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Distribution, stock structure, and growth of the squid *Berryteuthis magister* (Berry, 1913) (Cephalopoda, Gonatidae) during summer and fall in the western Bering Sea

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Abstract.—Distribution, abundance, and length-frequency composition of schoolmaster gonate squid, *Berryteuthis magister*, were studied during seven trawl surveys in the western Bering Sea between June and November 1993. Statolith age analysis was undertaken for 1,381 *B. magister* to estimate age, stock structure, and both growth and maturation rates. Three kinds of growth increments were revealed in *B. magister* statoliths. Daily periodicity of the second-order increments was confirmed by two independent, indirect methods. According to our data, *B. magister* live >1 yr; the oldest specimen was about 16 months old. *Berryteuthis magister* is a slow-growing and slow-maturing squid, and males exhibit slower growth and earlier maturation than do females. Growth in length was best described by a logistic curve, with a larger asymptotic parameter for females. In summer, concentrations of *B. magister* were low within the whole region, whereas in September–October squids aggregated into dense shoals over the continental slope of the Navarin–Olyutorsky region and Olyutorsky Bay. Stock structure of *B. magister* was complicated: each month, from 5 to 12 (usually 7–8) monthly classes of squid were encountered in the western Bering Sea. Three seasonal groups of *B. magister* occurred in the region: winter-, summer- and fall-hatched squids utilizing resources of the continental slope in different ways. A possible life cycle for the *B. magister* fall-hatched group includes a longevity of ca. 2 yr: 6 mo of embryonic development and 18 mo of postembryonic growth.

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The schoolmaster gonate squid, *Berryteuthis magister* (Berry, 1913), is an abundant near-bottom species occurring over the continental slopes in the North Pacific from southern Japan, the Sea of Okhotsk, and the Kurile Islands to the northwestern coast of the United States (Roper et al., 1984; Nesis, 1987). This species is one of the important fishery resources in the North Pacific. It is captured mainly by Russian trawlers around the Kurile Islands, in the Sea of Okhotsk, and in the western Bering Sea with an annual catch of 30,000–60,000 metric tons (t) (Fedorets, 1986a). In Japan, *B. magister* is taken seasonally by the coastal fishery and yields an annual catch of 5,000–9,000 t (Kasahara et al., 1978).

Some aspects of the distribution, reproductive biology, and growth of *B. magister* have been investigated in the Sea of Japan (Naito et al., 1977; Kasahara et al., 1978; Nazumi et al., 1979), where spawning occurs from December to May (with a peak between February and March). With the use of length-frequency analysis, the life cycle of *B. magister* was estimated to be 2 years or more, and growth of both sexes was approximated with a logistic function (Yuuki and Kitazawa, 1986). Natsukari et al. (1993) used statolith ageing techniques for age and growth analysis of *B. magister* captured in Kitamiyamato and Rebun Banks and suggested a longevity of four years, with females attaining a larger size than males at any given age.

Patterns of vertical and spatial distribution of *B. magister* juveniles and adults were analyzed in the Sea of Okhotsk and waters of the Kurile Islands (Railko, 1983; Alexeev and Bizikov, 1986; Nesis, 1989). Preliminary data on age were obtained by comparing increment number between statoliths and gladii in five immature specimens with mantle lengths ranging from 220 to 250

mm. The age of these individuals was estimated to be less than one year (Arkhipkin and Bizikov, 1991). Feeding, shoal, and escaping behaviors have also been examined from manned submersibles (Alexeev et al., 1989).

The first studies on *B. magister* biology in the Bering Sea appeared in the seventies (Shevtsov, 1974; Fedorets, 1977, 1979). During the next decade, investigations were focused on distribution and stock dynamics (Fedorets, 1986a), feeding rhythms (Fedorets, 1986b; Kuznetsova and Fedorets, 1987), gametogenesis, fecundity, and spawning (Reznik, 1982; Fedorets and Kozlova, 1986). *B. magister* was common along the continental slope of the Bering Sea at depths varying from 100 to 1,500 m. In the western Bering Sea, and near the Commander and Aleutian Islands, dense seasonal aggregations formed at depths ranging from 300 to 500 m. According to Fedorets and Kozlova (1986), spawning occurred near the Commander Islands in winter and in the northwestern part of the Bering Sea in summer. Hatchlings were hypothesized to be transported by currents into the Bering Sea and Kurile Islands region. Total stock size in the Bering Sea was estimated to be about 350,000 t (Fedorets, 1986a).

Research has been carried out on the presence of intraspecific groupings of *B. magister* in the Sea of Okhotsk (Nesis and Nezlin, 1993). However, genetic studies on protein variability have revealed a high polymorphism and heterozygosity without any significant differences within the species range (Katugin, 1991, 1993).

In contrast to a relatively good understanding of distribution, reproductive biology, and genetic variability, the growth and age-length dynamics of *B. magister* in the Bering Sea remain unknown. The present paper describes distribution, length frequency, stock-structure dynamics, and age and growth of *B. magister* in the western Bering Sea by using statolith and gladius ageing techniques.

Materials and methods

Data were collected on *B. magister* during seven trawl surveys in the western Bering Sea (lat. 59°30'N–61°30'N; long. 166° 00'E–179°30'W) by three Japanese trawlers: *Tenyu-Maru N 57, Kaiyo-Maru N 28*, and *Kashima-Maru N 8* between June and November 1993. Each survey was carried out during the first 10–11 days of each month and consisted of 12 transects (Fig. 1). Additional surveys were performed in the second half of June and November. On each transect, three near-bottom trawls were made at depths of 170–250 m, 370–450 m, and 600–750 m. Trawls were conducted with the standard Japanese

