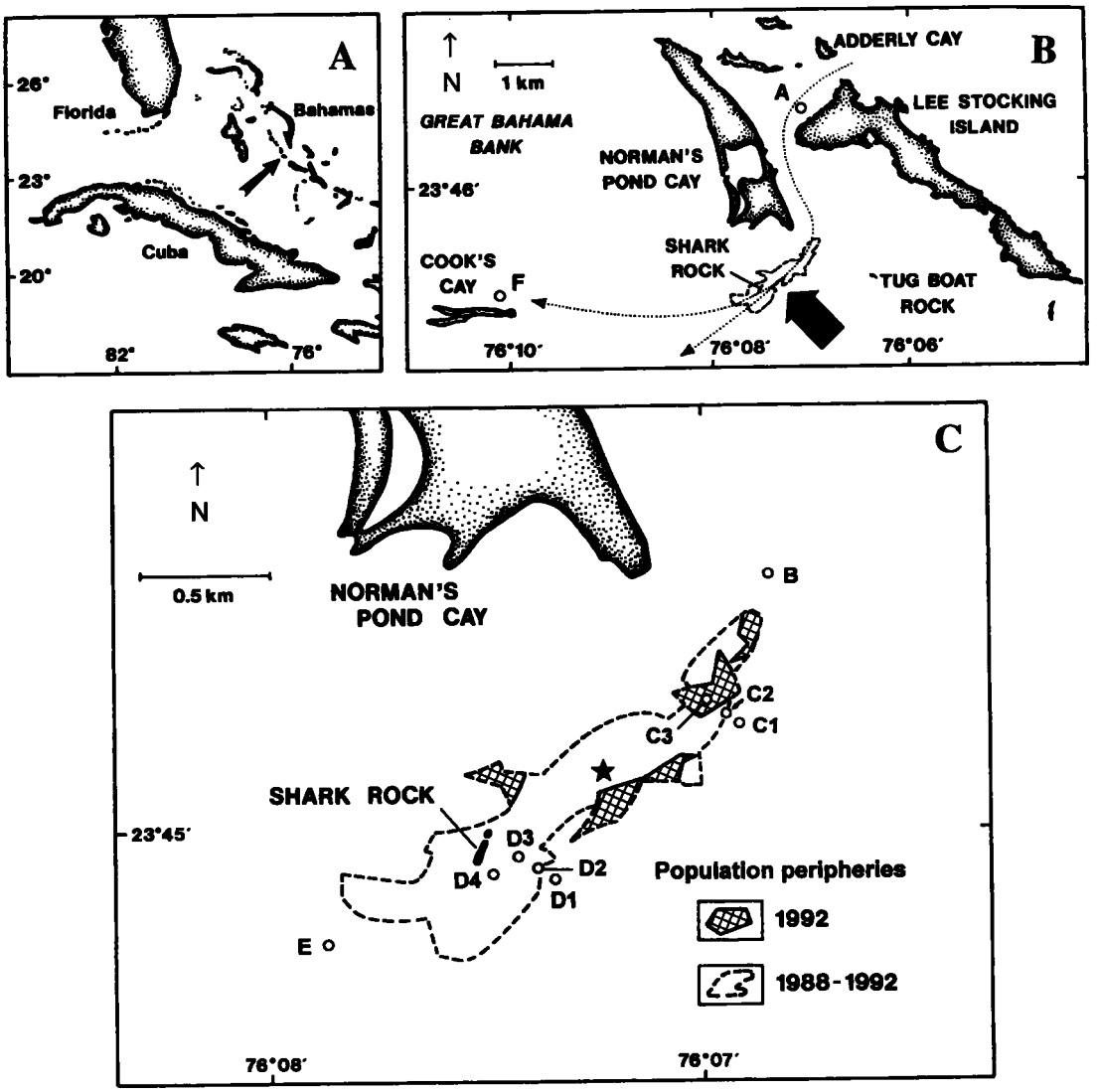



**Figure 1**

(**A**) Study area in the southern Exuma Cays, central Bahamas. (**B**) On the flood tide, water from Exuma Sound passes between Adderly Cay and Lee Stocking Island, flowing in an S-shaped pattern past Shark Rock towards Cook's Cay (dotted arrow). Stations A and F represented ends of the flow field. (**C**) Nine more stations were selected with respect to the long-term (1988–92) location of the juvenile queen conch aggregation, delineated by dashed line. In July 1992, just before dredge sampling was conducted, the aggregation occupied the areas shown in hatched polygons. Star indicates center of aggregation.

consequently, no station was directly comparable to D4. Other environmental characteristics, such as depth and certain sediment characteristics, also varied across the flow field (see "Results" section, Tables 1 and 2).

## Methods

### Dredge sampling

Given that maximum densities of conch veligers are observed during midsummer (June through August) and that the larval period lasts 3–4 weeks (Davis et al., 1993), dredge sampling for newly settled conch was conducted at the end of the summer, 24 August to 1 September 1992. Scuba equipment was used for all underwater work. At each of the 11 stations, water depth was measured and corrected to mean low water (MLW), and duplicate sediment samples were collected with a PVC core (diameter=40 mm, depth=5 cm) prior to dredging.

Sediment samples were rinsed with freshwater and dried at 80°C to constant weight. A subsample (~15–20 g) was incinerated at 550°C in a muffle furnace

for 4 h to determine organic content, calculated as the percent difference between dry weight and ash-free dry weight. A second rinsed subsample (~20 g) was analyzed by using standard dry sieve procedures (Folk, 1966), and product moment statistics were used to calculate mean grain size (McBride, 1971). The silt-clay fraction (>4.0 ø, <62 mm), always < 9% of sediment dry weight, was not fractionated.

Replicate dredge sample plots ($n$=5 for all stations, except C3, where $n$=6) were delineated by a circular enclosure made of aluminum sheet metal (area=0.5 $m^2$, height=0.3 m) that was placed haphazardly at each station. The enclosure was pushed securely into the sediment to prevent escape of motile fauna. In the middle of each sample plot, the number of *Thalassia testudinum* shoots was counted in a quadrat (25 × 25 cm). A gasoline-powered suction dredge (modified from Brook, 1979) was used to collect year-class 0 queen conch, other macrofauna, and associated macrophytes from each plot. The dredge created high-pressure water flow which, as a result of Venturi principle, drew algae, detritus, sediments, and macrofauna through a PVC intake tube (diameter=7.6 cm) into a mesh bag (40 × 70 cm, 1.2 mm mesh). Preliminary sampling in the study area and observations of year-class 0 conch (<45 mm SL) indicated that conch in the nursery ground buried no deeper than 5 cm into the sediment. Therefore, sediments from plots with seagrass were removed to the depth at which *T. testudinum* rhizomes occurred (usually 8–15 cm); in bare sand, dredging was 8–10 cm deep. Unlike the other macrophytes, living seagrass did not detach easily and was not collected with the dredge material. The mesh bags holding the dredged materials were tied securely underwater and later fixed in a 10% formalin-seawater mixture containing rose bengal as a staining agent. After 24 hours, each sample was rinsed onto a sieve (1.2 mm) and preserved in 70% ethanol until sorted.

Macrophytes were sorted into three components: *T. testudinum* detritus (senescent blades and fragments), the green macroalga *Batophora oerstedi*, and the red algae *Laurencia* spp. Occasionally fronds of calcareous green algae (including *Halimeda* spp., *Penicillus capitatus*, *Udotea* spp., and *Rhipocephalus phoenix*) were collected, but they were sparsely distributed and not quantified. Each fraction was rinsed with freshwater to remove salts and dried at 80°C to constant weight (~24 h) so that biomass (g dry wt/ $m^2$) could be calculated.

For ease in extracting newly settled queen conch and their potential predators, sediments were divided into two fractions, those retained on 1.2- and 2.0-mm sieves. A conch was classified as alive if its soft tissue and operculum were intact. Shortly after death, the operculum detaches from the foot, and soft tissues decompose quickly. Therefore, dead and living conch were easily distinguished. We do not believe that conch shells were damaged during collection because the dredge apparatus lifted samples off the bottom by suction that could be controlled and the materials collected did not pass through an impellor. Care was also taken so that the fauna were not damaged in sieving. None of the conch classified as alive at collection had damaged shells, and most other taxa, such as polychaetes and crabs, were in good (i.e. whole) condition.

To gain insight into modes of predation, shells of dead conch were classified as 1) whole and undamaged, 2) drilled, 3) peeled back along the spire line, or 4) crushed. Whole shells of dead conch were attributed to predation by mollusks or asteroids (Jory, 1982; Iversen et al., 1986; Ray and Stoner, 1995), drilled shells were probably the result of mollusk kills (Vermeij, 1987), and peeled and crushed shells were attributed to crustaceans (Randall, 1964; Vermeij, 1982, 1987; Davis, 1992). Whole shells can also result from nonpredatory mortality. The proportion of dead individuals was used as an indicator of post-settlement mortality.

Whole shells (from both live and dead conch) were measured for shell length. When only a shell spire or shell aperture was found, total shell length for the dead animal was calculated on the basis of regression formulae derived from measurements of 20 whole shells ranging in size from 3 to 40 mm total length:

$$Length = (spire\ length \times 2.4) - 1.8; \qquad [r^2=0.991]$$

$$Length = (aperture\ length \times 1.6) + 0.5. \qquad [r^2=0.998]$$

Given that queen conch settle into nursery grounds during a distinct season, it was possible to determine if an individual had indeed settled in 1992 on the basis of its size, color, and the amount of biological encrustation. Settlement of queen conch can occur at the beginning of May, and growth rates during the early postsettlement period may be as great as 0.45 mm/d (Ray and Stoner, 1994); therefore, we considered conch ≤45 mm in total shell length to be members of year-class 0. Also, conch shells lose their pink interior color within a few weeks after death. Animals that settled in 1992 were easily discerned on the basis of shell size and color.

Xanthid and portunid crabs and alpheid shrimps were extracted from samples because they were abundant and known to be significant predators of postsettlement conch (Ray-Culp et al., 1997). Olivid and marginellid gastropods were also removed and counted as potential predators. Carapace width (includ-

ing lateral spines) of crabs was measured, carapace length for shrimps, and shell length of gastropods.

### Data analysis

To discern station differences, density data from the dredge sampling were log-transformed ($\log_{10}(n+1)$) to improve homogeneity of variance (Cochran's test, $P>0.05$) and analysed by using 1-way ANOVA following the guidelines of Day and Quinn (1989). Tukey's multiple comparison test was performed to determine pairwise relationships. Seven measures of density were examined: live conch, dead conch, total conch, alpheids, portunids, xanthids, and total predators.

Relationships between these seven density measures and eight environmental variables (water depth, distance of the station from the center of juvenile queen conch aggregation, sediment grain size, sediment organics, *Thalassia testudinum* shoot density, weight of *T. testudinum* detritus, and biomass of the macroalgae *Batophora oerstedi* and *Laurencia* spp.) were examined with pairwise correlation. Log-transformation improved the relationships, and Pearson correlation coefficients are reported for the log-transformed variables.

The relationships between conch density (live, dead, and total) and each of the five predator families were also examined with correlation. Variables were not transformed in the analysis because transformation did not improve the correlations.

## Results

### Habitat characteristics

Depth down the flow field was relatively uniform, ranging from 2.8 to 3.3 m at MLW, except at E where depth was 2 m (Table 1). Across the flow field at transect D, depth increased from bare sand (1.3 m) to high seagrass density (3.3 m), and, at transect C, greatest depth (3.5 m) occurred in low density seagrass (C2). Sediments were fine to medium sands (1.4–2.6 ø), with mean grain size decreasing slightly (increasing ø) with depth over both transects C and D (Table 1). Organic content of the sediments across transect D also increased with depth, ranging from 2.7% (station D1) to 5.2% (station D4). The range of organic content in the down flow-field dimension was 3.0–4.6%.

*Thalassia testudinum* shoot density decreased down the flow field from 784 to 320 shoots/m$^2$ (Table 2). Across the channel, shoot density increased rapidly from 0 to >500 shoots/m$^2$ in both transects, as had been in-

**Table 1**

Habitat characteristics for 11 dredge stations in the Shark Rock flow field. Depth was at mean low water and distance was measured from each station to the center of the juvenile queen conch nursery (see Fig. 1). Means and the range of values (parentheses) are given for sediment grain size and organics ($n$=2 for all stations except C3, where $n$=3). Data for stations C3 and D3 are given twice for ease of comparison in both flow-field dimensions.

| | | | Sediments | |
|---|---|---|---|---|
| Station | Depth (m) | Distance (km) | Grain size (ø) | Organics (% dry wt) |
| Down flow field, midchannel | | | | |
| A | 2.8 | 3.60 | 2.57 (2.56–2.58) | 4.08 (3.68–4.50) |
| B | 3.0 | 1.00 | 1.81 (1.78–1.84) | 4.05 (3.46–4.65) |
| C3 | 3.1 | 0.55 | 1.84 (1.63–1.95) | 3.54 (3.17–3.75) |
| D3 | 2.8 | 0.55 | 2.07 (2.04–2.10) | 4.56 (4.43–4.69) |
| E | 2.0 | 1.10 | 1.89 (1.86–1.92) | 2.95 (2.95–2.95) |
| F | 3.3 | 4.50 | 2.04 (1.97–2.12) | 3.99 (3.98–4.00) |
| Across flow field | | | | |
| Transect C | | | | |
| C1 | 2.0 | 0.70 | 1.51 (1.27–1.74) | 2.18 (2.16–2.21) |
| C2 | 3.5 | 0.70 | 1.78 (1.73–1.83) | 3.31 (3.09–3.53) |
| C3 | 3.1 | 0.55 | 1.84 (1.63–1.95) | 3.54 (3.17–3.75) |
| Transect D | | | | |
| D1 | 1.3 | 0.60 | 1.44 (1.27–1.60) | 2.72 (2.60–2.84) |
| D2 | 2.1 | 0.55 | 1.73 (1.72–1.74) | 3.12 (3.06–3.19) |
| D3 | 2.8 | 0.55 | 2.07 (2.04–2.10) | 4.56 (4.43–4.69) |
| D4 | 3.3 | 0.70 | 1.87 (1.60–2.14) | 5.24 (5.12–5.37) |

**Table 2**

Macrophyte characteristics for 11 dredge stations in the Shark Rock flow field (see Fig. 1). Shoot count and detritus values are for *Thalassia testudinum*. All values are mean ±SE ($n$=5 for all stations except C3, where $n$=6). Data for stations C3 and D3 are given twice for ease of comparison in both flow-field dimensions.

| Station | Shoot density (no./m$^2$) | Biomass (g dry wt/m$^2$) | | |
|---|---|---|---|---|
| | | Detritus | *B. oerstedi* | *Laurencia* spp. |
| Down flow field, midchannel | | | | |
| A | 784 ± 36 | 353 ± 49 | 0.02 ± 0.01 | 0.20 ± 0.05 |
| B | 640 ± 65 | 144 ± 20 | 0.80 ± 0.40 | 0.04 ± 0.03 |
| C3 | 536 ± 26 | 30 ± 11 | 0.007 ± 0.004 | 0.20 ± 0.18 |
| D3 | 528 ± 36 | 139 ± 20 | 24.08 ± 6.00 | 0.84 ± 0.27 |
| E | 352 ± 22 | 29 ± 10 | 44.76 ± 4.77 | 0.66 ± 0.13 |
| F | 320 ± 17 | 34 ± 8 | 2.18 ± 0.57 | 0 ± 0 |
| Across flow field | | | | |
| Transect C | | | | |
| C1 | 0 ± 0 | 0.06 ± 0.04 | 0.02 ± 0.03 | 0 ± 0 |
| C2 | 288 ± 44 | 37 ± 14 | 1.76 ± 0.45 | 0.34 ± 0.18 |
| C3 | 536 ± 26 | 30 ± 11 | 0.007 ± 0.004 | 0.20 ± 0.18 |
| Transect D | | | | |
| D1 | 0 ± 0 | 0.08 ± 0.04 | 0.06 ± 0.04 | 0 ± 0 |
| D2 | 240 ± 36 | 14 ± 4 | 3.68 ± 0.32 | 1.60 ± 0.04 |
| D3 | 528 ± 36 | 139 ± 20 | 24.08 ± 6.00 | 0.84 ± 0.27 |
| D4 | 544 ± 22 | 180 ± 17 | 0.22 ± 0.23 | 1.58 ± 0.83 |

tended in the sampling design. A similar increase occurred with *T. testudinum* detritus, with the exception of a relatively low value at station C3 (Table 2), where the aggregation of year-class 1 and 2 juvenile conch undoubtedly had a grazing effect (Fig. 1). As was intended, shoot density and detritus biomass increased across transect D, and values were highest at station D4. Algal biomass was noticeably high only at stations D3 and E (where standing crops of *Batophora oerstedi* were 24 and 45 g dry wt/m$^2$, respectively), and particularly low at station C3 (grazed by conch). Biomass of *Laurencia* spp. was low at all stations (≤1.6 g dry wt/m$^2$).

## Newly settled conch

Newly settled queen conch were collected in dredge samples at all 11 stations except F (Fig. 2). Down the flow field, mean total density was relatively high (8–12 conch/m$^2$) at stations B, C3, and D3, and low (0–2.4 conch/m$^2$) at stations A, E, and F, although differences were only significant between C3 and F (Fig. 2). There was a significant negative correlation between total conch and distance from the geographic center of the long-term aggregation (Table 3); both total density and density of dead conch decreased with distance from C3 (Fig. 2). All of the conch collected at stations A and E were dead, as were most (60–86%) from the other down flow field stations. Live conch were collected at stations B, C3, and D3, with maximum density (4 conch/m$^2$) observed at B.

Across the flow field, mean total conch density appeared to increase with seagrass density in transect C (Fig. 2), although differences were not significant. Values were relatively uniform at all of the stations in transect D, ranging from 4.0 to 8.4/m$^2$. Live newly settled conch were most abundant at stations C3 (1.7/m$^2$) and D3 (1.6/m$^2$), where seagrass density was moderate. Significant numbers of live individuals were also collected at the other stations with at least some seagrass (C2, D2, D4). However, all of the conch dredged from the bare sand stations (C1, D1) were dead.

When data for 11 stations were included in the analysis, live conch density (the index of recruitment) had a significant positive correlation with total conch density (the index of settlement) (coefficient of correlation [$r$]=0.703, $P$=0.016). The percentage of the total conch that were dead provides an index of mortality. This index was negatively correlated with settlement ($r$=0.654, $P$=0.04).