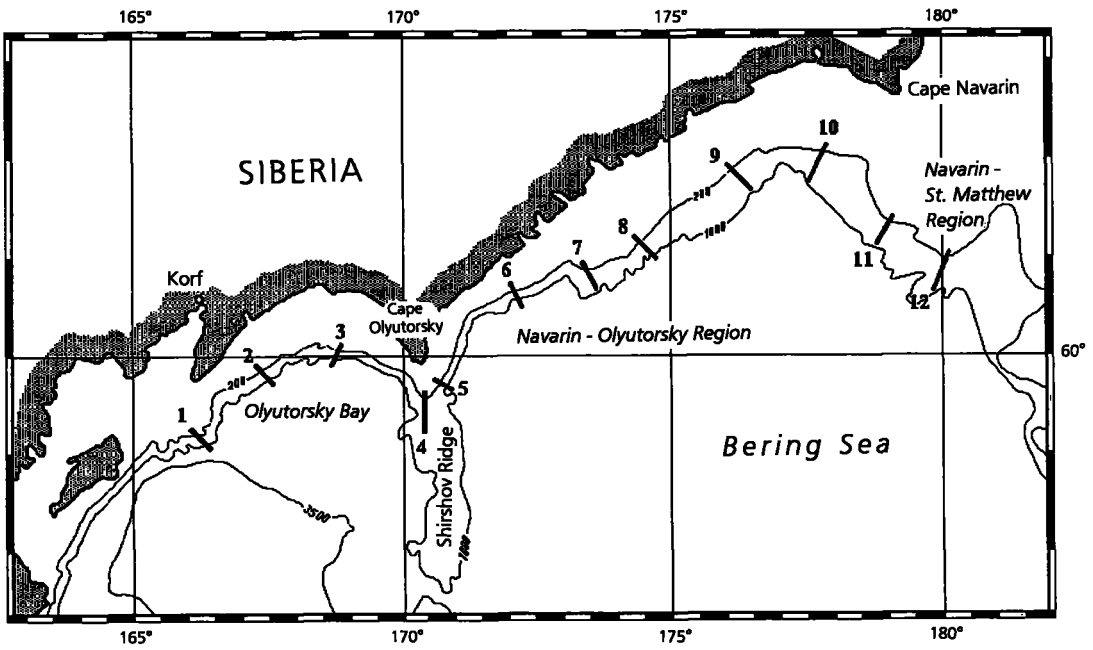

Figure 1

Location of the twelve transects of the scientific survey on *Berryteuthis magister* in the western Bering Sea.

pelagic trawl "Suketodara" with horizontal opening of 75 m, vertical opening of 20 m, and a 70-mm mesh size at the codend. The duration of each trawl was about one hour and the average speed of each trawl was 6.5–7.8 km·h^{-1}.

Length-frequency sampling

A total of 23,765 squids were analyzed during the expeditions, including 3,533 juveniles. A random sample of one hundred specimens was taken from each catch. If the number of squid in a given catch was less than 100, the entire squid catch was examined. Dorsal mantle length (ML) was measured to the nearest 1 mm and total body weight (BW) weighed to the nearest 1 g (during periods of calm sea only). Sex and maturity stage were identified according to the maturity scale for *Illex argentinus* (Nigmatullin, 1989). Evidence of mating and indices of stomach contents (fullness) were examined according to the methods of Zuev et al. (1985). The sex ratio was also determined. Because sex can be determined by eye only in squid >120 mm ML, all individuals <120 mm ML were considered juveniles and analyzed separately from males and females. Because juveniles were taken from the mesh of the trawl wings, we could not precisely estimate their abundance and occurrence.

For each sample, four length-frequency curves for each sex were constructed for the following ontogenetic periods: immature (maturity stages 1–2), maturing (maturity stages 3–4), mature (maturity stage 5), and spent (maturity stage 6). After preliminary analysis of the samples, length frequencies of all the catches taken within a given month were pooled together for each maturity period and for the three regions: Olyutorsky Bay, and both Navarin–Olyutorsky and Navarin–St. Matthew regions (Fig. 1).

Age sampling

Every month from June to October, statoliths were removed from one hundred randomly sampled individuals of *B. magister* from one successful catch (>100 kg). In addition, statoliths were dissected from 50 juveniles and from specimens of uncommon sizes and maturity stages (i.e. large-size males and females and spent animals) that were not found in the sample but occasionally occurred in other catches within each month. Statoliths were sampled and analyzed separately in two regions: Olyutorsky Bay and the central part of the Navarin–Olyutorsky region. In June and October, statoliths were taken from two samples from the first and second halves of each month. A total of 1,453 statoliths were collected, washed in distilled water, and stored in oil-paper envelopes in 96% ethanol.

In June and July, 87 gladii and pairs of statoliths were dissected from the same specimens for a comparison of the number of growth increments between ageing structures.

Statolith ageing analysis

From a total of 1,453 statoliths, 740 were processed and read by two of the authors (AIA and VAB) aboard the *Tenyu-Maru N 57*; the rest were analyzed in the Laboratory of Commercial Invertebrates of AtlantNIRO by AIA. From the entire sample, 1,381 (95.1%) statoliths were successfully read. Statolith processing was rather time consuming because sizes (especially in adults) were unusually large: total statolith length (STL) ranged from 2.5 to 3.2 mm. Statolith terminology followed Clarke (1978) and Lipinski et al. (1991).

Statoliths were processed according to standard techniques (Arkhipkin and Murzov, 1985) with minor modifications. They were ground (on 600 grit) and polished (on 1,000 grit) wet waterproof sandpaper. Because the direction of the maximum growth within statoliths changed during ontogenesis, it was necessary to grind the convex side of the same statolith in two planes: one plane running through the lateral and dorsal domes and spur, and the other plane running through the spur and along the central axis of the rostrum. This method of grinding exposes the growth increments lying immediately below the wing. The ground statolith was not flat and thin as in Natsukari et al. (1993) but thickened in the region of the lower part of the lateral dome and the proximal part of the rostrum. This feature allowed all increments from the nucleus to the most distal part of the rostrum to be unambiguously resolved.

Ground statoliths were embedded in glycerin and covered with glass for immediate reading. Statoliths were read under a Biolam R14 light microscope with 450–500× magnification. Growth increments were counted from the nucleus to the distal part of the rostrum and from farther within the rostrum as described by Natsukari et al. (1993) by using the eyepiece (as described in Dawe and Natsukari, 1991). To avoid possible counting errors, each statolith was counted at least twice by two observers, and if the difference between readings was less than 5%, squid age was taken as the mean of these counts. Readings were made only after achievement of the maximum resolution of growth increments with fine-adjustment focusing. Because the periodicity of different types of growth increments was unknown for the northern populations of *B. magister*, their number was calculated separately for each type.

Gladius ageing analysis

A total of 87 gladii were extracted from squid captured from the Navarin–Olyutorsky region during June and July. The gladii were processed according to the techniques elaborated by Bizikov (1991). Each gladius was dissected from the animal through the dorsal section of the mantle, then washed carefully with warm soapy water, labeled, and stored in 6% formaldehyde. The periodic laminae were counted in the cross sections of the inner shell layer of the gladius by using the same microscope (100–200×) as that used for statoliths. The sections were made at the area of greatest thickness of the gladius inner layer, near the ventral anterior margin of the conus. These sections were placed on slides with a drop of glycerine and covered with glass for viewing. In some intact gladii, periodic laminae on the dorsal plate (proostracum) were analyzed by using a zoom microscope under reflected light (32–56× magnification).

Validation of the periodicity of increment formation within ageing structures

Two indirect methods were applied for validation of the periodicity of statoliths and gladii increment formation. The first involved comparison of increment number in both gladius and statoliths taken from the same specimen (Arkhipkin and Bizikov, 1991). The second method included a comparison of the difference between the mean number of statolith increments from the modal groups of two successive samples with the number of days elapsed between these samples (Uozumi and Ohara, 1993; Uozumi and Shiba, 1993). To analyze both relationships, a predictive regression model was applied (Ricker, 1973). The estimated values of slopes (SL) of both regressions were tested with the null hypothesis (SL=1) at the 0.05% level for SL by using the statistic $t = (SL-1)/SD$, where SD is a standard deviation of SL (Wesolowsky, 1976).

Age and growth parameters

Unfortunately, we had no opportunity to validate directly the periodicity of growth increments within statoliths and gladii. However, after examination of increment number and microstructure within statoliths taken from the same specimen and after comparison of these with daily growth increments in the statoliths of validated species (*Loligo opalescens*, Hixon and Villoch, 1984; *Illex illecebrosus*, Dawe et al., 1985; *Alloteuthis subulata*, Lipinski, 1986; *Sepioteuthis lessoniana*, Jackson, 1990; *Todarodes pacificus*, Nakamura and Sakurai, 1990), we assumed that growth increments were deposited daily (see the corresponding section in Results section). We considered the total number of increments beyond the "natal ring" (observed by Natsukari et al., 1993) to be the age of squid in days. Hatching dates were backcalculated. Month classes of hatching (further "month classes") were defined by the pooling of squid into each month of hatching.

Length-at-age data were analyzed separately for both sexes and hatching months. Monthly age structure in a given region was defined by routine procedures of age-length key construction. For more precise construction of age-length keys, we determined the numbers of squid of each month class separately for each sex and maturity period (Table 1A). With these keys, month-class compositions in each month were estimated from the monthly length-frequency compositions (Table 1B). The similarity of age structures observed in different months was estimated by applying a coefficient of similarity (as %, 0% as absolute difference, and 100% as absolute resemblance) elaborated by Shorygin (1952) during studies of fish food spectra.

The relatively short period of investigation in this study did not permit the resolution of ontogenetic growth curves for each hatching month of squid. However, it was possible to construct a growth curve for the species by pooling the individual age-at-length data over various hatching months. Curves (logistic, Gompertz, and von Bertalanffy) were fitted to the age-at-length data by using the method of iterative nonlinear least squares. As a result, the values of ML were calculated by using the formula of the best fitted curve. Unfortunately, pitching and rolling of the vessel during frequently occurring storms prevented us from weighing precisely almost half of the specimens analyzed, especially small-size ones. For investigation of growth in weight, we constructed at first length-weight curves for both sexes, and then calculated age-weight curves. Daily growth rates in length or weight (DGR; mm or g per day) and instantaneous growth rates (G) were calculated after Ricker (1958) as

$$DGR = (M_2 - M_1)/T$$

and

$$G = (\ln M_2 - \ln M_1)/T,$$

where M_1 and M_2 are mantle length (mm) or weight (g) at the beginning and end of a time interval (T=30 days).

Results

Distribution and abundance

Berryteuthis magister occurred in most trawl catches along the continental slope of the western Bering Sea

Table 1

An example of "raw" and calculated age-length key for *B. magister* females trawled in the Navarin–Olyutorsky region in August (n=87; N=253). Maturity state: imm = immature; ming = maturing; and mat = mature. FD = frequency distribution, as a percentage.

A Number of specimens observed with respect to the month class (raw age-length key)

ML interval (cm)	Maturity state	Month class (month of hatching)									Number of aged squid	FD of age sample
		Jan	Feb	Jun	Jul	Aug	Sep	Oct	Nov	Dec		
13–14	imm	3	1							1	5	5.75
15–17	imm		1							1	2	2.30
	ming										0	0
18–20	imm							1	3	3	7	8.05
	ming									1	1	1.15
	mat										0	0
21–23	imm								8	2	10	11.49
	ming					1	3	2			6	6.90
	mat										0	0
	spent					1					1	1.15
24–26	imm								2		2	2.30
	ming				1	3	13	6			23	26.44
	mat				1	2		1			4	4.60
	spent			1	3	2					6	6.90
27–29	imm										0	0
	ming				1	3	4	2			10	11.49
	mat							1			1	1.15
	spent							1			1	1.15
30–32	ming					1		1			2	2.30
	mat					1	1				2	2.30
	spent				1						1	1.15
33–35	ming										0	0
	mat				1	2					3	3.45
	spent										0	0
Total		3	2	1	8	16	21	15	13	8	87	100
Percent		3.45	2.30	1.15	9.20	18.39	24.14	17.24	14.94	9.20	100	

(Fig. 2). Although spatial distribution varied greatly in different regions and seasons, vertical distribution showed the same general pattern throughout the entire period of study. During the day, squid occurred near bottom at depths ranging from 150 m to 800 m, with the greatest densities usually between 350 and 450 m. At night, *B. magister* was generally dispersed throughout the water column. Females always predominated over males, the sex ratio (males/females) varying from 0.6 to 0.8.