Live individuals ranged in size from 3.3 mm to 38.5 mm with the mode at 10–14.9 mm (Fig. 3). Dead individuals ranged in shell length from 1.5 to 44 mm with the mode at 1.0–4.9 mm. The percentage of dead conch with whole, undamaged shells decreased across the flow field along both transects in the direction of increasing seagrass density and increasing density of

**Table 3**

Pearson correlation coefficients ($n$=11) for the pairwise relationship between each of seven dependent variables (i.e. newly settled queen conch and predators) and eight independent variables. Depth was at mean low water; distance was measured from station to center of juvenile queen conch aggregation (see Fig. 1); grain size and organics are for sediments; shoot density and detritus values are for *T. testudinum*. * $0.01 < P < 0.05$; ** $0.001 < P < 0.01$; *** $P < 0.001$. All of the dependent variables were transformed ($\log_{10}(x+1)$) prior to analysis.

| | Live conch | Total conch | Xanthids | Alpheids | Portunids | Olivids | Marginellids |
|---|---|---|---|---|---|---|---|
| Depth | 0.474 | 0.123 | 0.710* | 0.428 | –0.081 | 0.063 | 0.231 |
| Distance | –0.393 | –0.770** | 0.141 | 0.358 | –0.158 | 0.165 | –0.346 |
| Grain size | –0.027 | –0.312 | 0.533 | 0.821** | 0.337 | –0.254 | –0.233 |
| Organics | 0.346 | 0.196 | 0.868*** | 0.694* | 0.041 | –0.398 | 0.304 |
| Shoots | 0.454 | 0.168 | 0.812** | 0.924*** | 0.496 | –0.460 | 0.273 |
| Detritus | 0.085 | 0.038 | 0.537 | 0.947*** | 0.515 | –0.707* | 0.103 |
| *B. oerstedi* | –0.106 | –0.260 | 0.120 | –0.091 | –0.013 | 0.164 | –0.020 |
| *Laurencia* spp. | –0.026 | 0.182 | 0.237 | 0.164 | –0.311 | –0.205 | 0.082 |

year-class 1 and 2 conch (Table 4). The pattern of crushed shells was reverse. In the down flow-field dimension, the percentage of whole empty shells was lowest at stations within the nursery ground and at station F. Crushed shells made up the highest proportion of dead, newly settled conch within the nursery area. Overall, few shells were drilled (2.8%) or peeled (13.5%), and most were crushed (56.7%).

**Table 4**

Number of dead newly settled queen conch dredged from 11 stations for each of four shell conditions (see text for definitions). Values are station percentages followed by ($n$). Data for stations C3 and D3 are given twice for ease of comparison in both flow field dimensions.

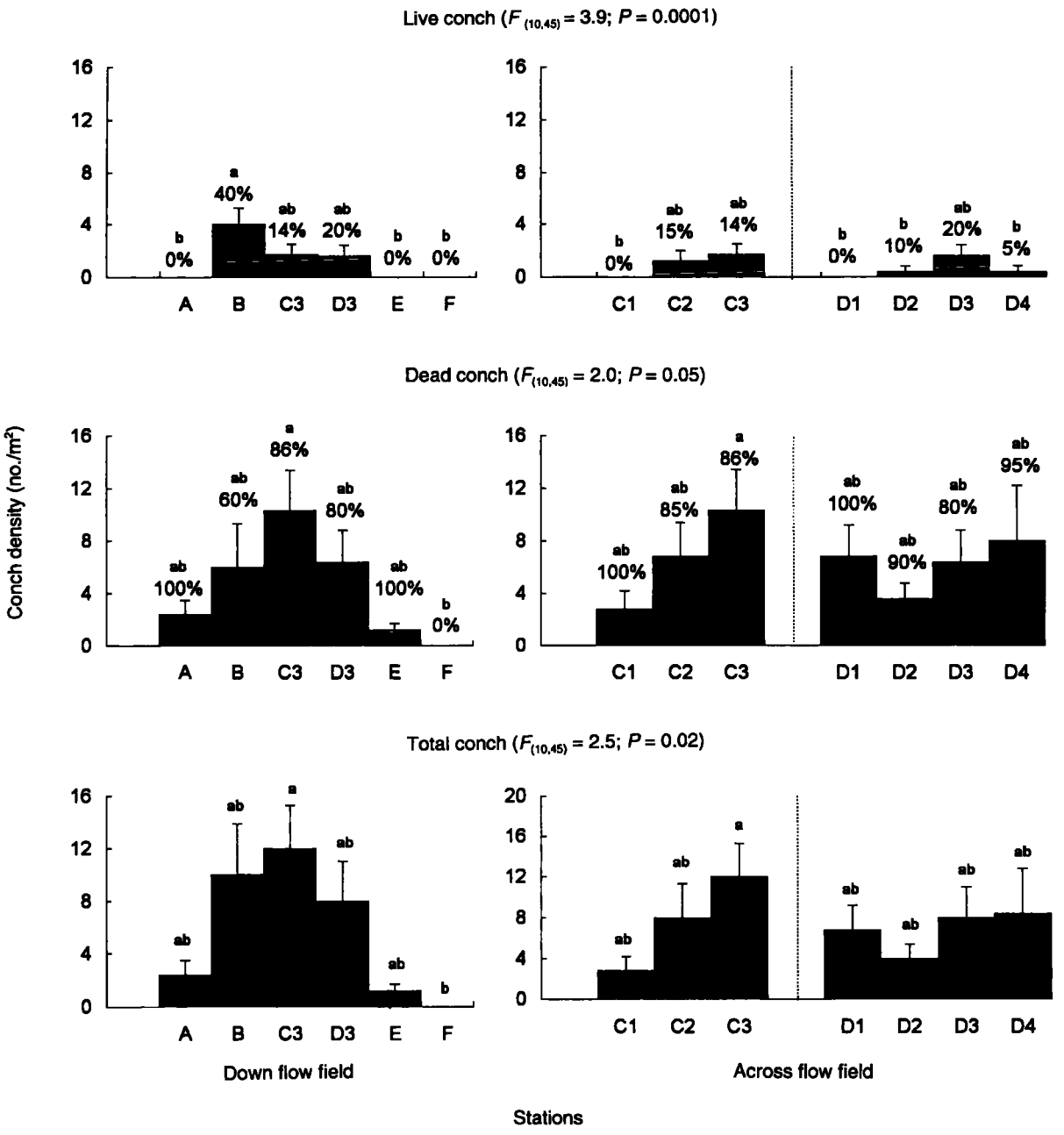
| Station | Whole | Drilled | Peeled | Crushed | Total |
|---|---|---|---|---|---|
| Down flow field, midchannel | | | | | |
| A | 33.3 (2) | 16.7 (1) | 0 (0) | 50.0 (3) | (6) |
| B | 6.7 (1) | 0 (0) | 13.3 (2) | 80.0 (12) | (15) |
| C3 | 9.7 (3) | 0 (0) | 25.8 (8) | 64.5 (20) | (31) |
| D3 | 18.7 (3) | 0 (0) | 12.5 (2) | 68.8 (11) | (16) |
| E | 33.3 (1) | 0 (0) | 33.3 (1) | 33.3 (1) | (3) |
| F | 0 (0) | 0 (0) | 0 (0) | 0 (0) | (0) |
| Total | 14.1 (10) | 1.4 (1) | 18.3 (13) | 66.2 (47) | (71) |
| Across flow field | | | | | |
| Transect C | | | | | |
| C1 | 57.1 (4) | 0 (0) | 28.6 (2) | 14.3 (1) | (7) |
| C2 | 17.6 (3) | 0 (0) | 5.9 (1) | 76.5 (13) | (17) |
| C3 | 9.7 (3) | 0 (0) | 25.8 (8) | 64.5 (20) | (31) |
| Total | 18.2 (10) | 0 (0) | 20 (11) | 61.8 (34) | (55) |
| Transect D | | | | | |
| D1 | 64.7 (11) | 0 (0) | 5.9 (1) | 29.4 (5) | (17) |
| D2 | 55.6 (5) | 11.1 (1) | 22.2 (2) | 11.1 (1) | (9) |
| D3 | 18.7 (3) | 0 (0) | 12.5 (2) | 68.8 (11) | (16) |
| D4 | 25.0 (5) | 10.0 (2) | 0 (0) | 65.0 (13) | (20) |
| Total | 38.7 (24) | 4.8 (3) | 8.1 (5) | 48.4 (30) | (62) |
| Grand total[1] | 27.0 (38) | 2.8 (4) | 13.5 (19) | 56.7 (80) | (141) |

[1] Stations C3 and D3 are included only once in grand total.

## Conch predators

Xanthid crabs (mostly *Micropanope* spp.) composed the predator group with the greatest densities and governed the density distribution of total predators in both flow-field dimensions (Fig. 4). Xanthids were most abundant (102–286 per $m^2$) at stations B, D3, and D4, and were $\leq 36/m^2$ at all other stations. Alpheid density decreased down the flow field (Fig. 3), increased with seagrass density across the flow field (Figs. 3 and 4), and had a high positive correlation with detritus ($r$=0.947, Table 3). Xanthid and alpheid densities also had high positive correlations with *Thalassia testudinum* shoot density and sediment organics (Table 3). Portunid crab densities were relatively low, compared with the two other crustacean families. They decreased down the flow field from a maximum at A ($7.6/m^2$) to 0 at F (Fig. 4).

Of the two predaceous mollusc families observed, the Olividae were most abundant at stations C2 ($18/m^2$) and F ($25/m^2$) (ANOVA, $F_{10,45}$=5.69, $P$<0.001). Values were $\leq 7.2/m^2$ at all other stations and the data were not plotted. Olivids were negatively correlated with detritus (Table 3). The Marginellidae were most abundant at B ($9.2/m^2$) and D4 ($6.8/m^2$) and densities were $\leq 2/m^2$ at all other stations, but the differences




## Figure 2

Density of live, dead, and total queen conch collected from 11 dredge stations located down and across the Shark Rock flow field. Stations C3 and D3 are illustrated in both dimensions for comparison. Values are mean ± SE ($n$=5 for all stations except C3, where $n$=6). Percentage of the total count represented by live and dead conch at each station is also given. $F$ and $P$ values are for 1-way ANOVAs made for each variable and flow-field dimension. Means that were not statistically different ($P$>0.05) are designated by similar letters (Tukey multiple comparison test on log-transformed data).

were not significant ($F_{10,45}$=1.92, $P$=0.067). Neither olivids nor marginellids were collected at station A.

Because size-frequency distribution of each predator group varied little among the 11 stations, measurements from all stations were considered together (Table 5). The majority of xanthids were very small, with a mode of just 1.5 mm carapace width. The largest predator collected was a portunid (36.1 mm carapace width); all others were <15 mm. Modal size of alpheids was 4.2 mm carapace length.

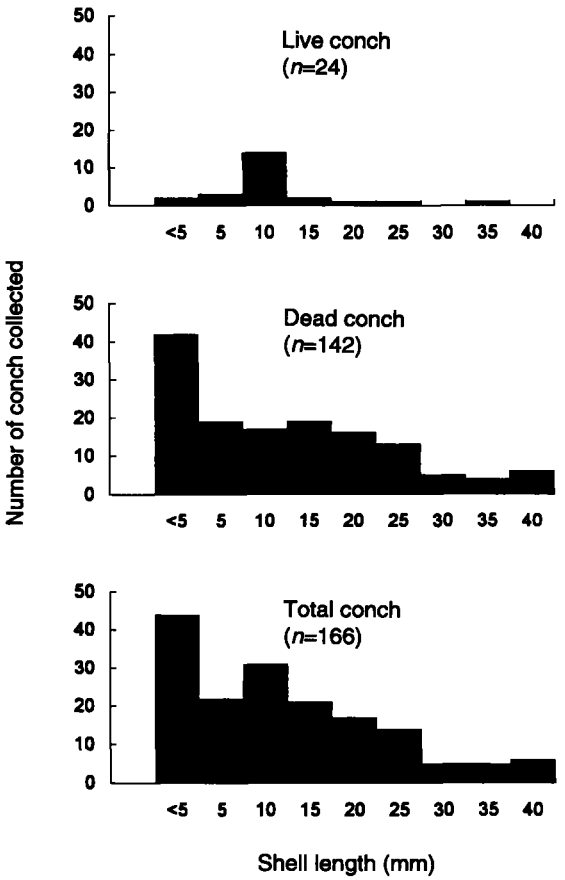



**Figure 3**

Length-frequency distribution for newly settled queen conch derived from all individuals, live and dead, collected from 11 dredge stations. Each value on the x axis represents a range of sizes starting with the lower end of the size interval (e.g. 5 represents 5.0–9.9 mm).

Live conch density had a high positive correlation with xanthid density ($r$=0.825, $P$=0.002), marginellid density ($r$=0.695, $P$=0.02), and total predator density ($r$=0.794, $P$=0.004), whereas relationships with densities of alpheids, portunids, and olivids were not significant ($P \geq 0.38$). There were no significant relationships with any of the predator families ($P \geq 0.15$) for dead or total conch densities.

## Discussion

### Age of postlarvae and settlement dates

The shell lengths of dredged newly settled conch provide insight into when settlement occurred. Using the middle of the week-long sampling period as the endpoint (28 August 1992), we estimated a summer average growth rate of 0.39 mm/day (Ray and Stoner, 1995), and considering settlement at 1.2 mm shell length (Davis, 1994), we determined that animals in the 10–15 mm modal size class would have settled 3–4 weeks earlier, between 24 July and 5 August. The largest live individual (38.5 mm) would have settled on about 24 May, and the smallest (3.3 mm) would have settled on 23 August. Dead conch ranged from 1.5 to 44 mm SL. According to the same assumptions, they would have been in the benthos for 1–110 days at the time of death. Therefore, settlement recorded in our samples began in early May and continued through at least late August. It should be pointed out that our intent was to collect young conch as close to the peak settlement period as possible, near the end of August. However, it is known that larvae are present in the water column near Lee Stocking Island until at least late September (Stoner and Davis, 1997), and our collections probably do not represent total settlement at Shark Rock in 1992.

There are three possible explanations for the fact that dredging yielded relatively few live conch outside the 10–14.9 mm modal class. First, there could have been a major settlement event between late-July and early August. Queen conch larvae were collected at the Shark Rock nursery ground on 13 dates between late May and mid-September 1992 (Stoner and Davis, 1997); however, relatively few late-stage larvae were found in these collections, and it is impossible with the available data to determine if the modal size of survivors resulted from a period of high settlement rate. Nevertheless, this is the most parsimonious explanation. Second, the high number of year-class 0 conch in the 10–14.9 mm range may also be related to high survivorship in conch settling between late July and early August, compared to conch settling at other times. However, the steep decline in numbers of individuals with size could be a reflection of the natural, high mortality of small conch (dis-

**Table 5**

Size range and mode for three crustacean and two molluscan families of potential predators of newly settled conch collected at 11 dredge stations.

| Family | Measurement | Range (mm) | Mode (mm) |
|---|---|---|---|
| Xanthidae | carapace width | 1.0–14.5 | 1.5 |
| Alpheidae | carapace length | 1.0–7.8 | 4.2 |
| Portunidae | carapace width | 1.5–36.1 | 3.4 |
| Marginellidae | shell length | 1.7–6.1 | 3.2 |
| Olividae | shell length | 2.0–11.6 | 3.2 |

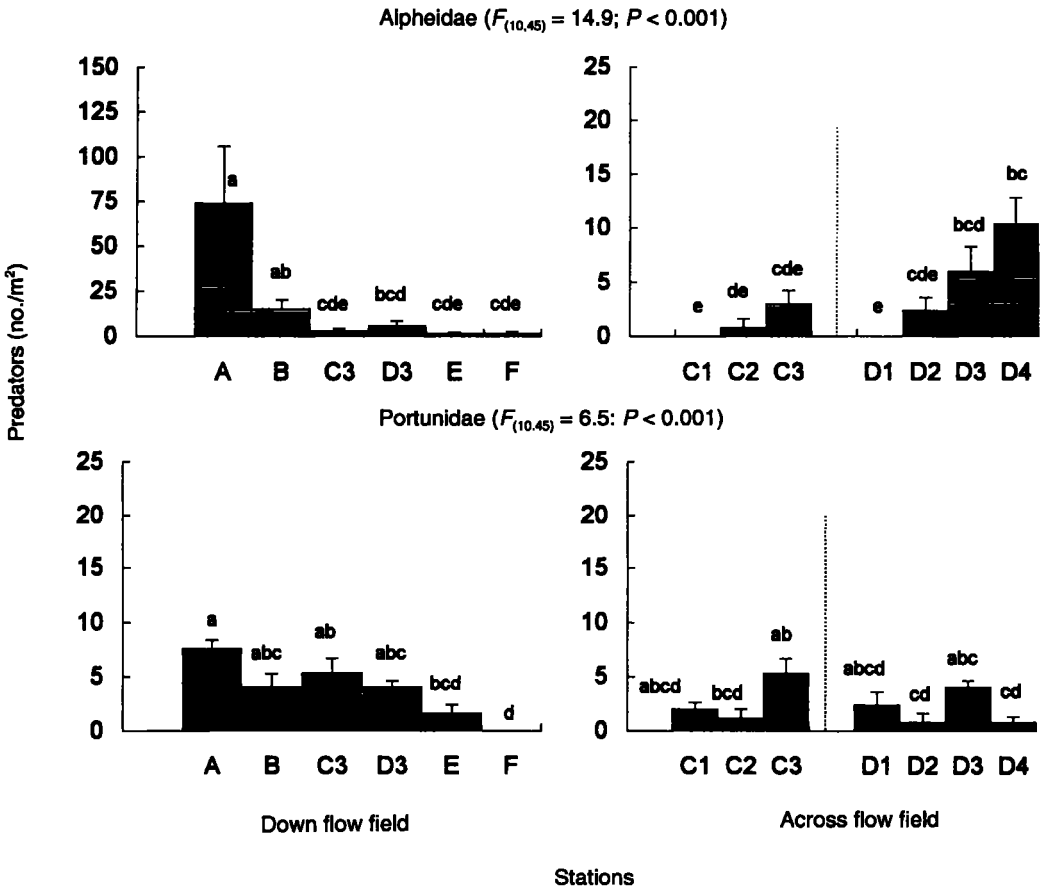



**Figure 4**

Density of three families of queen conch predators and total predators collected from 11 dredge stations located down and across the Shark Rock flow field. Total predators include alpheids, portunids, xanthids, as well as two mollusc families—olivids and marginellids (not shown individually). Stations C3 and D3 are illustrated in both dimensions for comparison. Values are mean ±SE ($n$=5 for all stations except C3, where $n$=6). Note different $y$ scale on each graph. $F$ and $P$ values are for 1-way ANOVAs made for each variable and flow-field dimension. Means that were not statistically different ($P$>0.05) are designated by similar letters (Tukey multiple comparison test on log-transformed data).

cussed below). This latter conclusion is supported by the fact that the modal size for dead conch was small (1–5 mm). Future studies should examine the interaction of settling date with food quality and quantity, growth, and predation rates. Few data of this type exist for sediment-dwelling invertebrates. Third, the smallest postlarval conch were probably undersampled. Despite the use of small mesh (1.2-mm), some of the smallest individuals may have passed through the dredge bags. Furthermore, shells of newly settled queen conch are frequently broken into fragments that would not be retained on a 1.2-mm mesh. Nevertheless, our study provides the first quantitative data on newly settled conch (<45 mm SL, <6 months postlarval age) and important insights into their early life history.