Olyutorsky Bay During June, July, and August, *B. magister* occurred in small numbers along the slope of Olyutorsky Bay and Shirshov Ridge with average catches <100 kg·h^{-1} at depths from 250 to 450 m. Local aggregations of mature squids (from 160 to 270 kg·h^{-1}) were found in the western part of Olyutorsky Bay and south of Cape Olyutorsky. Dense concentrations appeared in the eastern part of the Bay and Shirshov Ridge in September, reaching the highest values (1,100–1,400 kg·h^{-1}) in the first ten days of October. Later, smaller numbers of squid were observed and by the second half of November had decreased to 100 kg·h^{-1} or less.

Navarin–Olyutorsky region In June, density of *B. magister* shoals along the Navarin–Olyutorsky slope was low; average catches were around 50 kg·h^{-1}. A few large catches (up to 400 kg·h^{-1}) were taken in the eastern part of the region between 176°E and 177°E. From July to September, numbers of squids increased steadily and catches averaged 700–800 kg·h^{-1} by the end of September. The most dense aggregations (1,000 to 1,500 kg·h^{-1}) were captured at depths of 350–450 m between 172°E and 174°E in September and October. By the second half of November, catches of *B. magister* decreased rapidly to 90–100 kg·h^{-1}.

Navarin–St. Matthew region From June to August, catches of *B. magister* were very low (<50 kg·h^{-1}). Catches increased steadily during September and

Table 1 (continued)

B Calculated month-class–length key

ML interval (cm)	Maturity state	Month class (month of hatching) Jan	Feb	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Number of squid	FD of total sample
13–14	imm	0.47	0.16							0.16	2	0.79
15–17	imm		2.37							2.37	12	4.74
	ming										0	0
18–20	imm							1.30	3.90	3.90	23	9.04
	ming									0.40	1	0.4
	mat										0	0
21–23	imm								6.32	1.58	20	7.91
	ming					0.99	2.96	1.98			15	5.93
	mat										5	1.98
	spent					0.79					2	0.79
24–26	imm								0.79		2	0.79
	ming				1.50	4.40	19.44	8.97			87	34.39
	mat				3.06	6.13		3.06			31	12.25
	spent			0.40	1.19	0.79					6	2.37
27–29	imm										0	0
	ming				1.03	3.08	4.11	2.06			26	10.28
	mat							4.74			12	4.74
	spent							0.40			1	0.4
30–32	ming					0.40		0.40			2	0.79
	mat					0.40	0.40				2	0.79
	spent				0.40						1	0.4
33–35	ming										0	0
	mat				0.40	0.79					3	1.19
	spent										0	0
Total											253	100
Percentages of month classes in total sample		0.47	2.53	0.40	7.56	17.84	26.91	22.90	11.01	8.40		

reached 800–900 kg·h^{-1} in the first half of October. However, these aggregations quickly disappeared by the middle of November.

Length-frequency composition

Olyutorsky Bay In Olyutorsky Bay (Fig. 3), proportions of immature and maturing males gradually decreased from June to October, then expanded in November. Among males, mature males always predominated in catches. Their numbers increased steadily from June to October, then decreased slightly in November. The size range of mature males was wide (170–270 mm) and unimodal (210 mm), remaining invariable throughout the period of study. Spent males were rare; greatest numbers were observed in June (2–3%) and in November (2%).

Immature females were not abundant in June, very abundant in July (46%), then successively diminished to 11% in October and November. During summer, length distribution of immature females was bimodal; their modal sizes increased slightly from 190–200 mm and 220–230 mm in June to 200–210 mm and 230–240 mm in August. In fall, when the number of immature females was low, their length composition did not reveal well-defined modes. The proportion of maturing females increased steadily from June to September and decreased rapidly in October–November. Their length composition was unimodal, with modal lengths slightly increasing from June (230–240 mm) to September (240–260 mm).

Mature females were abundant in June. From July to September, their numbers diminished, then increased again in October. Length composition of mature females was always unimodal and wide (200–330 mm); their modal lengths remained constant between June and August (230–250 mm), then increased slightly in September–November (250–270 mm). Evidence of mating was observed in mature females as one or two bundles of spermatophores attached to the inner mantle surface near the gills. The number of mature females with evidence of mating grew from

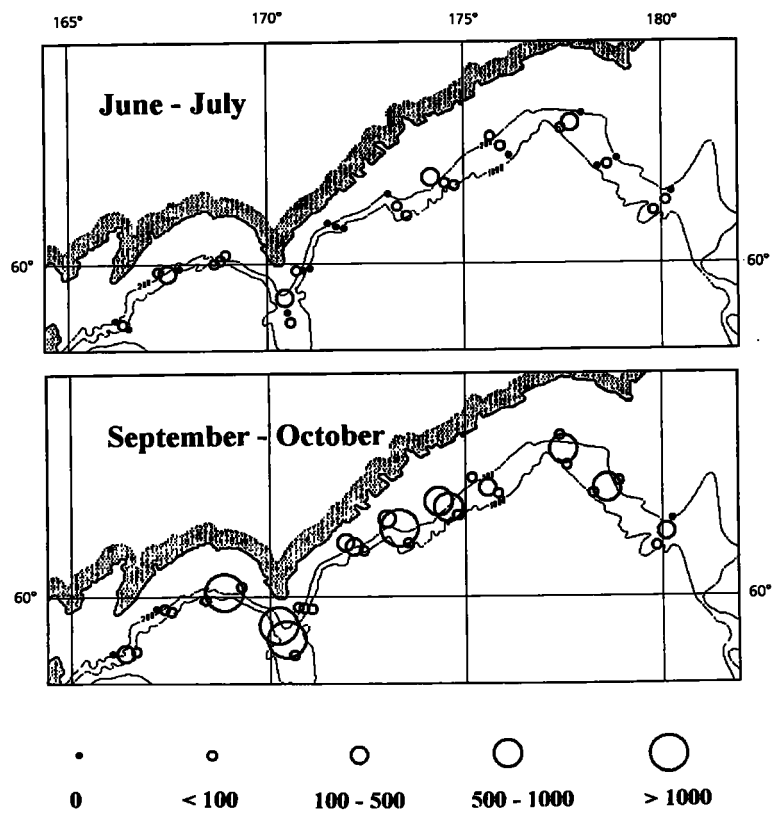

Figure 2

Distribution of *Berryteuthis magister* in the western Bering Sea, June–July and September–October 1993. Circles indicate trawl catches of squids ($kg \cdot h^{-1}$).

June (75%) to July–August (90%), then decreased abruptly in October (37%). Spent females appeared in July (1%). In August–October, their numbers were low, except for a few catches along the Shirshov Ridge. Spent females were most abundant in November (11–12%).

Juveniles were seldom caught from July to October. Their size range was wide (20–120 mm). Juvenile length composition was bimodal in summer and without well-expressed modes in fall.

Navarin–Olyutorsky region In the Navarin–Olyutorsky region (Fig. 4), proportions of immature and maturing males gradually decreased from June to August. During September and October, both groups almost vanished from catches (<2% each) and appeared again in November. Length composition of immature males was roughly unimodal (160–170 mm). Mantle length of the largest immature males never exceeded 200 mm. Length composition of maturing males was unimodal and wide (150–240 mm), with modes shifting slightly from June (170–180 mm) to October (190–200 mm).

Among males, mature animals always predominated in catches, with the greatest number in September and October (95%). The size range of mature males was wide (170–290 mm) and did not vary considerably from June to November. The size composition was distinctly unimodal (modal length was 210 mm during the entire period of study). The number of spent males was extremely low from June to October and increased slightly in November (3%). Their sizes always coincided with modal lengths of mature males.

Numbers of immature females decreased successively from June to September. In October, their proportion remained low, then expanded slightly in November. The size range of immature females was always wide, with largest individuals of about 280 mm ML. Length composition had two modes in June (180–190 mm and 220–230 mm), and three in July (130 mm; 190–200 mm; and 240 mm). In August, only one very broad mode was traced among this group (190–240 cm). From September to November, length composition of immature females had no clear modes.

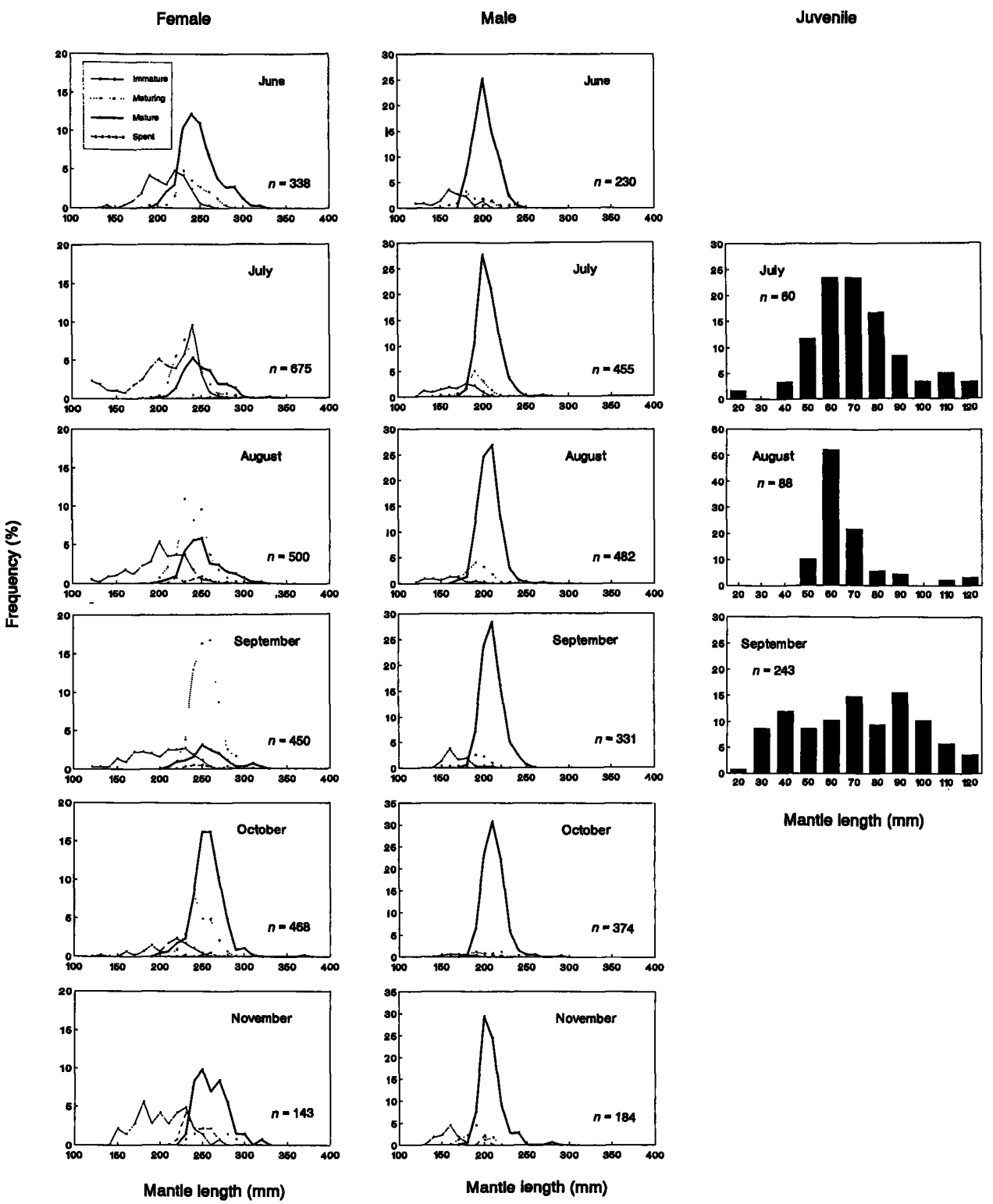

Figure 3

Length composition of *Berryteuthis magister* in the Olyutorsky Bay, June–November 1993.