## Role of settlement and habitat on conch recruitment

In this study, large volumes of sediment had to be sorted to detect relatively low settlement densities (≤12/m$^2$) of queen conch over the traditional nursery. These densities were not surprising given that 1- and 2-year-old queen conch typically occur in aggregations with just 0.2–1.0 individual/m$^2$ (Stoner and Ray, 1993). The most intriguing findings are that settlement was concentrated in the traditional nursery ground and that recruitment to early benthic stages was directly correlated with settlement density over a large spatial scale. This is compatible with the prediction (Connell, 1985) that settlement will be most influential in predicting the recruitment of

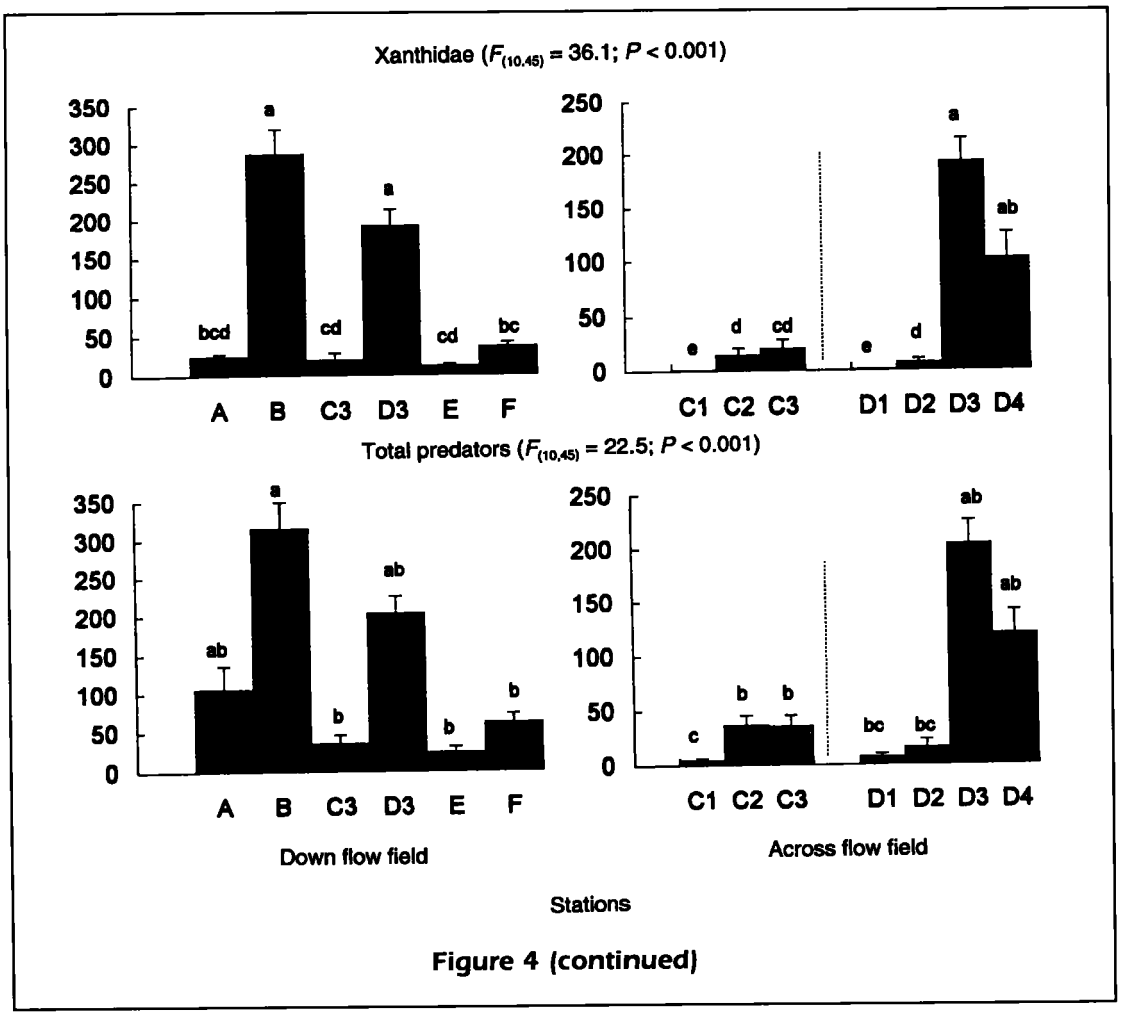



**Figure 4 (continued)**

benthic invertebrates when settlement occurs in low density

After an extensive review of the literature, Butman (1987) concluded that settlement patterns in invertebrates associated with soft sediments are a function of passive accumulation and deposition of larvae over spatial scales of kilometers and that active habitat selection occurs primarily over smaller scales (centimeters to meters). Data on the abundance of queen conch veligers over the Shark Rock tidal flow field (Stoner and Davis, 1997) may support this conclusion. Although newly hatched larvae (300–500 μm) were collected well beyond the Shark Rock nursery, at station F on 12 of 13 sampling dates in 1992, neither midstage larvae (500–900 μm), competent larvae (>900 μm), nor newly settled conch were ever collected there, suggesting that late-stage larvae are somehow concentrated at the nursery location. At maximum flood-tide current, velocity near the surface decreases by approximately 75% between station A, north of Lee Stocking Island, and Shark Rock. Near the bottom, the decrease in velocity is more than 95% (Stoner and Ray-Culp[1]). We also know that maximum flood tidal excursion in this flow field occurs near the Shark Rock nursery area on neap tide; therefore, the nursery is bathed in oligotrophic water (and perhaps larvae) from the Exuma Sound on every tide, whereas areas farther out on the bank are not (Jones, 1996; Stoner et al., 1996b). These hydrographic characteristics may result in the deposition of larvae in the long-term nursery area, or the lower botom-water velocities may allow them to settle.

Density of newly settled conch had a strong negative correlation with distance from the center of the traditional nursery ground but was relatively independent from all other environmental characteristics tested (i.e. depth and various qualities of sediments, seagrass, and macroalgae). This finding indicates that conch settlement cannot be explained

[1] Stoner, A. W., and M. Ray-Culp. 1997. Northeast Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, 74 Magruder Road, Highlands, NJ 07732. Unpubl. data.

simply by fine-scale hydrodynamic relationships associated with seagrasses and macroalgae, as observed for certain other invertebrates including mollusks (Eckman, 1987; Harvey et al., 1993, 1995). In fact, conch larvae settled in approximately equal densities across the seagrass gradient at transect D which spanned only 250 m. Therefore, the structure provided by macrophytes appears not to influence settlement of conch larvae even though older juveniles prefer seagrass habitats and are associated with an optimal shoot density (Stoner and Waite, 1990).

Although accumulation of competent larvae near the Shark Rock nursery is the most parsimonious explanation for the observed settlement and recruitment patterns, earlier experiments indicate that seemingly similar seagrass beds offer different qualities that have significant effects on larval and juvenile conch. Laboratory experiments have shown that macrophytes collected from stations within the Shark Rock nursery (B, C3, D3, D4) induced significantly higher metamorphosis than the same types of substrata collected outside the general nursery area (stations A, F) (Davis and Stoner, 1994). Growth rates of newly settled conch (1.2 mm) fed seagrass detritus from the different sources reflected metamorphic responses on the same substrata (Stoner et al., 1996a), and when 1-yr-old juvenile conch were transplanted to stations A and F, growth rates were low in comparison with those in the Shark Rock nursery (Stoner et al., 1994). It is clear, therefore, that the nursery area is trophically unique, despite visual similiarity to surrounding areas.

Micro-organism films that coat the sediment in soft-bottom communities are known to be important inducers of metamorphosis in conch and other invertebrates, most likely because they are associated with favorable nutritional requirements for postlarvae (Scheltema, 1961; Gray, 1974; Davis and Stoner, 1994; Stoner et al., 1996a). Characteristics that make the Shark Rock nursery an attractive location for settling larvae and an ecologically suitable habitat for juveniles probably stem from hydrodynamic properties of the location that affect nutrient cycling and productivity patterns in certain algal foods for conch (Stoner et al., 1994, 1996b). Field manipulations will be needed to distinguish direct effects of hydrodynamics (i.e. larval transport and retention) from indirect effects such as hydrographic mediation of biological productivity, habitat choices, and postsettlement processes.

Postlarval conch recruited to the same habitats traditionally occupied by 1- and 2-yr-old animals. This association is probably not the result of conspecific attraction because settlement was equally high at stations with and without older conspecifics. This result corroborates an earlier laboratory study showing that cues associated with previously settled juveniles (slime trails, feces, and the older conch themselves) did not elicit larval metamorphosis (Davis and Stoner, 1994).

### The role of micropredators on conch recruitment

Although settlement of queen conch was relatively independent of habitat features other than location, predator distributions were highly correlated with seagrass shoot density, detrital abundance, and sediment organics and grain size. Numerous studies have shown that animal abundances in seagrass beds are correlated with certain measures of habitat complexity such as seagrass blade density or biomass, detrital biomass, leaf characteristics, or rhizome structure (Orth et al., 1984; Stoner and Lewis, 1985). The association between benthic macrofauna and physical structure may be related to food abundance or predation, or both. There is abundant experimental evidence that the physical structure provided in seagrass beds reduces predation rates on invertebrates (Heck and Wilson, 1987; Heck and Crowder, 1991). Potential conch predators dredged in this study were prey species themselves, and they undoubtedly derived some measure of protection or nutrition from the habitat, or both.

Predation on early postsettlement stages can be an important process affecting the number of invertebrate settlers that survive to recruit into a population (Thorson, 1966; Keough and Downes, 1982; Osman and Whitlach, 1995). Heavy losses to micropredators during the first days or weeks after settlement can severely diminish or eliminate a prey species, and even regulate community composition (Osman et al., 1992; Osman and Whitlatch, 1995). It is apparent from the length frequency of dead conch collected in this study that very high mortality occurs immediately after settlement, when conch are <5-mm shell length. Queen conch have many predators at this size (Ray-Culp et al., 1997), and one of the most important is probably the xanthid crab *Micropanope* sp., which was the most abundant invertebrate counted in dredge samples. The crab is capable of killing conch that are up to 0.5 times its own carapace width (Ray-Culp et al.[2]). Although a large proportion of the xanthids collected were too small (mode=1.5 mm) to kill even newly settled conch

[2] Ray-Culp, M., M. Davis, and A. W. Stoner. 1998. Escaping the xanthid crab gauntlet—the role of size, density and habitat for newly-settled queen conch. Caribbean Marine Research Center, 805 E. 46th Place, Vero Beach, FL 32963. Unpubl. manuscr.

(1.2 mm), xanthids up to 10 mm were far more abundant than conch, and they undoubtedly play a major role in conch mortality. The high positive correlation between live conch and xanthids suggests that conch settle in areas prone to high predator abundance. However, with typical summer growth rates, mentioned earlier, conch would escape predation by xanthids in about 10 days when they reach 5 mm shell length. Consequently, predator-prey relationships associated with the early postsettlement stages may be highly dynamic, with suites of predators shifting rapidly over time.

There was an increase in conch survivorship from bare sand to moderate density seagrass over both cross-channel transects. A similar trend was obtained experimentally when year-class 0 and 1 juveniles were tethered over an analogous seagrass gradient near transect D (Ray and Stoner, 1994, 1995). Highest mortality occurred on bare sand and in highest seagrass biomass whereas lowest mortality occurred in moderate biomass. It appears that a certain amount of seagrass structure provides protection, but too much is detrimental. However, in the down flow field dimension, survivorship was highest within the traditional nursery ground, and distribution is clearly related to both settlement and survivorship in this dimension.

### Identifying critical habitats

Our findings have important management implications for queen conch and other species associated with seagrass beds. First, it may not be possible to determine the value of a particular site for a species on the basis of simple habitat maps. Even descriptions of the beds that include seagrass species composition, biomass, and shoot density do not provide adequate information to identify critical habitats for conch. Value of specific seagrass bed locations also depends upon hydrography, larval retention, larval settlement, predator abundance, and the related survivorship. Persistence in the locations of queen conch nurseries near Lee Stocking Island (Stoner et al., 1996b; Jones, 1996) indicates that these factors are relatively constant over periods of several years, and that the specific locations may be as "critical" as habitat type. Only certain seagrass beds are suitable for queen conch; these must be identified and protected. Furthermore, in many areas of the Caribbean, conch populations have been devastated by overfishing, and there is an intense interest in rehabilitating them through releases of hatchery-reared juveniles. Transplant experiments have shown that juvenile conch will survive and grow only in very specific locations, and releases must be made in locations that ensure economically acceptable survivorship (Stoner, 1994). Clearly, thorough knowledge of distributional mechanisms is necessary to make predictions on the habitat requirements of queen conch and other managed species.

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# Growth trajectory of the larval Japanese sardine, *Sardinops melanostictus*, transported into the Pacific coastal waters off central Japan

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**Abstract.**—Late larvae (15–30 mm TL) of the Japanese sardine, *Sardinops melanostictus*, are commercially exploited in fishing grounds along the Pacific coast of western and central Japan. Concentrated shoals of late larvae in the shallow (15–30 m deep) coastal (4–6 miles from the coast) fishing grounds enable fishermen to catch as much as several hundred metric tons (t) (several billion larvae in number) per month. Growth trajectories of sardine larvae caught in the fishing ground off Atsumi Peninsula in central Japan were individually backcalculated by using the biological intercept method based on the allometric relationship between otolith radius and fish length. Growth rates for larvae up to 13–21 d were high, ranging from 0.79 to 0.85 mm/d, but declined after reaching size of immigration (13–19 mm TL) from the offshore waters to the coastal fishing grounds. The decline of growth rate in the late larval stage seemed to be related to the concentration of late larvae in the fishing grounds, the result of onshore intrusions of offshore Kuroshio waters. Total lengths at age 20 d were significantly smaller in 1990 (total catch of larval sardine was 720 t) than in 1991 (total catch 300 t) in spite of a higher sea surface temperature in 1990 in the coastal habitat. This may have resulted from a larger population of late larvae on the fishing ground in 1990 than in 1991.

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Late larvae of the Japanese sardine *Sardinops melanostictus* and the Japanese anchovy, *Engraulis japonicus*, termed *shirasu* in Japan, are fished by boat seiners in waters along the Pacific coast of western and central Japan. The coastal waters (4–6 miles from the coast) off Atsumi Peninsula (Fig. 1) are one of the major fishing grounds for *shirasu*. Depth of the sea bed of the fishing grounds is about 20 m, with a range from 15 to 30 m. The *shirasu* fishery for sardine larvae begins in March and continues to December, with the major effort shifting to anchovy in early summer. The annual catch of sardine larvae in the waters ranged from 700 to 2000 metric tons (t), 7–20 billion larvae, 1980–88. However, between 1989 and 1991 the catch declined to 300–700 t (Fig. 2). Since 1992, catches have been as low as several tens of tons, with an exception of about 400 t in 1993.

Growth rates of fish larvae affect their survival and recruitment to the adult population (Anderson, 1988). From life-stage table analyses, growth rate has been shown to be an important determinant of year-class strength by delimiting the duration of a particular life stage with high instantaneous mortality (Lo et al., 1995; Butler et al., 1996). Watanabe et al. (1995) showed that recruitment failures of the Japanese sardine in 1988–91 could not be explained by mass mortality at the first feeding stage. Cumulative mortality after the first feeding stage of the sardine, which may be a function of growth rate, is likely to have determined the recruitment in these years. Meekan and Fortier (1996) examined early life growth and survival of the Atlantic cod, *Gadus morhua*, and showed that fast-growing pelagic larvae survived better through the larval stage and dominated in the cohort of demersal juveniles. Campana (1996) found a positive correlation between growth rates in juvenile Atlantic cod and subsequent year-class strengths, which enabled him to predict recruitment from the juvenile growth rates.

Available population size of late larval sardine in the *shirasu* fishing grounds could be affected by larval growth. The size range of larvae caught in the *shirasu* fishery is usually from 15 to 30 mm TL. Because the duration time of this size

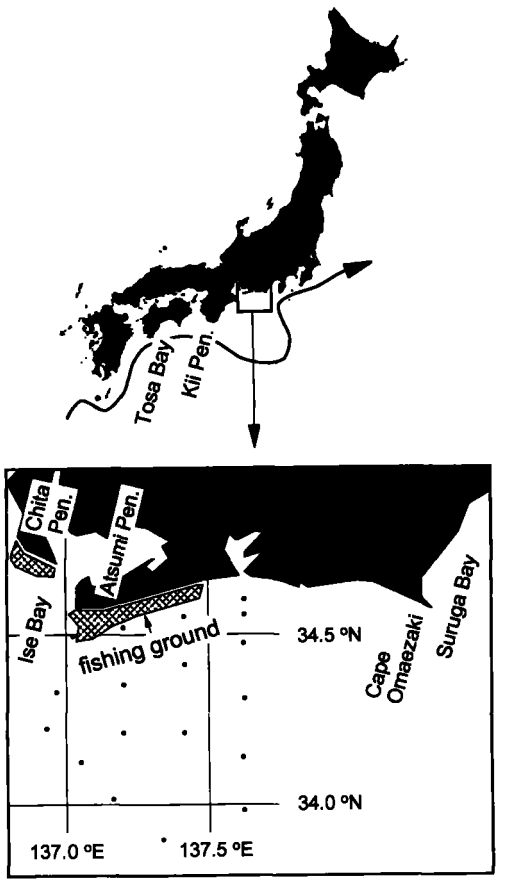


**Figure 1**

Location of *shirasu* fishing grounds in the coastal waters along Atsumi Peninsula. Minor fishing grounds are found in Ise Bay at the tip of Chita peninsula. Dots indicate locations of monthly SST observations. A solid line along the Pacific coast of western and central Japan denotes an example of the meandering Kuroshio current axis.