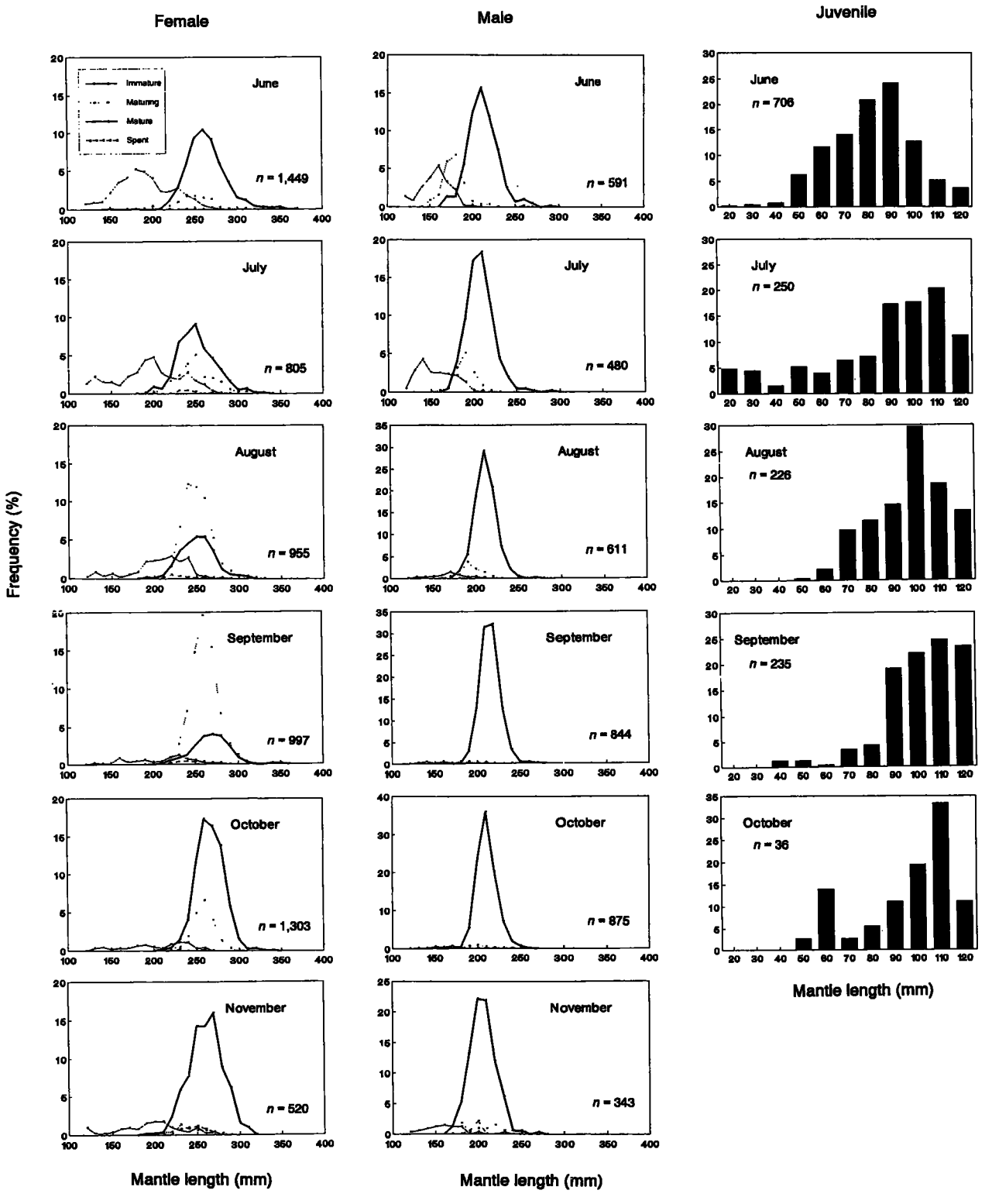

Figure 4

Length composition of *Berryteuthis magister* in the Navarin–Olyutorsky region, June–November 1993.

The proportion of maturing females increased during the summer; this group predominated in catches (70%) in August–September. In October, maturing females decreased rapidly in numbers and almost disappeared in November. Their size range gradually narrowed from 170–320 mm in June to 210–280 mm in November. The length composition of maturing females was unimodal. Their modal classes remained constant (240–250 mm) from June to August, then increased slightly to 260 mm in September–October.

Mature females were predominant among females in June (53%). Subsequently their numbers decreased constantly until September (20%), then increased abruptly in October–November (70%). Length composition of mature females was always unimodal and wide (180–370 mm). Their modal lengths did not change from June to August (250–260 mm), but increased slightly in September–November (260–270 mm). The proportion of mature females that had mated was very high during June–August (86–90%), then diminished considerably by the beginning of October (34%). The numbers of spent females were low from June to September (<2%). In October, they almost vanished from catches, appearing again in November (5%). Their size range was wide (220–330 mm) with an indistinct mode at 240–250 mm.

Juvenile abundance was greatest in June–July and diminished successively until November. The length composition for this group varied greatly throughout the period of study, with one distinct modal size in June (80–90 mm), two in July (30 mm and 70 mm), one in August and September (100 mm and 110 mm, respectively), and two in October (60 mm and 119 mm).

Navarin–St. Matthew region In the Navarin–St. Matthew region (Fig. 5), immature and maturing males were most abundant in June (22% and 44%, respectively). They decreased progressively in number from July to September and almost disappeared in October (about 3% each). The largest immature specimens were 190–200 mm ML. Their size composition was unimodal (160–170 mm) and constant throughout the study. The size range of maturing males was narrow (150–220 mm). Their length distribution was unimodal, the modes shifting slightly from 170–180 mm in June–July to 190–200 mm in September–October.

The percentage of mature males steadily increased from June (35%) to September (60%). In October, almost all males were mature (92%). The size range of mature males was wide in June–July (160–290 mm) and narrowed slightly in October (170–260 mm). Their length composition was unimodal (200–210 mm) throughout the study. Spent males appeared in August and represented about 4% of all males in September.

Immature females predominated in June–July (70–75%), then decreased abruptly in August (10%) and remained at this level until October. Size of the largest immature females diminished from 280 mm in June to 250 mm in October. Length composition was distinctly unimodal, the modes increasing from June (180–190 mm) to October (220–230 mm). The percentage of maturing females expanded from June (12%) to September (38%), but in October this group almost disappeared. Mantle length of maturing females ranged from 160 mm to 330 mm. Their length composition was unimodal (250–260 mm).