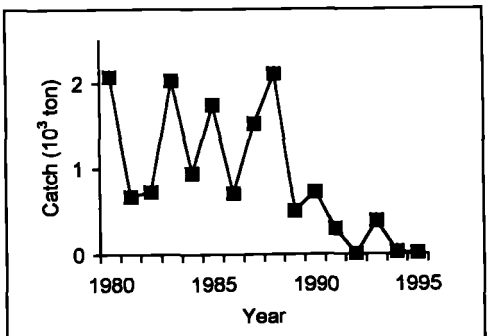


**Figure 2**

Annual catch of sardine *shirasu* in the coastal waters of Atsumi and Chita Peninsulas after 1980.

range is a function of growth rate, slower growth results in longer duration time and an increase in the available number of larvae. Watanabe and Kuroki (1997) backcalculated the growth history of larval sardine *Sardinops melanostictus* in the coastal waters off Miyazaki in western Japan. They found that growth rates reached a maximum (0.80–0.85 mm/d) at around 10–12 mm in total length (TL) but slowed thereafter, exhibiting asymptotic growth trajectories. According to this growth pattern, duration time from 15 to 30 mm TL was calculated to be 35 days. If, however, growth rates of 0.80–0.85 mm/d were maintained in the late larval stage, duration time of the same size range could be as short as 18 days.

Growth rate in early life stages is thus important as a potential determinant of year-class strength as well as of available stock sizes of *shirasu* larvae of the Japanese sardine. The daily growth rate of fish can be estimated by regressing size-at-age data to a growth model (Campana and Jones, 1992). When we apply this method, we need data points throughout an age range, from first feeding up to the fish size of concern (Watanabe et al., 1997). Because the size range of sardine larvae fished by the boat seine fishery is usually from 15 to 30 mm, we do not have a complete range of data points for early larvae, and therefore the regression method is not applicable to describe the growth history from first feeding to size at capture. Instead, backcalculation of size at age from the relationship between otolith radius and fish length makes it possible to draw a growth trajectory for individual fish (Campana, 1990; Campana and Jones, 1992). We backcalculated growth trajectories of individual larval sardines caught in coastal waters off Atsumi Peninsula, 1990 and 1991, and compared them with growth trajectories of larvae from other waters.

## Materials and methods

### Larval sampling

Two *shirasu* fishing boats, towing a seine net, were used to sample waters off Atsumi Peninsula and in Ise Bay (Fig. 1). They usually departed before dawn from the fishing port, together with a catch-loading boat, set the net several times in the morning, and returned to the port for offloading. Catches were stored with ice before landing. In our study, we randomly sampled *shirasu* larvae from catches in the ports of Morozaki and Toyohama (tip of Chita Peninsula) four times in 1990 (11, 16, 27 April and 7 May) and four times in 1991 (15, 23 April and 7, 14 May).

The larvae were classified as Japanese sardine, *S. melanostictus*, Japanese anchovy, *E. japonicus*, and round herring, *Etrumeus teres*. Sardine larvae were preserved in 80% ethanol for otolith examinations.

### Otolith measurement

Total lengths (TL) of sardine larvae were measured to the nearest 0.1 mm with an optical comparator. Sagittal otoliths were dissected and cleaned under a binocular microscope, mounted on a glass plate with enamel resin, and used for measurements and counts of daily growth rings. We used the otolith measurement system (Ratoc System Engineering Inc.) composed of a light microscope, a video camera and monitor, and an image analyzer controlled by computer. Because the otolith had not yet developed a rostrum and because we were not able to determine its orientation at the larval stage, we measured radii of all daily rings along the maximum radius of the otolith.

### Growth backcalculation

The relationship between larval TL and maximum otolith radius (OR) was considered for larvae sampled. Plots of TL against OR can be expressed by an allometric relationship (see "Results" section). An allometric OR-TL relationship has previously been demonstrated in larval *S. melanostictus* from different waters (Watanabe and Kuroki, 1997). Otolith growth rings have been found to be deposited on a daily basis in *S. melanostictus*, with the first ring being formed on the third day of hatching (the day of first feeding) when larvae are reared at 18°C (Hayashi et al., 1989). The relationship of the *i*th otolith ring radius ($OR_i$) and *TL* on the day of the *i*th ring formation ($TL_i$) is considered to be expressed by an allometric formula, $TL_i = a \times OR_i^b$, for individual larvae. We determined the allometric parameters *a* and *b* for each larva by using the biological intercept method (Campana, 1990; Campana and Jones, 1992) and a size of first feeding larvae (first otolith daily ring deposition) of 5.0 mm TL (Watanabe and Kuroki, 1997). The solution of the following two equations gives us *a* and *b* for each larva:

$$TL_1 = a \times OR_1^b \text{ and } TL_{capture} = a \times OR_{capture}^b,$$

where $TL_1$ = total length (mm) at the first ring deposition which was fixed at 5.0 mm;
$OR_1$ = the measured radius of the first daily ring;
$TL_{capture}$ = the measured total length (μm) at capture; and
$OR_{capture}$ = otolith radius (μm) at capture.

$TL_i$ of each larva was thus calculated from the formula for each larva independently. Mean ±SD (standard deviation) of TL at ages from 4 d up to a certain age, with at least 10 backcalculated TLs, was calculated for the March- and April-hatched cohorts for the two years of study. Differences in mean TLs at ages 10, 15, 20, and 25 d were examined between the same month of hatch cohorts in 1990 and 1991 by using Student's *t*-test, when variances were equal, or by Welch's *t*-test when they were not equal.

### Sea surface temperature distribution

Sea surface temperatures (SST) in and around the *shirasu* fishing ground were measured monthly at fixed stations off Atsumi Peninsula (Fig. 1). We used data from April and May, 1990 and 1991, to describe temperature distributions in coastal waters.

## Results

The SST in coastal waters off Atsumi Peninsula was in the range of 16–19°C during 23–25 April and 8–9 May 1990. From 23 to 25 April, the isotherms ran nearly parallel to the coast line but from 8 to 9 May offshore waters warmer than 18°C intruded into the coastal fishing ground (Fig. 3). In 1991, the SST during 2–3 April and 8–9 May ranged from 11 to 18°C. Cold waters extruded from Ise Bay covered part of the coastal fishing ground. The SST in the fishing grounds were 1.5–2.5°C lower in 8–9 May 1991 than in the corresponding season in 1990.

Local government permits the *shirasu* fishery to operate year round in these fishing grounds, but catches were zero in January–February 1990 and January–March 1991 (Fig. 4). Japanese sardine larvae were caught mainly in April in these years. The major target species of the *shirasu* fishery shifted to Japanese anchovy after May. A monthly catch of sardine larvae was 430 t in April 1990, declining to 175 t in April 1991. Annual catches of sardine larvae were 724 t and 298 t in 1990 and 1991, respectively.

Total length of larval sardines caught in the *shirasu* fishery were 15–27 mm in mid-April 1990 (Fig. 5). Frequency of larvae smaller than 15 mm TL increased after late April in this year, with sizes of 11–20 mm. In 1991, the modal size and range of the larvae remained relatively constant at 22–25 and 20–27 mm TL, respectively, mid-April to mid-May (Fig. 5).

Sardine larvae fished on 11 and 16 April 1990 were aged from 14 to 39 d after hatching. All of them hatched in March (Fig. 6). Larvae caught on 27 April

and 7 May were young, from 10 to 23 d. Except for one larva hatched on 31 March (not used for backcalculation), all larvae caught on 27 April and 7 May hatched in April 1990. In 1991, ages of sardine larvae were 19–30 d. Larvae caught on 15 April were all hatched in March. Those caught on 23 April were composed of March- and April-hatched fish. All larvae caught on 5 and 14 May were hatched in April except one which was hatched on 24 March (not used for backcalculation).

Plots of TL (mm) on OR (μm) of all individuals could be expressed in an allometric formula (Fig. 7). Size at age of individual larva was backcalculated on the basis of allometric OR-TL relationship for each larva from first feeding to capture. The 1990 March-hatched cohort grew linearly to 25 d when fish reached 20.5 mm TL (Fig. 8). Mean growth rate of the cohort from 4 d (6.3 mm TL) to 25 d was 0.68 mm/d. Growth in the April-hatched cohort in 1990 was linear to about 13 d (13.1 mm TL, 0.83 mm/d), then slowed down. In the 1991 March- and April-hatched cohorts, growth was linear to 21 d (21.2 mm TL, 0.85 mm/d), and 20 d (19.2 mm TL, 0.79 mm/d), respectively, declining thereafter. Larval TL at which growth started to decline occurred at the approximate size when immigration into the coastal fishing grounds occurred in both months.

Total lengths at 15 d in the 1990 March- and April-hatched cohorts were 14.2 ±1.2 and 14.9 ±1.4 mm, respectively, whereas in 1991 the March-hatched cohort reached 16.3 ±1.5, and the April cohort 15.8 ±1.3 mm. Backcalculated TLs of March- and April-hatched cohorts were significantly smaller in 1990 than in corresponding hatching month in 1991 at 15, 20, and 25 d (Table 1).

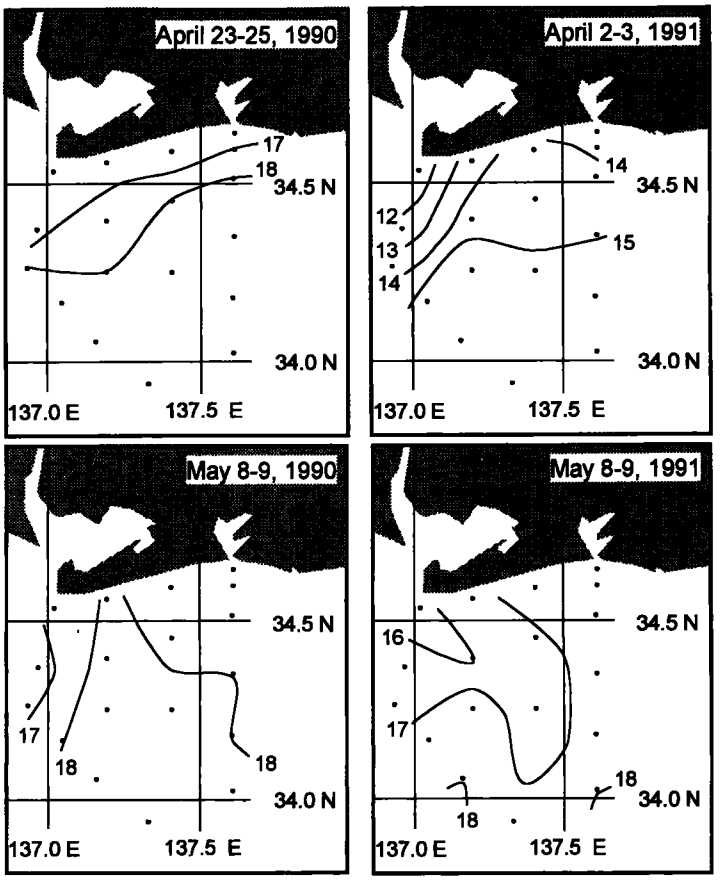


**Figure 3**
Sea surface temperature distribution off Atsumi Peninsula in April and May of 1990 and 1991.

## Discussion

Larvae of *S. melanostictus* and *E. japonicus* have been reported to be transported from the offshore Kuroshio area to the coastal fishing grounds along the Pacific coast in central Japan by onshore intrusions of Kuroshio waters (Tsuji, 1983; Muranaka, 1984; Mitani, 1990). This is the case in the coastal fishing grounds off Atsumi Peninsula, because great densities of *S. melanostictus* eggs were detected in the offshore waters along the Kuroshio Current in 1990 and 1991 (Ishida and Kikuchi, 1992; Zenitani et al., 1995; Watanabe et al., 1996). Onshore intrusions of Kuroshio waters often develop when the Kuroshio meanders in the waters off central Japan (Kobayashi et al., 1986; Kasai, 1995). The available population size of *S. melanostictus* larvae in coastal fishing grounds off Atsumi Peninsula and adjacent waters is a positive function of the latitudinal distance from Cape Omaezaki to the Kuroshio axis (Fig. 1) (Kishida et al., 1994). This distance in April and May 1991 measured approximately 125 nautical miles (n mi) (Maritime Safety Agency, 1991), which was less than that in 1990 (200 n mi) (Maritime Safety Agency, 1990). Oceanic conditions were less favorable for onshore larval transport in 1991 than in 1990. As seen in Figure 3, SSTs in coastal waters were lower in 1991 than in 1990, a feature that was indicative of limited intrusion of the warm Kuroshio waters to the coastal area. Annual catch of sardine *shirasu* in 1991 in the waters off Atsumi Peninsula (including small catches in Ise Bay) decreased to 41%

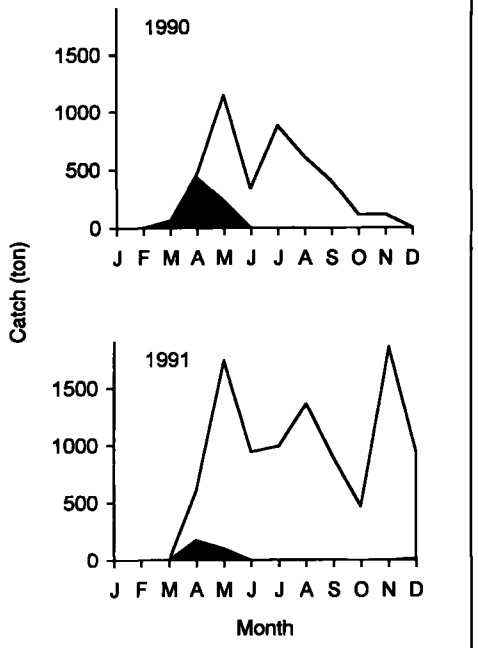


**Figure 4**

Monthly catch of late larvae of sardine (closed) and anchovy (open) by the *shirasu* fishery in the coastal waters off Atsumi and Chita Peninsulas.

of the 1990 catch. This was due partly to unfavorable oceanic conditions.

Growth rates of sardine larvae estimated in this study were 0.79–0.85 mm/d to a size when they immigrated to the fishing grounds as 1990 April- and 1991 March- and April-hatched cohorts, but later declined to 0.6–0.7 mm/d (Fig. 8). This decline in growth was similar to the asymptotic growth of larval *S. melanostictus* in the *shirasu* fishing grounds in western Japan (Watanabe and Kuroki, 1997). Fishermen for *shirasu* locate a concentrated larval shoal by echo sounder (Mitani, 1987) and catch large numbers of larvae in relatively narrow fishing grounds (Fig. 1). In mid-April 1990, 100 t (ca. one billion in number) per day of sardine larvae were caught in the fishing ground in our study.[1] Turbidity is a factor that helps to retain concentrated larval shoals in the coastal fishing grounds (Funakoshi, 1988). Uotani et al. (1993) demonstrated experimentally that *E. japonicus* larvae showed a strong positive taxis to turbidity and tended to stay in the turbid water. Reduction of larval growth, after reaching the size when immigration to the *shirasu* fishing grounds occurred, is likely to be related to concentrations of large numbers of larval sardines in the narrow fishing grounds as a result of intrusions of offshore waters (Muranaka, 1984).

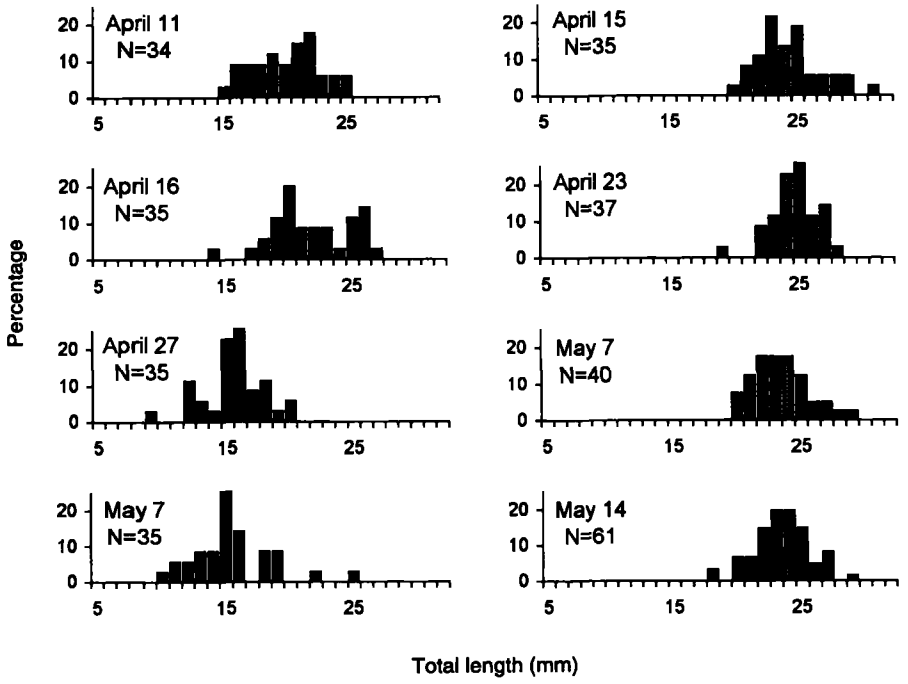


**Figure 5**

Frequency distributions of TL of sardine larvae caught in 1990 (left) and 1991 (right). Sampling date and sample size ($n$) are shown in each panel.

The modal size of sardine larvae caught on April 27 and May 7 (April-hatched cohort) in 1990 was exceptionally smaller (15–16 mm TL) than those in the other larval groups (Fig. 5). The mesh aperture of the net of the *shirasu* fishery is 2.1 mm at the codend. The diagonal of the mesh is 3.0 mm, which is much larger than the body depth of 15–16 mm sardine larvae (about 1.3 mm). A large proportion of larvae smaller than 15 mm could, therefore, be extruded from the mesh at the codend (Smith and Richardson, 1970). Nevertheless, many larvae smaller than 15 mm

[1] 1990. Marine Resources Research Center of Aichi Fisheries Research Institute, 2-1 Toyoura, Toyohama, Minami-Chita, Chita-gun, Aichi 47034, Japan. Unpubl. data

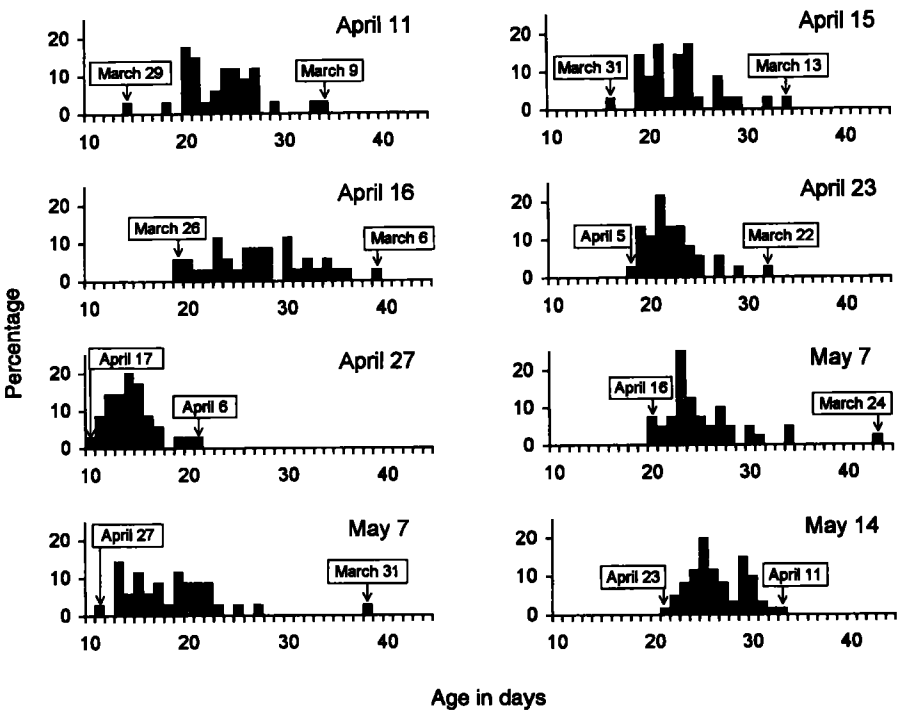


**Figure 6**

Frequency distribution of age of sardine larvae caught on different dates in 1990 (left) and 1991 (right). Boxes show the earliest or latest hatch date of the group.

**Table 1**

Back-calculated TLs (in mm) of sardine larvae at ages 10, 15, 20, and 25 d after hatching.

| | | 10 | | | 15 | | | 20 | | | 25 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Hatching month | | Mean | SD | *n* | Mean | SD | *n* | Mean | SD | *n* | Mean | SD | *n* |
| 1990 | March | 10.8** | 0.9 | 69 | 14.1** | 1.2 | 68 | 17.5** | 1.4 | 65 | 20.5** | 1.3 | 35 |
| | April | 11.5 | 1.0 | 69 | 14.9** | 1.4 | 39 | 17.9* | 2.0 | 14 | | | |
| 1991 | March | 12.3 | 1.1 | 62 | 16.3 | 1.5 | 62 | 20.4 | 2.1 | 61 | 23.1 | 2.6 | 33 |
| | April | 11.7 | 0.9 | 110 | 15.8 | 1.3 | 110 | 19.2 | 1.7 | 110 | 21.6 | 1.8 | 74 |

* Significantly smaller ($P<0.01$) than the same hatching month cohort in 1991.
** Significantly smaller $P<0.001$) than the same hatching month cohort in 1991.

(April-hatched cohort) were caught from late April to early May. This finding indicates that large numbers of small larvae were carried to the coastal fishing grounds after April 16 in 1990. The SST distribution in 8–9 May indicated that there was a substantial amount of intrusion of the offshore warm water after 23–25 April. Because the size of immigration to the fishing ground was smaller in this April-hatched cohort than in others, decline of growth in this cohort started earlier, at 13 d old (13.1 mm TL), compared with other cohorts from 20 to 21 d (19–20 mm TL) (Fig. 8).

Larval TLs at 20 d were 20.4 ±2.1 and 19.2 ±1.7 mm, as March- and April-hatched cohorts in 1991, respectively, which were comparable to the sizes at 20 d (19.1 ±0.6–19.4 ±1.6 mm) of the January- to March-hatched cohorts of *S. melanostictus* in the waters off Miyazaki in 1991 (Watanabe and Kuroki, 1997). In our current study, however, TLs of the 1990 larvae at 20 d ranged from 17.5 to 17.9 mm, significantly

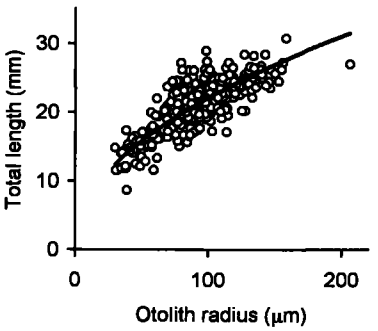


**Figure 7**

Allometric relationship of fish TL (mm) on OR (μm). $TL=2.34 \cdot OR^{0.482}$ ($r^2=0.685$, $n=312$, $P<0.001$).

smaller than the sizes in 1991. The difference in growth rates between 1990 and 1991 could not be explained by SST because in our study area, slower growth was recorded in 1990, when SST was higher, than in 1991. Relative abundance of sardine *shirasu* in the coastal waters of central Japan in 1991 decreased to about 50% of the 1990 (Kishida et al., 1994). The catch of sardine larvae in 1991 declined to 41% of that in 1990 (Fig. 2). Funakoshi (1996) demonstrated that abundance of macrozooplankton was negatively correlated with the biomass of young-of-the-year sardines in Ise Bay (Fig. 1). He considered that large biomasses of young-of-the-year sardines resulted in a reduced abundance of macrozooplankton, followed by a decline in growth of the sardines through density-dependent processes. The greater population of sardine larvae in the *shirasu* fishing grounds in 1990 than in 1991 may have resulted in the slower growth of the sardine larvae in 1990. We need to study the density of food items for sardine larvae in the *shirasu* fishing grounds to examine if sardine larval growth is limited by food availability. We also need to know interspecific competition for food between sardine and anchovy larvae in a coastal ecosystem, because they coincided in April and May in our study area (Fig. 4).

The offshore Kuroshio frontal waters provide sardine larvae with sufficient foods. Nakata et al. (1995) calculated that the total food requirement of carnivorous macrozooplankters and sardine larvae was about 11% of the total production of small copepods (<1.0 mm prosome length) in Kuroshio frontal waters. This resulted in a higher feeding incidence in the early larval stage of *S. melanostictus* in the frontal waters compared with the inshore and offshore waters of the frontal area (Nakata, 1995). Juvenile *S. melanostictus* (32–48 mm fork length) collected in

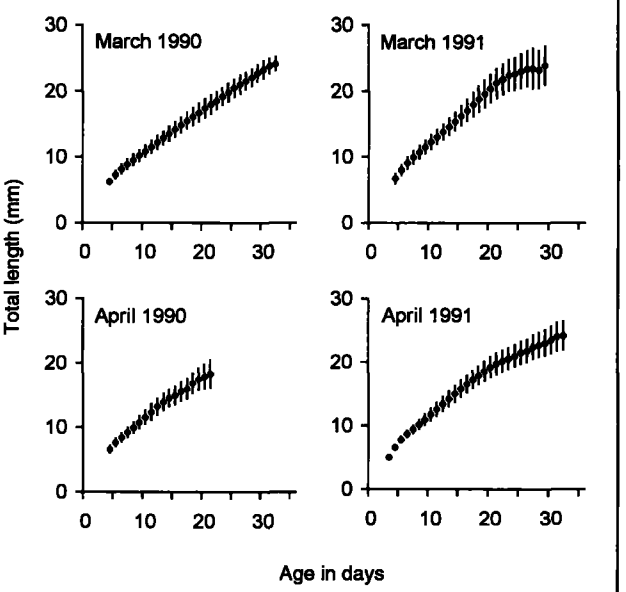


**Figure 8**

Backcalculated growth trajectories of sardine larvae hatched in March and April in 1990 and 1991. Small diamond represents mean TL at age and vertical bar one SD of the m

the Kuroshio frontal waters had stomach contents (mostly copepods and larvaceans) of 7–10% of wet body weight and were backcalculated to have grown at 0.8–0.9 mm/d in the larval stage (Watanabe and Saito, 1998). Perhaps the coastal waters in and around the *shirasu* fishing grounds are a less favorable feeding area for sardine larvae than the Kuroshio frontal waters.

## Acknowledgments

We thank Shigeo Funakoshi for comments on ecology of larval sardine and anchovy in the study area. Masao Bando sampled the sardine larvae in the fishing ports. Hisae Furukawa prepared and read otolith specimens. This work was supported in part by Grants-in-Aid from the Ministry of Agriculture, Forestry, and Fisheries (Biocosmos project, BCP-98-IV-A-8) and from the Ministry of Education, Science and Culture.

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# Transition from pelagic to benthic prey for age group 0–1 Atlantic cod, *Gadus morhua*

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Atlantic cod, *Gadus morhua* L., settle to the bottom early in life at standard lengths of 30 to 40 mm (Bowman, 1981; Hawkins et al., 1985; Hop et al., 1994; Methven and Bajdik, 1994). After settlement into benthic habitats, Atlantic cod continue to feed on pelagic prey but then shift to benthic prey. The rate at which cod make this transition has not been quantified at a level usable in trophic dynamic studies. To quantify the rate at which this shift in diet occurs, the volumetric proportion of pelagic prey in the diet of 98 juvenile Atlantic cod (age group 0 and 1) was measured. The data were used to evaluate a method that enables the calculation of food quantities with high accuracy for incorporation in trophic studies.

## Materials and methods

Juvenile Atlantic cod (ages 0 and 1) were collected at Bellevue, Trinity Bay, Newfoundland, from July to December 1989 and from August to October 1991. Refer to Methven and Bajdik (1994) for additional information on fish collection and the collection site. A sample of 98 group-0 (40.2–100.1 mm standard length [SL]) and group-1 (85.1–192.0 mm SL) cod were used. Stomach contents were analyzed by using prey volume to quantify the transition from pelagic to benthic prey.

For each individual, prey were identified to the lowest taxon possible, then counted. Displacement volume was measured for each taxon with a 5-mL graduated cylinder or a 200-µL micropipette. Prey volume was estimated as a proportion of the total volume of the pipette by using a millimeter ruler (200 µL measured 90.5 mm, i.e. 1 mm=approx. 2.2 µL). If a prey group was too small for volumetric displacement, measurements of length, width, and depth were taken for each individual prey item by using a dissecting microscope with an ocular micrometer. Measurements were made by using eye piece units and converted to millimeters to calculate volumes with geometric formulae (Table 1).

To evaluate the accuracy of calculated volumes, both displacement volume and calculated volume were measured for various prey items. Calculated volume tended to be higher than displacement volume by a constant rate, therefore linear regression was used to calibrate calculated volume against displacement volume. The intercept was not significantly different from zero ($P$=0.1453, $F_{[1,33]}$=116.43), therefore the parameters were re-estimated without the intercept ($P$=0.0001, $F_{[1,33]}$=258.02). The regression equation was

$$\textit{Displacement volume} = (0.72)(\textit{calculated volume}).$$

A correction factor of 0.72 was applied to all calculated volumes to obtain estimated displacement volumes.

The following references were used to identify invertebrate prey items and to determine whether they were benthic or pelagic with respect to habitat: Smith, 1964; Allen, 1967; Russell-Hunter, 1969; Schultz, 1969; Feeley and Wass, 1971; Meglitsch, 1972; Naylor, 1972; Bousfield, 1973; and Gardner and Szabo, 1982. Scott and Scott (1988) was used to identify vertebrate prey.

Percent pelagic prey in the diet was plotted against standard length to determine the relation between the two.

## Results

Both group-0 and group-1 cod fed on a broad range of prey. However, few occurred in large amounts

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**Table 1**

Prey shapes and volume formulae used in the study. spl = species length; spw = species width; spd = species depth.

| Prey type and species | Shape | Formula |
|---|---|---|
| Copepoda, Polychaeta, and shrimp and crab zoea | cylinder | $V = 3.14\ r^2 \times spl$<br>$r = spw/2$ |
| Amphipoda (straight) and Mysidicae | cylinder | $V = 3.14 \times r^2 \times spl$<br>$r = [(spw + spd)/2]/2$ or<br>$r = spw/2$ |
| Amphipoda (curved) | 1/2 cylinder | $V = 3.14 \times r^2 \times spw$<br>$r = spl/2$ |
| Crab (adult) | disc | $V = 3.14 \times r^2 \times spd$<br>$r = [(spl + spw)/2]/2$ |
| Crab (megalopa), Isopoda, and Ostracoda | box | $V = spl \times spw \times spd$ |
| Crustacean eggs and eyes | sphere | $V = 4/3 \times 3.14\ r^3$<br>$r = spl/2$ |
| Snail | circular<br>cone | $V = 1/3 \times 3.14\ r^2 \times spd$<br>$r = [(spl + spw)/2]/2$ |

**Table 2**

Prey of age group 0–1 cod based on two measurement methods. B = Benthic, P = Pelagic, U = Unknown, Unid. = Unidentified. Mean number = number of individuals per stomach; mean volume = microliters per stomach.

| Method | Group 0 | | Group 1 | |
|---|---|---|---|---|
| Mean number | Calanoida (P) | 22.7 | *Jaera marina* (B) | 37.9 |
| | Harpacticoida (B) | 3.6 | Eggs (U) | 17.7 |
| | Unid. Copepoda (U) | 3.2 | *Gammarus oceanicus* (B) | 3.0 |
| | *Jaera marina* (B) | 2.7 | *Pontogeneia inermis* (P) | 3.0 |
| | *Pontogeneia inermis* (P) | 2.1 | Harpacticoida (B) | 1.2 |
| | Other (U) | 5.7 | Other (U) | 5.8 |
| Mean volume | Unid. Gammaridae (B) | 27.4 | *Crangon septemspinosa* (B) | 297.7 |
| | *Gammarus oceanicus* (B) | 24.9 | *Gammarus oceanicus* (B) | 98.4 |
| | Unid. Mysidacea (U) | 12.9 | *Jaera marina* (B) | 84.0 |
| | *Calliopius laeviusculus* (P) | 12.3 | *Urophycis tenuis* (B) | 62.5 |
| | *Pontogeneia inermis* (P) | 11.2 | Unid. Teleostei (U) | 42.6 |
| | Unid. Copepoda (U) | 10.7 | Unid. Decapoda (U) | 40.9 |
| | Calanoida (P) | 6.5 | Unid. Crustacea (U) | 31.1 |
| | *Jaera marina* (B) | 6.1 | Unid Polychaeta | 28.9 |
| | Other (U) | 100.0 | Other (U) | 317.1 |

(Table 2). Group-0 cod fed predominately on amphipod taxa (*Pontogeneia inermis*, *Gammarus oceanicus*, *Calliopius laeviusculus*, and unidentified Gammaridae) and copepod taxa (Calanoida and Harpacticoida). Predominate prey of group-1 cod were more diverse, including two amphipod taxa, an isopod (*Jaera marina*), invertebrate eggs, a shrimp (*Crangon septemspinosa*), white hake (*Urophycis tenuis*), and other unidentified teleosts, decapods, and polychaete worms.

Figure 1 indicates a rapid shift from pelagic to benthic prey at standard lengths of 60 to 100 mm. Four group-0 fish, represented by triangles in Figure 1, had <5% pelagic prey. Prey of these fish consisted of a large volume of unidentified prey and a single benthic prey item (e.g. one ostracod or one amphipod head). These fish were omitted in the calculation of the mean proportion of pelagic prey for the three size groups of cod in Table 3.

The rapid shift to benthic prey by juvenile Atlantic cod was related to body size. This change was quantified for use in food web computations. The diet of cod 40–59.9 mm SL was 98% pelagic prey, that of

cod 60–100 mm SL was 39% pelagic prey, and the diet of cod greater than 100 mm SL was 13% pelagic prey by volume. A simple explanation for this rapid shift is that the mouth opening of smaller size classes is too small to enable predation upon many benthic prey species. However, it is important for juvenile cod to settle to benthic habitats as soon as possible to find protection against predators. Therefore, they quickly shift to a benthic diet as soon as their gape size is large enough.

A series of hypotheses were examined to decide whether the rapid shift in diet was associated with conditions of the study: time of day, time of year, and breakdown of the thermocline. The pattern of change in Figure 1 was not due to time of day, because cod were captured primarily at night (18:10 to 04:30 hours). Data were then replotted by month of capture, which proved not to be responsible for the rapid shift in diet. Data were then replotted by date to investigate relation to the breakdown of the thermocline in mid-October. It was hypothesized that the thermocline keeps pelagic and benthic prey well separated (i.e. pelagic prey are unavailable to demersal juveniles). After the breakdown of the thermocline, the pelagic prey may occur lower in the water column. However, the change in percentage of pelagic prey did not change suddenly at the time of thermocline breakdown.

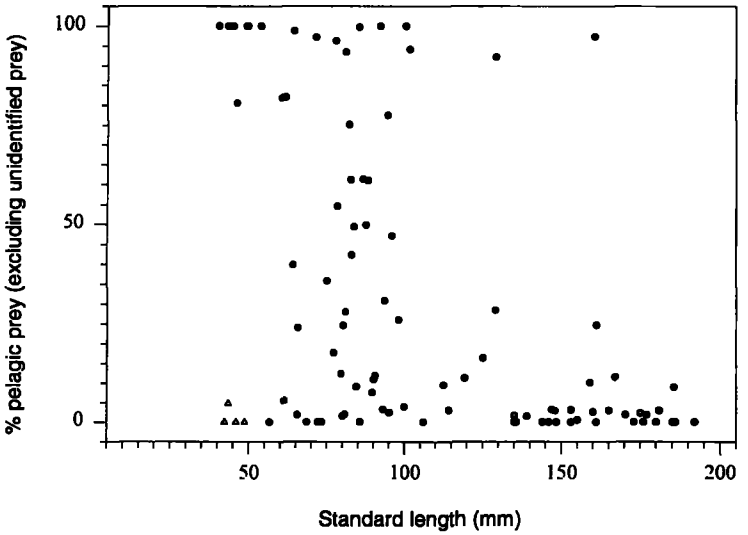


**Figure 1**

Percent pelagic prey (excluding unidentified prey) as a function of standard length (mm) for juvenile Atlantic cod. Four fish, indicated by the four triangles at the bottom left, had a single prey item identified.