Numbers of mature females decreased from June (23%) to July (8%), later increased gradually until October (83%). Mantle-length range for mature females was wide in June (200–370 mm) and slightly narrower in October (200–320 mm). Length distribution was roughly unimodal at 260–270 mm. The proportion of mature females that had mated was high in summer (70–80%), then decreased abruptly in September (30–40%). A few spent females were encountered in this region, with mantle lengths largest in June (250–290 mm) and smallest in October (200–250 mm).

Juveniles were very abundant in June. In summer, they gradually decreased in numbers and almost disappeared by October. The minimum length of juveniles increased from 20 mm in June–July to 50–60 mm in September. Their length composition was unimodal; modal lengths increased from June (60–70 mm) to September (110–120 mm).

Gladius microstructure

The gladius of *B. magister* exhibits the typical oegopsid plane in structure (Arkhipkin and Bizikov, 1991; Bizikov, 1991) and is composed of three layers: the middle layer, forming the rigid chitinous frame of the gladius; the inner layer, filling the conus inside and forming a thick cartilaginous layer on the ventral surface in the posterior part of the gladius; and the outer layer, which is reduced to a film-like pellicle covering the conus.

Microstructure of the inner layer A cross section of the anterior part of the conus has the shape of a broad isosceles triangle, the inner layer filling the entire space between the dorsal and lateral walls of the conus (Fig. 6A). Regular laminae were observed on sections within the inner layer. In contrast to statoliths, no distinct growth zones were visible on the

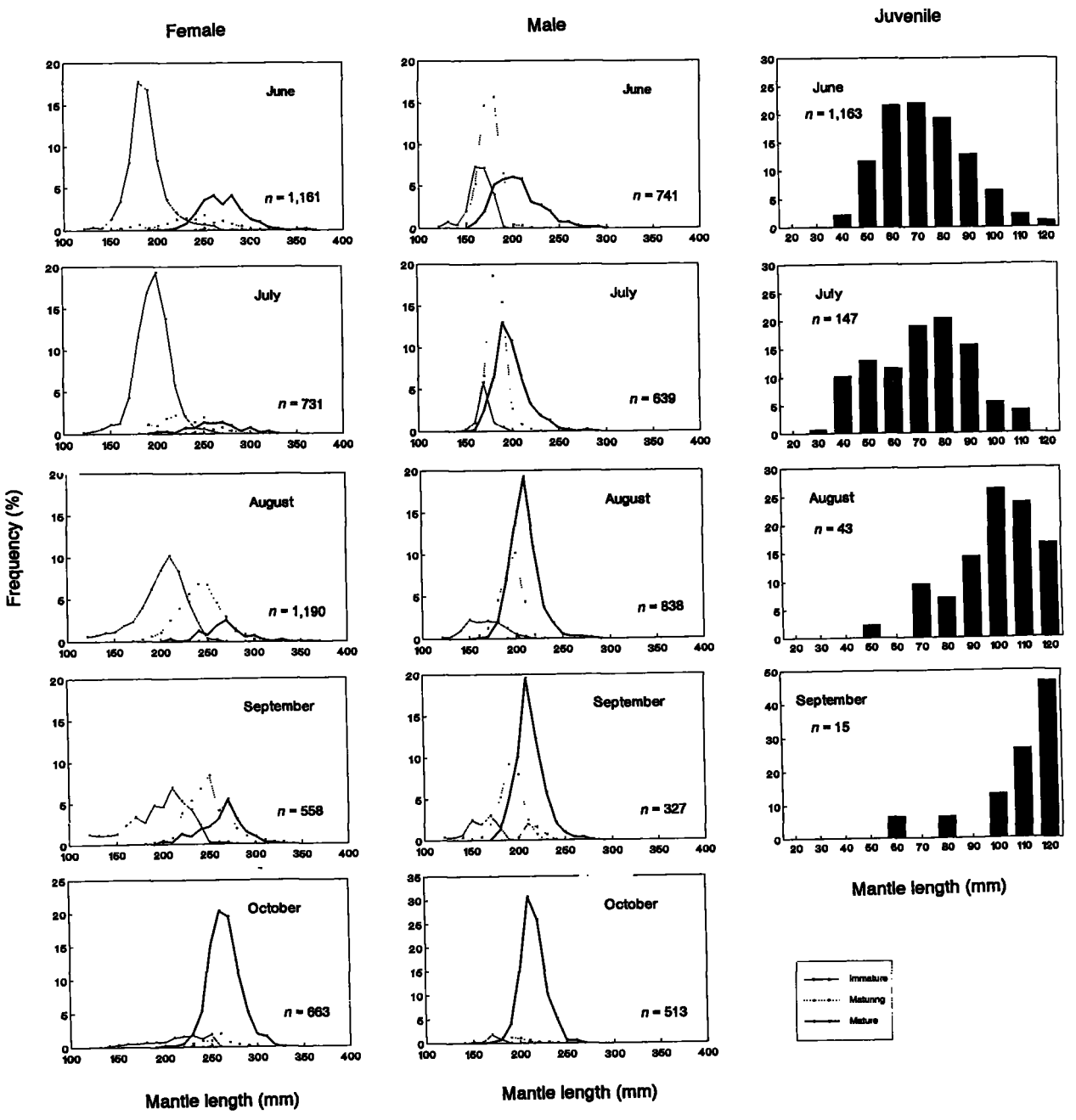

Figure 5

Length composition of *Berryteuthis magister* in the Navarin–St. Matthew region, June–October 1993.

sections. Laminae were rather quite uniform from the dorsal apex to the broad ventral side. Each lamina consisted of a broad translucent layer and a narrow dark layer. Counting of laminae commenced from the border between the middle and the inner shell layers in the dorsal apex of the section. The width of laminae varied greatly along the section. The first 35–45 laminae in the dorsal angle of the section usually were narrow: (ca. 3.0–4.0 μm, Fig. 6B). The middle part of the sections was formed by wide, uniform laminae (ca. 7–9 μm, Fig. 6C), and the last 20–30 peripheral laminae narrowed to 4–5 μm (Fig. 6D).