**Table 3**

Percent pelagic prey in the diet of three size groups of juvenile Atlantic cod.

| Size group (mm) | Mean % pelagic prey | Standard error | Number of stomachs |
|---|---|---|---|
| 40–59 | 97.56 | 2.44 | 8 |
| 60–100 | 38.5 | 5.32 | 45 |
| >100 | 13.06 | 4.43 | 41 |

## Conclusions

The diets of group-0 and group-1 Atlantic cod at Trinity Bay, Newfoundland, are comparable to those of other areas (Daan, 1973 [northeastern Atlantic]; Arntz, 1974 [western Baltic]; Pálsson, 1980 [Iceland]; Bowman, 1981 [western Atlantic]; Keats et al., 1987 [eastern Newfoundland]; Paz et al., 1991 [Flemish Cap]; Keats and Steele, 1992 [eastern Newfoundland]; Hop et al., 1992, 1994 [northeastern Atlantic]). Demersal group-0 cod fed on both pelagic and benthic organisms, whereas group-1 cod fed more on benthic organisms as the principal components of the diet. The diets of group-0 and group-1 cod overlapped within a narrow range of body size (85.1 to 100.1 mm SL). Small pelagic prey, such as calanoid copepods, became less important in the diet of group-1 cod, whereas larger benthic prey items, such as decapods, amphipods, teleost fish, and polychaetes, became more important.

Results of the present study indicate that the ontogenetic shift from pelagic to benthic prey occurs within a narrow size range (from 60 to 100 mm SL) and hence more rapidly than previously believed (Daan, 1973; Bowman, 1981). This rapid shift may have been overlooked in previous studies that did not examine the diet of small cod in as much detail as in our study (i.e. volume in microliters of individual prey taxa). However, results of our study do not indicate that all cod less than 100 mm rely solely on benthic food. For example, it is well documented (e.g. Kohler and Fitzgerald, 1969) that, at particular times of the year, large juvenile and adult cod can forage far off the bottom on pelagic prey. One implication of this finding is that any investigation of cod recruitment variability, in relation to food supply, should include postsettlement stages.

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# Metazoan parasites as potential markers for selected Gulf of Alaska rockfishes

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Rockfishes (family Scorpaenidae) of the genus *Sebastes* constitute some of the most important groundfish resources in the northeastern Pacific Ocean. In Alaska waters, shortraker rockfish, *S. borealis*, and rougheye rockfish, *S. aleutianus*, are especially prized because their large size and red color make them valuable on the Asian market. Both species reside in offshore waters of the upper continental slope, and they often co-occur. Commercial catches of these two species in the Gulf of Alaska (GOA) have averaged 1700 metric tons per year during this period, and the estimated exvessel value of the fishery in 1991 (the most recent year with good economic data) was $3 million.

Knowledge of stock structure and the degree of mixing among populations is important for the rational management of commercially important marine species. At present, such information is lacking for shortraker and rougheye rockfish, and questions, such as whether these species perform lengthy migrations or whether discrete populations exist, are unanswered. Traditional tag-and-release experiments, which are often used to investigate stock structure, are not feasible for physoclistic fish such as rockfish because they cannot survive the barotrauma of initial capture. One alternative to human-implanted tags is the use of parasites as naturally occurring tags. Because necropsies of rockfishes are time consuming, we examined 100 fish of each species from the GOA to identify the feasibility of targeting selected parasites as tags for these species.

## Methods

Adult shortraker and rougheye rockfish were captured in the GOA in summer 1990 during an annual longline survey conducted on the upper continental slope by the National Marine Fisheries Service. Sampling covered five statistical management areas established by the International North Pacific Fisheries Commission (Zenger and Sigler, 1992): Shumagin, Chirikof, Kodiak, Yakutat, and Southeast (Fig. 1). The survey area extended from the Island of the Four Mountains (52°50'N, 170°W) eastward to Dixon Entrance (54°29'N, 134°W). Forty-five stations were sampled along the upper continental slope at depths from 150 to 1000 m. Of the 7836 rockfishes of various species caught in the cruise, a subsample of 20 rougheye and 20 shortraker rockfish (21 from Shumagin) from each management area were frozen on board for later necropsy. Total sample size was 101 shortraker and 100 rougheye rockfish from 21 stations.

In the laboratory, we conducted complete necropsies for metazoan parasites on an initial sample of 54 shortraker and 69 rougheye rockfish. As a result of preliminary analysis of the parasite data from these fish, we restricted the necropsies on the remaining 47 shortraker and 31 rougheye rockfish to examinations for the presence of gill and fin copepods, monogenetic gill trematodes, and visceral acanthocephalans. Identities of representative parasite specimens were verified by D. J. Whitaker of the Canadian Department of Fisheries and Oceans. Both prevalence (the proportion of fish with a given parasite) and intensity (the mean number of parasites per infected fish) were calculated for each management area.

Geographic trends were examined by grouping samples into the five management areas. Categorical analysis of variance (SAS procedure CATMOD; SAS Inst., 1989) was used to determine whether parasite prevalence differed among areas. For this analysis, the prevalence of a particular parasite was used as the dependent variable, and area and fish size as independent variables. For each fish species, median fork length was used to divide the areawide sample into two groups, hereafter referred to as large and small. Data on parasite intensity for each fish were divided by fish length to account for the possible influence of fish size on parasite intensity. Distribution of the intensity data was highly nonnormal, even after transformation. Therefore, intensity data were analyzed by using the nonparametric Mann-Whitney *U* test. These analyses allowed us to account for differences in fish size by area while test-

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ing for dependence of parasite prevalence and intensity by area. Fish size was chosen as a variable because the size of fish sampled in some areas differed, and fish size may influence parasite prevalence and intensity (Sekerak, 1975). A probability of 0.10 or less was judged to be statistically significant.

## Results

Seventeen species of parasites were found in our preliminary examinations: six species of copepod on the gills and fins and in the cephalic canal and nasal cavities; two species of monogenetic trematodes on the gills; three species of digenetic trematodes, two species of acanthocephalans, one species of cestode, and three species of nematodes in the viscera and mesenteries. All these species had been described previously from northeastern Pacific rockfishes, although parasites of shortraker and rougheye rockfishes in the western GOA had not been described previously. Many of the fish contained both larval nematodes *Contracaecum* spp. and *Hysterothylacium* spp. Because it is time consuming to separate these two genera, they were lumped together as a single species as *Contracaecum*-type spp. On the basis of these preliminary results, nematodes, digenes, and cestodes were eliminated from further examination. These helminths were infrequent in the samples or showed no difference between management areas. Further examinations focused on enumeration of copepods, acanthocephalans, and monogenes.

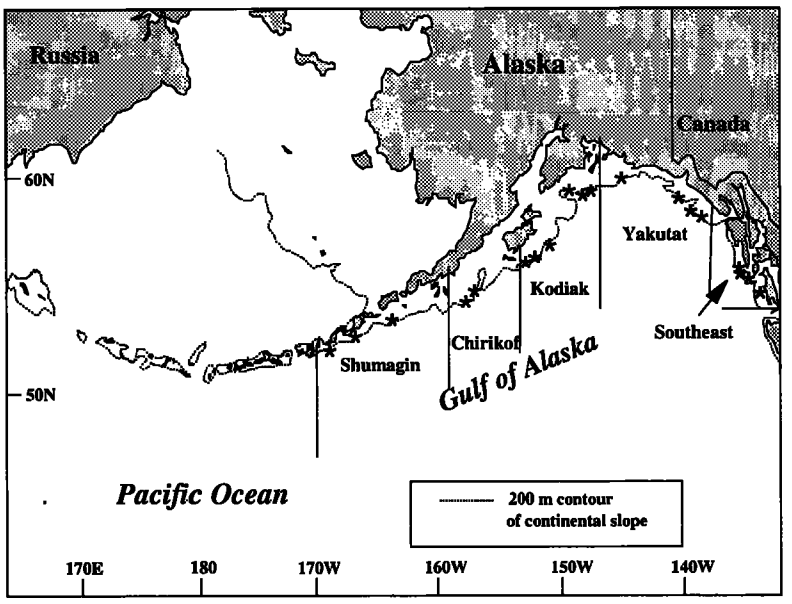


**Figure 1**

Northeastern Pacific Ocean, showing management areas of the Gulf of Alaska. Asterisks show sampling stations along the continental slope.

Prevalence (Table 1) and intensity (Table 2) of several parasite species differed distinctly among shortraker and rougheye rockfish populations in the GOA; they varied between areas, rather than being present in one area and absent in another. Three of these—*Neobrachiella robusta* (copepod), *Trochopus trituba* (monogenetic trematode), and *Corynosoma* sp. (acanthocephalan)—had the most distinctive changes in prevalence between areas. For shortraker rockfish, the highest prevalence of *N. robusta* and *T. trituba* parasites was in Kodiak samples. In rougheye rockfish, prevalence of all three parasites was significantly reduced in the Southeast. Several species of parasites were scarce in some areas and absent in others.

Of the six species of copepods in our survey, the gill copepod *N. robusta* was sufficiently prevalent to be potentially useful in stock discrimination studies. Prevalence of *N. robusta* differed significantly between areas for both shortraker ($P$=0.076) and rougheye ($P$=0.087) rockfish. *Neobrachiella robusta* was present in 80% of the Kodiak shortraker rockfish sampled as opposed to 35–55% of those sampled in the other four areas. Larger rougheye rockfish also had a significantly ($P$=0.028) greater prevalence of *N. robusta* than smaller specimens. Among shortraker rockfish, intensities ranged from a mean of 2.4 in Shumagin to 7.6 in Chirikof; the differences were also significant between areas ($P$=0.029), especially when corrected for the size of the fish ($P$=0.016). Among rougheye rockfish, however, intensity of *N. robusta* infection did not differ between areas ($P$=0.667). Mean infection levels were lower among rougheye rockfish than among shortraker rockfish for *N. robusta* but still averaged 1–5 parasites per fish.

Other copepods were prevalent in the GOA samples. *Naobranchia occidentalis* was found in shortraker rockfish from Chirikof, Kodiak, and Yakutat in low prevalence (10%) and in rougheye rockfish from Yakutat (20%), but not from other areas. Prevalence of *Chondracanthus pinguis* was above 40% in Yakutat and Southeast rougheye rockfish, but below 10% in all other samples. This difference, however, was a function of size rather than area. Prevalence was significantly greater ($P$=0.069) in large rougheye rockfish than in small ones. *Colobomatus kyphosus* was present in one shortraker rockfish from Yakutat and in two rougheye rockfish from Yakutat and Southeast. *Chrondracanthus triventri-*

**Table 1**

Comparison of parasite prevalence (proportion of fish having the parasite) by area for shortraker and rougheye rockfish in the Gulf of Alaska, 1990. The number of fish examined in each area is given in parentheses. Significance probability is given for a categorical analysis of variance model with area and fish size as main effects. Asterisks indicate $P < 0.10$.

| | Parasite prevalence | | | | | Significance probability | |
|---|---|---|---|---|---|---|---|
| | Shumagin | Chirikof | Kodiak | Yakutat | Southeast | Area | Size |
| Shortraker rockfish | (*n*=21) | (*n*=20) | (*n*=20) | (*n*=20) | (*n*=20) | | |
| *Neobrachiella robusta* | 0.48 | 0.55 | 0.80 | 0.35 | 0.40 | 0.076* | 0.724 |
| *Naobranchia occidentalis* | 0.00 | 0.10 | 0.10 | 0.10 | 0.00 | 0.980 | 0.493 |
| *Chondracanthus pinguis* | 0.10 | 0.05 | 0.10 | 0.10 | 0.10 | 0.971 | 0.301 |
| *Colobomatus kyphosus* | 0.00 | 0.00 | 0.00 | 0.05 | 0.00 | 0.954 | 0.583 |
| *Trochopus trituba* | 0.62 | 0.60 | 0.86 | 0.55 | 0.45 | 0.081* | 0.262 |
| *Microcotyle sebastis* | 0.14 | 0.10 | 0.00 | 0.00 | 0.00 | 0.927 | 0.655 |
| *Corynosoma* sp. | 0.81 | 0.75 | 0.60 | 0.65 | 0.65 | 0.606 | 0.914 |
| *Echinorhynchus gadi* | 0.10 | 0.00 | 0.00 | 0.05 | 0.00 | 0.929 | 0.633 |
| *Clavella parva* | 0.62 | 0.80 | 0.90 | 0.30 | 0.20 | 0.013* | 0.370 |
| Rougheye rockfish | (*n*=20) | (*n*=20) | (*n*=20) | (*n*=20) | (*n*=20) | | |
| *Neobrachiella robusta* | 0.25 | 0.40 | 0.30 | 0.50 | 0.10 | 0.087* | 0.028* |
| *Naobranchia occidentalis* | 0.00 | 0.00 | 0.00 | 0.20 | 0.00 | 0.897 | 0.823 |
| *Chondracanthus pinguis* | 0.10 | 0.00 | 0.00 | 0.40 | 0.50 | 0.152 | 0.069* |
| *Colobomatus kyphosus* | 0.00 | 0.00 | 0.00 | 0.10 | 0.10 | 0.960 | 0.165 |
| *Trochopus trituba* | 0.70 | 0.60 | 0.55 | 0.50 | 0.20 | 0.045* | 0.822 |
| *Microcotyle sebastis* | 0.15 | 0.00 | 0.00 | 0.15 | 0.00 | 0.906 | 0.895 |
| *Corynosoma* sp. | 0.80 | 0.75 | 0.75 | 0.75 | 0.20 | 0.001* | 0.283 |
| *Echinorhynchus gadi* | 0.00 | 0.00 | 0.15 | 0.00 | 0.05 | 0.674 | 0.356 |
| *Clavella parva* | 0.48 | 0.10 | 0.10 | 0.70 | 0.55 | 0.105 | 0.704 |

*cosus*, a common parasite in the nasal cavities of Canadian rockfishes, was largely absent from our samples, occurring in only a single specimen. The fin copepod *Clavella parva* was present in all areas, with increased prevalence among shortraker rockfish in the western GOA; this difference was significant ($P$=0.013) between areas. Although we examined all parasites in our sample, *C. parva* was never a candidate for separation, because fin parasites could be lost in capture and sampling.

The parasites showing the most potential for providing insights into the population structure for both species of rockfishes were the monogenetic trematodes *T. trituba* and *Microcotyle sebastis*, because of their high and low prevalences, respectively. Prevalence and intensity of *T. trituba* were significantly lower for rougheye rockfish in the Southeast (20% prevalence, mean intensity of 1.8) than in other management areas (50–70% prevalence, mean intensity of 2–9). For shortraker rockfish, prevalence and intensity of *T. trituba* were highest in Kodiak (86%, intensity of 16) and declined farther southward (45% and 8 in the Southeast, 62% and 4 in Shumagin). Both prevalence and intensities of *T. trituba* differed significantly among areas and did not depend on fish size. *Microcotyle sebastis*, common among many species of British Columbia rockfishes, was rare in the GOA.

The only internal parasite showing potential as a tag was *Corynosoma* sp., which, with the less common acanthocephalan *Echinorhynchus gadi*, infected nearly every Shumagin shortraker rockfish (90% infected with an acanthocephalan at an average of three *Corynosoma* sp. per fish). Most other shortraker rockfish were also infected (60–75%). Although prevalences of *Corynosoma* sp. in shortraker rockfish did not differ among areas, intensities and intensities/cm differed significantly ($P$=0.024 and 0.019, respectively) by area, largely owing to high numbers of *Corynosoma* sp. among Yakutat fish. Rougheye rockfish were also infected with *Corynosoma* sp. at 75–80%, except in the Southeast (20%; significantly lower [$P$=0.001] than in other areas).

## Discussion

Williams et al. (1992) proposed six criteria to assess the value of a parasite as a marker for stock separation. The parasite should differ in levels of infection across geographic regions, not be detached easily with handling, be easily assessed, have no harmful effect

**Table 2**

Comparison of mean parasite intensity by area for shortraker and rougheye rockfishes in the Gulf of Alaska, 1990. Range of intensity is in parentheses. Significance probability for differences in intensity and for intensity per cm fish length between areas is also given (Mann-Whitney $U$ test). Asterisks indicate $P < 0.10$. Dash means insufficient number of infected fish to perform statistical tests. Int = intensity.

| | Mean parasite intensity (no. of parasites per infected fish) | | | | | Significance probability | |
|---|---|---|---|---|---|---|---|
| | Shumagin | Chirikof | Kodiak | Yakutat | Southeast | Intensity | Int/cm |
| Shortraker rockfish | | | | | | | |
| *Neobrachiella robusta* | 2.4 (1–9) | 7.6 (1–18) | 4.9 (1–12) | 4.4 (1–17) | 3.8 (1–8) | 0.029* | 0.016* |
| *Naobranchia occidentalis* | 0 | 1 (1) | 1 (1) | 4.5 (4–5) | 0 | 0.333 | 0.156 |
| *Chondracanthus pinguis* | 1 (1) | 3 (3) | 3.5 (3–4) | 1 (1) | 1.5 (1–2) | 0.131 | 0.189 |
| *Colobomatus kyphosus* | 0 | 0 | 0 | 1 (1) | 0 | — | — |
| *Trochopus trituba* | 3.8 (1–9) | 4.8 (1–9) | 16 (1–106) | 17 (2–89) | 8.3 (1–15) | 0.001* | 0.002* |
| *Microcotyle sebastis* | 1.3 (1–2) | 2.5 (2–3) | 0 | 0 | 0 | 0.133 | 0.083* |
| *Corynosoma* sp. | 3.3 (1–6) | 2.3 (1–12) | 2.7 (1–7) | 5.6 (1–26) | 3.7 (1–7) | 0.024* | 0.019* |
| *Echinorhynchus gadi* | 1 (1) | 0 | 0 | 3 (3) | 0 | — | 0.221 |
| *Clavella parva* | 1.2 (1–2) | 1.5 (1–5) | 1.5 (1–3) | 1.5 (1–2 | 1.3 (1–2) | 0.259 | 0.357 |
| Rougheye rockfish | | | | | | | |
| *Neobrachiella robusta* | 2.6 (1–4) | 2.7 (1–7) | 1.8 (1–4) | 5.2 (1–32) | 1 (1) | 0.667 | 0.478 |
| *Naobranchia occidentalis* | 0 | 0 | 0 | 1 (1) | 0 | — | — |
| *Chondracanthus pinguis* | 1 (1) | 0 | 0 | 9.6 (1–61) | 2.7 (1–5) | 0.235 | 0.211 |
| *Colobomatus kyphosus* | 0 | 0 | 0 | 3 (2–4) | 1.5 (1–2) | 0.333 | 0.121 |
| *Trochopus trituba* | 4.6 (1–19) | 1.7 (1–3) | 2.1 (1–8) | 9.1 (1–50) | 1.8 (1–3) | 0.023* | 0.069* |
| *Microcotyle sebastis* | 1 (1) | 0 | 0 | 1 (1) | 0 | — | — |
| *Corynosoma* sp. | 6 (1–17) | 5.1 (1–15) | 4.6 (1–8) | 5 (1–17) | 3.8 (1–7) | 0.973 | 0.916 |
| *Echinorhynchus gadi* | 0 | 0 | 1 (1) | 0 | 1 (1) | 1.000 | 0.180 |
| *Clavella parva* | 1.4 (1–3) | 1 (1) | 1 (1) | 1.8 (1–3) | 2.2 (1–5) | 0.427 | 0.443 |

on the host, have a long life span, and be present in only one part of the host. Based on coincident samples, it is clear that the monogenetic trematodes and copepods on the gills of the rockfishes in our study meet all these criteria, as do the visceral acanthocephalans. Gill parasites are protected by the operculum during capture, are sampled easily, and can be identified aboard ship. Notably, Leaman and Kabata (1987) previously proposed using *N. robusta* as a marker for separating stocks of *S. alutus* in British Columbia. Acanthocephalans, such as *Corynosoma* sp., also serve as excellent markers because they can be easily enumerated with a pepsin enzyme. In contrast, the lack of digenes and cestodes in the preliminary survey (probably due to regurgitation through barotrauma) makes these parasites poor candidates as tags for deepwater rockfishes. The nematodes are difficult to identify and their prevalences were similar throughout the Gulf of Alaska.

In addition to their potential use in determining stock structure, differences in prevalence between areas among the parasites in this study also give insight on differences in diet and parasite distributions. *Corynosoma* sp. is widely distributed in the northeastern Pacific Ocean as a parasite of marine mammals, birds, and fishes (Margolis, 1958); thus the different prevalences of Corynosoma sp. in our study were likely due to differences in diet rather than to parasite distribution. The intermediate hosts for *Corynosoma* sp. are amphipods; hence, the percentage of amphipods in the diet may be higher in the western part of the GOA than in the eastern part. Alternatively, rougheye and shortraker rockfishes may be more likely to consume infected amphipods than other prey items. In contrast, both copepods and monogenes have no intermediate host stage, and differences in parasitism between management areas probably reflect differences in parasite distribution or host habitat, rather than differences in diet.

Some of the parasite species reported in this study had very different prevalences than those reported for other species or locations of rockfishes. For example, *Corynosoma* sp. was less prevalent (<10%) in most species of British Columbia rockfishes (Sekerak, 1975; Stanley et al., 1992) than in our study. *Corynosoma* sp. may be more common in the GOA than in Canada or simply more prevalent in shortraker and rougheye rockfishes than in some other species. Sekerak (1975) examined 536 rockfishes of

26 species from British Columbia waters and the GOA: of the 40 *Corynosoma* sp. recovered, 12 were from rougheye rockfish and 23 were from the GOA.

Size did not appear significant in parasite prevalences except for *N. robusta* and *C. pinguis* infection in rougheye rockfish. Prevalences of several species of parasites, including *N. robusta*, differed significantly among fish of the same size. Nor was size a factor in parasite intensities, despite the observation of Sekerak (1975) that intensities of copepods and monogenetic trematodes increase with increasing fish size, largely due to increased gill surface area. Although the value of parasite tags would be enhanced by sampling similar-size fish, the statistically significant differences among areas, despite size variation, provide an indication of the potential power of parasite markers for these species.

In summary, the prevalence or intensity of *N. robusta*, *T. trituba*, and *Corynosoma* sp. may prove to be useful markers for population studies of GOA shortraker and rougheye rockfishes. It is interesting to note the major reduction in prevalence of all three parasites among Southeast rougheye rockfish. Possibly these fish may constitute a separate stock and support a localized fishery. More studies are needed to evaluate the effects of temporal and spatial variability on parasite prevalence and intensity, particularly among GOA rougheye rockfishes.

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# Catchability and retention of larval European anchovy, *Engraulis encrasicolus*, with bongo nets

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Whenever data on larval abundance are used in producing estimates or indices of stock size or recruitment, accurate length distributions are required. Factors that might bias sample distributions must be taken into account and, in broadscale ichthyoplankton surveys, the effect of environmental and behavioral factors on the content of the samples or collections must be considered (Zweifel and Smith, 1981). The objective is to standardize sampling gear by applying correction factors to make samples comparable (Smith and Richardson, 1977).

A factor contributing to a possibly serious source of bias in larval fish collections is net avoidance. Larvae may be agile and capable of avoiding nets, with the general effect of inaccurate abundance and mortality estimates (Clutter and Anraku, 1968). Catchability varies mainly with light regime and larval length. The visual stimulus of the sampling device is believed to be of crucial importance. This is indicated by numerous investigations showing diel variation in avoidance, catches being significantly smaller during daylight than at night (Morse, 1989, and references therein).

A second factor affecting larval fish collections is extrusion of captured material through the net mesh. According to the "diagonal rule" (Saville, 1958; Smith et al., 1968), the maximum cross-sectional diameter of an organism must be greater than the mesh diagonal if it is to be fully retained. However, the "diagonal rule" is often too conservative (Lenarz, 1972; Colton et al., 1980).

We examined the effects of time of day (day-night-twilight), fish length, and ontogeny on the catchability of European anchovy (*Engraulis encrasicolus*), by using a 60-cm bongo net. We also investigated biases resulting from differential retention of larvae of different lengths, and, further, we examined the effect of correction of catch for net avoidance on estimation of mortality.

Information on catchability and retention of anchovy with plankton nets is very limited and results are often contrasting. Catchability of European anchovy with bongo nets is unknown. Regarding retention, there is just a single study indicating full retention of European anchovy larvae with the 0.333-mm net (Aldebert et al., 1975), whose data are contradictory to Lo (1983) who has estimated a 0.63 retention rate for northern anchovy, *Engraulis mordax*, larvae <4.0-mm with a 0.333-mm net.

## Materials and methods

From 1992 through 1995, five ichthyoplankton surveys were carried out in the Aegean Sea. A total of 474 stations were occupied in continental shelf and slope waters and areas characteristic of larval anchovy habitat (Fig. 1). Plankton and hydrographic sampling were performed at each station and cruise information is given in Table 1. Most stations were positive (i.e. at least one larva was captured).

A 60-cm bongo net sampler (Hydrobios) was used during all cruises. Mesh sizes on the sampler were 0.250-mm, and 0.500- or 0.335-mm, depending on the cruise (Table 1). The 0.250-mm mesh net is considered to retain clupeoid eggs and larvae completely (Aldebert et al., 1975; Colton et al., 1980; Leslie and Timmins, 1989).

Tows at two knots were double-oblique, within 5 m of the bottom to the surface, or from 120 m depth to the surface at deep stations. All tows consisted of a wire released to the desired depth and retrieved to the surface at standard speeds. The depth of the sampler could be monitored onboard at any time during the tow by means of a recording depthmeter attached to the sampler. Plastic codend buckets, with side windows of 155 $cm^2$ covered with net gauze, were used in an effort to minimize damage to larvae. Volumes filtered were calculated from a calibrated flowmeter in the mouth of each net.

All samples were sorted in the laboratory and larvae were identified to the lowest possible taxonomic level. Larval anchovies were counted and measured (notochord

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Fish. Bull. 96: 917–925 (1998).

or standard length to the nearest 0.1 mm). If more than 100 specimens of anchovy were captured in a tow, 100 randomly selected larvae were measured, and subsequent length frequencies were raised to the total number of larvae. Lengths were rounded to 1-mm length groups (e.g. 2–2.99: 2.5 mm).

Each station was assigned to day, night, or twilight hours according to the recorded time at the beginning of the tow. Twilight was designated as one hour before or after sunrise and sunset (Morse, 1989).

The analysis of retention and catchability was made after pooling all available data and, subsequently, estimating mean catch per length group. For example, mean catch per $m^2$ in each length category was calculated for 227 day, 146 night, and 84 twilight positive stations (Table 1). Pooling data over large temporal and spatial regimes integrates areal and temporal heterogeneity in distribution and abundance, and results of the analyses represent average conditions (Hewitt, 1981; Morse, 1989).

Negative stations (where no anchovy larvae were caught by either of two nets) were not included in our analysis (*sensu* Hewitt, 1981); we assumed that they represent samples drawn from outside larval habitat. Given that the number of negative stations was very low in our data set (17 out of 474, of which 10 were from one cruise, 92ANC2, Table 1), inclusion or exclusion of such negative stations was not expected to affect results.

Catches were standardized to numbers per $m^3$. This standardization is sufficient for comparing larval retention in paired different mesh-size nets but, in comparing daytime or twilight and nighttime catches, data had to be standardized to numbers per $m^2$, by using maximum tow depth and volume of water filtered (Houde, 1977). Mean standardized catches per length group were used to calculate the following ratios: day:night and twilight:night as well as 0.500-:0.250-mm mesh and 0.335-:0.250- mm mesh. Variances of ratios were approximated as in Somerton and Kobayashi (1989).

The calculation of mean catch and its variance followed the methods of Pennington (1983) for the delta-distribution of catch frequencies (see also Morse (1989)). The estimators based on the lognormal model (delta distribution) are more efficient for marine data than the usual sample estimators (Lo et al., 1992; Pennington, 1996). In particular, they provide reasonable estimates for data sets that contain isolated large catches.

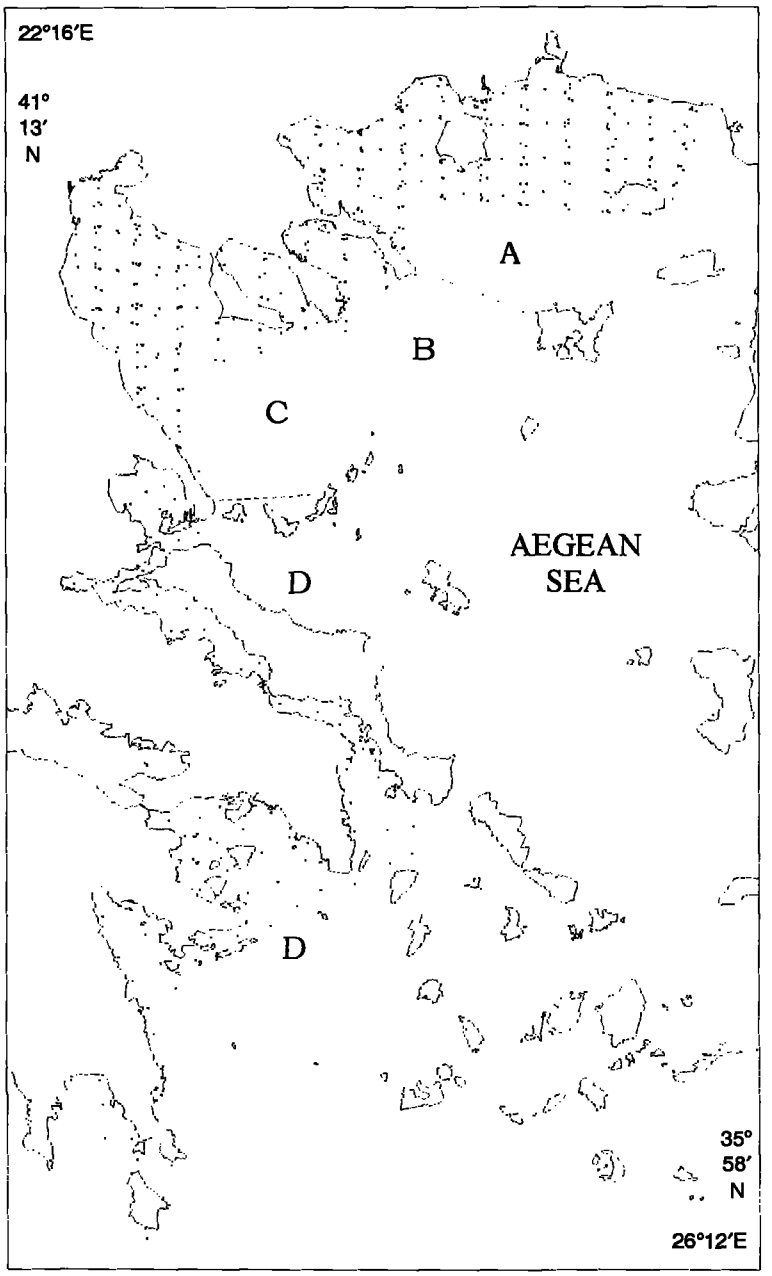


**Figure 1**

Map of the study area showing the location of sampling stations (black dots). A = Thracian Sea; B = Chalkidiki gulfs; C = Thermaikos Gulf; D = Gulfs of central and southeastern Greece.

Anchovies collected during 1995 were further sorted into yolksac, preflexion, flexion, and postflexion larvae. Eye pigmentation, functional mouth, and the formation of intestine (Regner, 1985; Palomera et al., 1988; Clarke, 1989) were used to distinguish yolksac from preflexion larvae. The flexion stage begins at initial notochord flexion and ends (postflexion stage starts)

**Table 1**

Cruise data. Subregions A, B, C (northern Aegean Sea), and D (central-southern Aegean Sea) are indicated in Figure 1. $n$ = number of stations. $n_p$ = number of positive stations. D = daytime stations. N = nighttime stations. T = twilight stations.

| Cruise | Date | Subregion | $n$ | $n_p$ | D | N | T | Mesh size (mm) | Larval abundance/m$^2$ |
|---|---|---|---|---|---|---|---|---|---|
| 92ANC1 | 16 Jul–3 Aug 1992 | A-B-C | 117 | 117 | 54 | 44 | 19 | 0.250, 0.500 | 97.25 |
| 92ANC2 | 3–9 Sep 1992 | D | 80 | 70 | 30 | 26 | 14 | 0.250, 0.500 | 21.02 |
| 93ANC3 | 7–14 Jul 1993 | A-B-C | 110 | 110 | 62 | 30 | 18 | 0.250, 0.500 | 233.91 |
| 94ANC4 | 19–24 Jan 1994 | A-C | 46 | 43 | 16 | 18 | 9 | 0.250, 0.335 | 114.55 |
| 95EP1 | 15–30 Jun 1995 | A-B-C | 121 | 117 | 65 | 28 | 24 | 0.250, 0.335 | 69.17 |
| Total | | | 474 | 457 | 227 | 146 | 84 | | |

when the posterior margin of the upper hypural plate is at 90° from the notochord axis (Moser, 1996).

Additionally, to determine whether the inferences drawn regarding retention rates were plausible in terms of the "diagonal rule," we plotted maximum head width values against standard length based on measurements of 74 staged anchovy larvae (for a justification of using head width, see Colton et al., 1980). In postyolksac larvae, maximum head width was the maximum body width and was greater than any body-depth measurement (Somarakis, unpubl. data). This is not the case for yolksac larvae because of the bulk of the yolk sac. Yolk sacs, however, may be easily compressed or crushed, hence, we considered head width to be the significant dimension.

## Correction for net avoidance and mortality estimates

In studies on mortality of European anchovy the usual practice has been to correct catches for net avoidance by using day:night catch ratios and the methods available for northern anchovy (e.g. Palomera and Lleonart, 1989) because catchability of European anchovy has been unknown. As a final step of this study we estimated mortality during 1994 and 1995 cruises without correcting catches for net avoidance, as well as after correction using three different methods:

**Method 1** The correction for avoidance of the net during day-light was calculated by the sinusoidal function (Hewitt and Methot, 1982):

$$f1 = \frac{(1+DN_L)}{2} + \frac{(1-DN_L)}{2}\cos\left(\frac{2\pi t}{24}\right),$$

where $DN_L$ = the midday-to-midnight catch ratio of $L$-length larvae; and
$t$ = the hour of the tow.

$DN_L$ data used were those available for *E. mordax*.[1]

**Method 2** The same as method 1, $DN_L$ data used were those calculated for *E.encrasicolus* in the present study.

**Method 3** The sinusoidal function was not used. Length-specific ratios of day:night and twilight:night catches calculated in the present study were used to correct catches of day and twilight stations.

The correction for duration of each size class (Hewitt and Methot, 1982; Lo et al., 1989) was calculated from growth of postyolksac larvae in the sea measured by daily increments in otoliths (see also Somarakis et al., 1997a). Age-(micro-increment count)-at-length data and respective growth curves were available from 336 postyolksac larvae collected during the 1994 cruise, and 294 postyolksac larvae from the 1995 cruise. Significant spatial or interannual differences in growth of the European anchovy larvae in the Aegean Sea can be found, which cannot be explained by temperature differences (Somarakis et al., 1997a; Somarakis et al., 1997b). Thus, we estimated mortality for only the 1994 and 1995 cruises for which otolith data were available.

Mean corrected catches at length (i.e. length-specific daily production of larvae per m$^2$) were calculated based on the lognormal model (delta distribution—see above). Mortality was estimated for larvae >4-mm and <10-mm. The 3–3.99 size class was not used because it includes both yolksac and feeding larvae (the yolksac stage is characterized by different mortality rates than the feeding stage [Lo, 1985a; Lo, 1985b]). Mean length-specific daily production of larvae per m$^2$ with its age (calculated from the

[1] Lo, N. C. H. 1996. Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038. Personal commun.

respective growth curve) constituted the database for nonlinear regression estimation of instantaneous mortality rate of postyolksac larvae in a simple exponential model,

$$P_t = P_0 \exp(-zt),$$

where $P_t$ = the daily production of larvae at age $t$;
$t$ = the age in days from the end of the yolksac stage;
$P_0$ = the daily larval production at $t = 0$; and
z = the daily instantaneous mortality rate.

The simple exponential mortality model fitted the data very well (Watanabe and Lo, 1988).

Mortality models resulting from the application of different methods of correcting (or not correcting) catches for light-induced net avoidance were compared by an analysis of the residual sum of squares (Chen et al., 1992).

## Results

### Estimates of mean catch

No larvae >12-mm were caught in any of the 227 day-time tows. Estimates of mean catch per length group (Table 2) indicated that catches of >10-mm larvae were very low and their coefficients of variation too great (generally >20%) to be useful in this study. Thus, our analysis was restricted to larvae <10-mm (see also Lenarz, 1972).

### Retention of anchovy larvae in the 0.335- and 0.500-mm mesh nets

Results of the catch analysis indicate that the 0.500:0.250-mm mesh catch ratio was less than one for larvae <7 mm but the 0.335:0.250-mm mesh ratio was not significantly different from one, at any length (Fig. 2).

Data of maximum head width against standard length of the 74 anchovy larvae, along with the mesh diagonals of 0.500-, 0.335-, and 0.250-mm, are presented in Figure 3. A comparison of head-width measurements with mesh diagonals indicates that the minimum lengths for complete retention in the 0.500- and 0.335-mm mesh nets were approximately 7.5 and 3.5 mm, respectively. The head-width measurements further suggest that to ensure full retention of larvae, it would be necessary to use netting with a mesh aperture of 0.250 mm or less. In terms of ontogenetic stages, the 0.335-mm mesh net is expected to retain all except the yolksac larvae, whereas the 0.500-mm mesh net seems to be inefficient for yolksac and preflexion larvae. It therefore appears that the "diagonal rule" is conservative for yolksac larvae of the European anchovy, when head width is used as the maximum cross-sectional diameter of the larva.

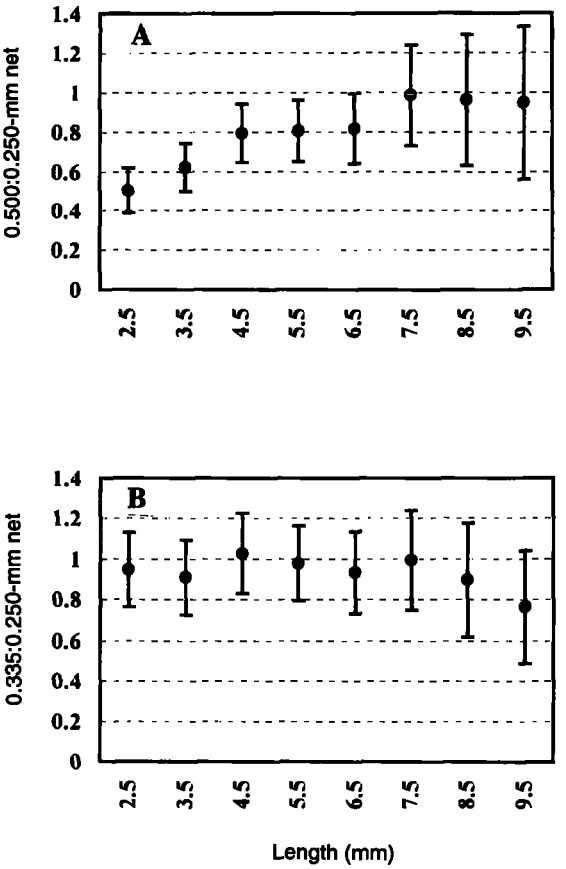


**Figure 2**

Catch ratios of 0.500:0.250 mm (**A**) and 0.335:0.250 mm (**B**) mesh nets as a function of larval length. Bars indicate 95% confidence intervals.

### Differences in day versus night and twilight versus night catches

Results of the catch analysis show a change in the day:night and twilight:night catch ratios at $L$ = 6.5 mm (Fig. 4). In general, both ratios are practically one for larvae <6 mm, at which point they drop substantially, continuing to decrease more or less linearly thereafter. This decrease is stronger for the day:night than for the twilight:night catch ratio, the day:night ratio being significantly less than one from 6 mm onwards and greater than the corresponding twilight:night ratio. Thus, for larvae >6 mm, it seems

**Table 2**

Estimates of mean catch and their coefficients of variation (in parentheses), by length class.

| | Length (mm) | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 2.5 | 3.5 | 4.5 | 5.5 | 6.5 | 7.5 | 8.5 | 9.5 | 10.5 | 11.5 |
| 0.500:0.250 | | | | | | | | | | |
| 0.500 | 0.419 (0.079) | 0.378 (0.067) | 0.323 (0.062) | 0.264 (0.064) | 0.187 (0.072) | 0.136 (0.082) | 0.078 (0.115) | 0.054 (0.131) | 0.020 (0.200) | 0.012 (0.248) |
| 0.250 | 0.836 (0.084) | 0.607 (0.071) | 0.408 (0.069) | 0.329 (0.072) | 0.230 (0.080) | 0.139 (0.101) | 0.080 (0.128) | 0.056 (0.156) | 0.021 (0.233) | 0.012 (0.306) |
| 0.335:0.250 | | | | | | | | | | |
| 0.335 | 0.581 (0.067) | 0.453 (0.067) | 0.438 (0.068) | 0.325 (0.064) | 0.225 (0.077) | 0.182 (0.089) | 0.098 (0.109) | 0.062 (0.132) | 0.023 (0.201) | 0.013 (0.249) |
| 0.250 | 0.614 (0.068) | 0.498 (0.076) | 0.427 (0.068) | 0.332 (0.069) | 0.241 (0.074) | 0.184 (0.085) | 0.109 (0.110) | 0.082 (0.124) | 0.024 (0.232) | 0.015 (0.287) |
| day:night and twilight:night | | | | | | | | | | |
| day | 4.008 (0.067) | 2.900 (0.072) | 2.047 (0.075) | 1.582 (0.082) | 0.890 (0.093) | 0.587 (0.107) | 0.326 (0.132) | 0.201 (0.167) | 0.059 (0.297) | 0.043 (0.335) |
| night | 4.002 (0.085) | 2.775 (0.087) | 2.090 (0.088) | 1.512 (0.102) | 1.352 (0.101) | 1.003 (0.111) | 0.623 (0.129) | 0.496 (0.145) | 0.221 (0.191) | 0.099 (0.280) |
| twilight | 3.864 (0.115) | 3.098 (0.113) | 2.322 (0.114) | 1.683 (0.114) | 1.146 (0.129) | 0.748 (0.156) | 0.454 (0.186) | 0.319 (0.217) | 0.161 (0.319) | 0.101 (0.397) |

that catchability changes with varying light conditions and length. On the other hand, the "sudden" change in catchability at 6.5 mm coincides with the onset of the development of the tail, i.e. the flexion stage (Fig. 5).

### Correction for avoidance and its effect on mortality estimates

Estimates of length-specific larval production for the 1994 and 1995 cruises obtained by using the three different methods of adjusting data for net avoidance, or without any correction, were very similar (Table 3). Method 1, which was based on length-specific day:night catch ratio values calculated for *Engraulis mordax*, gave slightly greater values for larvae 4–6 mm, although differences were not statistically significant (overlapping confidence intervals).

Consequently, analyses of the residual sum of squares showed that the resulting mortality curves (Table 4) were not statistically different (1994: $F$= 0.361, $P$>0.5; 1995: $F$=0.780, $P$>0.5).

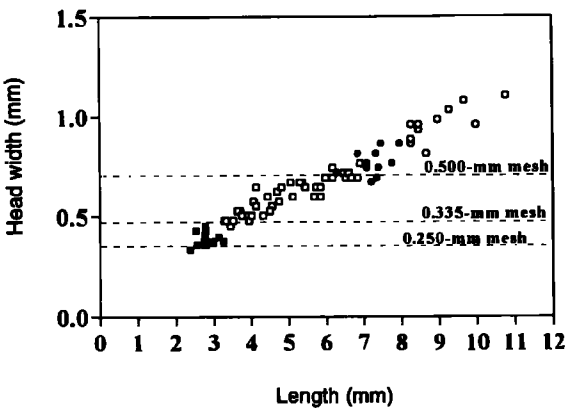


**Figure 3**

Relation between standard length and maximum head width for larval anchovy. The horizontal broken lines indicate the mesh diagonals of 0.500-, 0.335-, and 0.250-mm nets. Solid squares = yolksac larvae. Open squares = preflexion larvae. Solid circles = flexion larvae. Open circles = postflexion larvae.

## Discussion

### Retention of larvae

The results of this study indicate that the "diagonal rule" (maximum head width being considered as the maximum cross-sectional diameter of the larva) may adequately "predict" retention of anchovy larvae in the 0.500-mm mesh net but appears to be conservative in the case of the 0.335-mm mesh net. Specifically, yolksac larvae have a smaller head width than the diagonal of the 0.335-mm mesh net, but the latter seems to fully

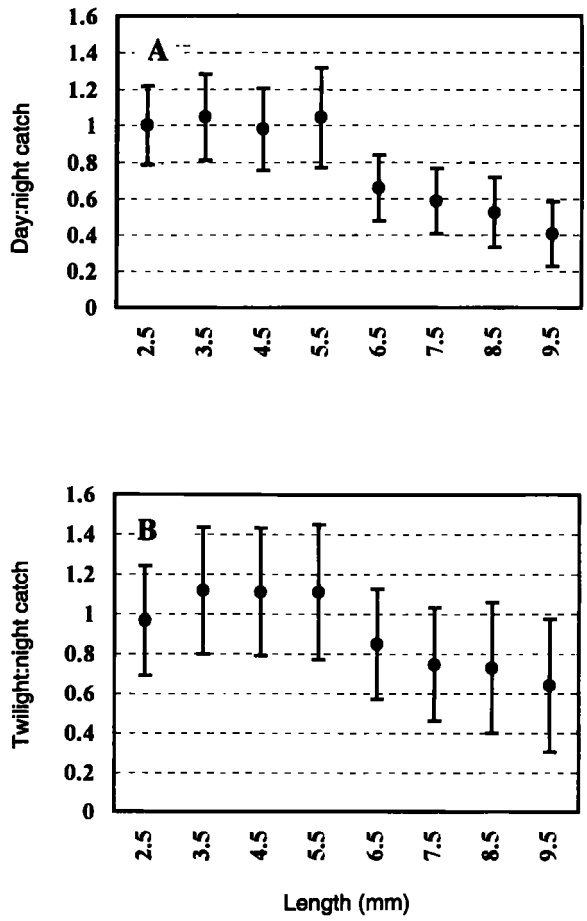


**Figure 4**

Day:night (**A**) and twilight:night (**B**) catch ratios as a function of larval length. Bars indicate 95% confidence intervals.

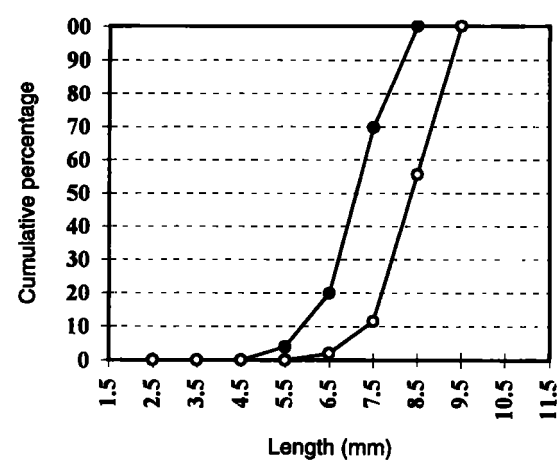


**Figure 5**

Cumulative percentages of flexion (solid circles) and postflexion larvae (open circles) as a function of larval length.

retain them. This is attributable to the fact that maximum head width is not the maximum cross-sectional diameter of the larva, because of the bulk of the yolk sac. Our method of towing (at low speed, with plastic codend buckets) did not seem to cause damage to yolk sacs and resulted in full retention of yolksac larvae by the 0.335-mm mesh. However, the degree of extrusion strongly depends on filtration velocity (Smith and Richardson, 1977; Colton et al., 1980). Thus, at high towing speeds yolk sacs may easily be crushed.

In his study on anchovy, Lenarz (1972) used depth of body at the insertion of the pectoral fin as the critical dimension to compare with mesh diagonal and concluded that the mesh "diagonal rule" was too conservative in the case of slowly towed nylon nets. However, body depth is not the critical dimension for clupeoids (Colton et al., 1980). The latter found no differences related to mesh size (0.253- and 0.333-mm mesh nets) in the length frequency distributions and abundances of larval herring in their collections at 1.5-knot towing speed. The mesh "diagonal rule" (with skull width as the critical dimension) was also conservative in their case, but for the length interval including only yolksac larvae. They found that most yolksac larvae caught in their slowly towed bongo nets, which were also equipped with plastic codend buckets, were undamaged.

We feel that at a low, constant towing speed (1.5–2.0 knots), bongo nets equipped with a 0.335-mm mesh net and plastic codend buckets are very efficient in retaining larvae of clupeoids.

## Net avoidance

Changes in catchability with varying light conditions and larval length are demonstrated in this study. These changes begin at notochord flexion. If visual detection of the net is the primary cue for net avoidance, flexion and postflexion European anchovy larvae show the expected relationship of night>twilight> day catches (Morse, 1989).

In another study, Murphy and Clutter (1972) compared catches of larval Hawaiian anchovy (*Stolephorus purpureus*) taken by conventional towed conical nets with catches taken by a miniature purse seine constructed of the same netting. The latter was considered to be a more effective sampler of the full size range of anchovy larvae than towed nets. In a way similar to the present study, larvae <6 mm long were captured with approximately equal efficiency by both the towed net and the seine (i.e. these larvae did not seem to avoid the towed net). For larger lar-

**Table 3**

Estimates of length-specific larval production for the 1994 and 1995 cruises (and their standard errors in parentheses) with different methods of adjusting data for net avoidance. Method 1 is based on day:night catch ratio values available for *Engraulis mordax*, and methods 2 and 3 are based on day:night and twilight:night values calculated in the present study (see text for details).

| | | Length (mm) | | | | | |
|---|---|---|---|---|---|---|---|
| Cruise | Correction | 4.5 | 5.5 | 6.5 | 7.5 | 8.5 | 9.5 |
| 1994 | none | 1.984 (0.198) | 1.655 (0.198) | 1.169 (0.139) | 0.893 (0.127) | 0.518 (0.110) | 0.413 (0.093) |
| | method 1 | 2.142 (0.214) | 1.793 (0.212) | 1.281 (0.152) | 0.972 (0.138) | 0.569 (0.121) | 0.450 (0.102) |
| | method 2 | 1.984 (0.198) | 1.655 (0.198) | 1.231 (0.146) | 0.944 (0.134) | 0.553 (0.118) | 0.445 (0.101) |
| | method 3 | 1.984 (0.198) | 1.655 (0.198) | 1.258 (0.150) | 0.979 (0.140) | 0.573 (0.122) | 0.475 (0.109) |
| 1995 | none | 1.537 (0.111) | 1.235 (0.090) | 0.928 (0.080) | 0.690 (0.071) | 0.472 (0.052) | 0.341 (0.046) |
| | method 1 | 1.721 (0.029) | 1.409 (0.015) | 1.076 (0.058) | 0.722 (0.045) | 0.559 (0.046) | 0.399 (0.047) |
| | method 2 | 1.537 (0.111) | 1.235 (0.090) | 1.009 (0.086) | 0.681 (0.062) | 0.531 (0.057) | 0.390 (0.051) |
| | method 3 | 1.537 (0.111) | 1.235 (0.090) | 1.026 (0.087) | 0.706 (0.064) | 0.549 (0.059) | 0.412 (0.054) |

vae, the efficiency of the towed net decreased with larval length relative to the seine.

The change in catchability at flexion, observed in our study, can be attributed to a change in the swimming ability of larvae, which is associated with flexion. Batty (1984) found that Atlantic herring larvae, as they grow, change from an anguilliform mode of swimming to a subcarangiform mode of swimming. This change of swimming mode occurs as the caudal fin develops (at a body length of about 22 mm). Subsequently, Heath and Dunn (1990) using the large (5 $m^2$), high-speed LOCHNESS sampler, found that the day:night catch differential increased with body length for larval herring in the North Sea, with a maximum fivefold difference between day and night catches for larvae >25mm. In another study, Osse and van den Boogaart (1995) reported results similar to those of Batty (1984) for common carp (*Cyprinus carpio*). The morphological differentiation of the caudal fin, which begins at flexion and is accompanied by ossification of the caudal-fin rays and the caudal part of the notochord, closely parallels a change in the swimming mode from anguilliform to carangiform. Burst-speed capability, which is believed to determine, in part, the ability of a larva to avoid plankton nets (Hunter, 1976), might also change with the development of the tail.

**Table 4**

Estimated parameters of the exponential mortality models ($P_t=P_0\exp(-zt)$) for the 1994 and 1995 cruises. A different model was fitted for each different method of adjusting data for net avoidance (see text for details). $r^2$ = coefficient of determination.

| Cruise | Correction | $P_0$ | $z$ | $r^2$ |
|---|---|---|---|---|
| 1994 | none | 2.931 | 0.143 | 0.980 |
| | method 1 | 3.156 | 0.142 | 0.979 |
| | method 2 | 2.872 | 0.135 | 0.979 |
| | method 3 | 2.832 | 0.131 | 0.978 |
| 1995 | none | 2.195 | 0.136 | 0.992 |
| | method 1 | 2.463 | 0.135 | 0.989 |
| | method 2 | 2.139 | 0.126 | 0.989 |
| | method 3 | 2.109 | 0.121 | 0.989 |

Alternatively, changes in catchability may have a behavioral component. A substantial change in day:night catches of northern anchovy (*Engraulis mordax*) with bongo nets occurs at approximately 11 mm (Fig. 2 in Hewitt and Methot, 1982). Flexion in this species occurs at around 11 mm (Watson and Sandknop, 1996). Laboratory and field studies (Hunter and Sanchez, 1976; Hewitt, 1981; Hunter

and Coyne, 1982) have shown that, at about 11 mm, swimbladder inflation and schooling begins, whereupon patchiness increases rapidly. Our field observations of European anchovy indicate initiation of swimbladder inflation at flexion. It is therefore possible that schooling behavior also begins during this stage in *E. encrasicolus*.

School formation during the day and dispersion of schools during the night could result in low day:night catches for two main reasons: 1) larvae are less vulnerable to plankton nets when in a school than when reacting individually, owing to the reduction in the reaction distance of the organisms in the school to the approaching net; and 2) increased patchiness resulting from schooling during the day produces a larger number of negative tows.

In summary, field data on the European anchovy suggest the existence of an ontogenetic change in catchability with slowly towed plankton nets, which can be attributed to a respective change in the swimming ability, or a change in behavior (i.e. onset of schooling), or both.

To our knowledge, the present study is the first to examine retention and catchability in a larval fish not only in terms of length but also of ontogeny. Surprisingly, this study also shows that, when sampling is undertaken on a 24-h basis, bias that results from light-induced avoidance of the net may not be great enough to affect significantly estimates of daily larval production or larval mortality. However, when only daytime sampling is undertaken, mean catches of postflexion larvae may well be biased and correction factors may have to be applied.

Size selectivity due to net avoidance by larvae is expected to lead to an overestimation of mortality rate, because older larvae are underrepresented in relation to younger larvae. In a recent simulation study, Somerton and Kobayashi (1992) have shown that approaches usually taken to eliminate the selection bias from sampled length frequencies (i.e. division of sampled length frequencies by length-specific estimates of capture probability or elimination of the biased portion of the length distribution) may be only partially effective in reducing the bias in estimated mortality rates. The latter, as well as the present paper, suggests that the effectiveness of methods that attempt to correct for net avoidance is largely unknown. Their effectiveness has to be fully addressed.

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