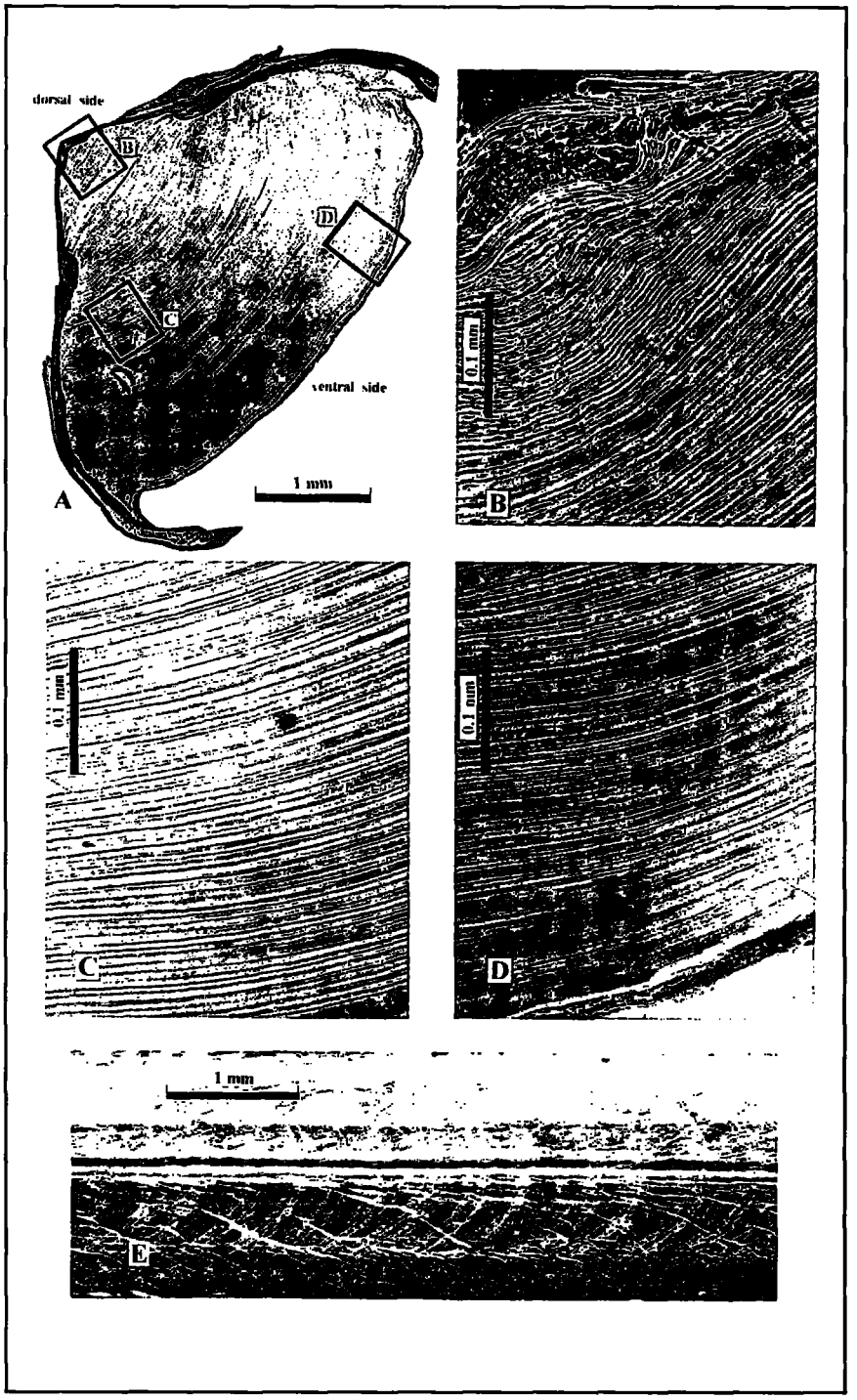

Figure 6

Microstructure of the gladius of *Berryteuthis magister* (light micrographs). (**A**) General view of a transverse cross section through the anterior part of the conus (mature male, ML 242 mm); (**B–D**) magnified views of the areas outlined by rectangles B–D in panel A; (**E**) increments of the middle layer visible on the dorsal surface of the gladius proostracum in reflected light (immature female, ML 273 mm; micrograph taken at 190 mm from the posterior end of the galdius).

Microstructure of the middle layer Laminae were visible as faint microstructural ridges on the dorsal surface of the proostracum (Fig. 6E). Each lamina consisted of a broad growth layer with a rather smooth surface confined by a narrow layer with a convoluted surface. Average width of laminae varied (depending on squid size) from 0.4–0.5 mm at 50 mm ML to 0.7–0.9 mm at 250–300 mm ML. In most specimens the laminae were best resolved in the middle part of the gladius. The general illegibility of laminae in the proostracum made it impossible to calculate individual growth rates with this gladius structure.

Statolith microstructure

Growth increments were observed in all statolith preparations. The nucleus was oval-shaped and had a maximum diameter of 40–45 μm along the rostrum axis (Fig. 7). The postnuclear zone lay beyond the nucleus; its color resembled that of the dark and peripheral zones. Approximately 10–12 narrow and rather uniform increments were observed within the postnuclear zone, each with a maximum width of 4.3–6.5 μm. Maximum radius of the postnuclear zone was 65–75 μm. The postnuclear zone was separated from the dark zone by the first prominent growth increment which was assumed (after Natsukari et al., 1993) to be the "natal ring." Within the dark zone and sometimes in the peripheral zone, three types of growth increments were revealed. The first-order growth increments occurred mainly within the inner part of the dark zone. They were very narrow (ca. 1–1.2 μm) and faint, corresponding to the "fine rings" of Natsukari et al. (1993). However, they could not be seen in all statolith preparations, especially within the outer part of the dark zone and in the peripheral zone. The second-order growth increments (corresponding to the "heavy rings" of Natsukari et al., 1993) were prominent and seen both in the dark and peripheral zones. Their width varied from 4.7–7.1 μm in the inner portion of the dark zone in the direction of the lateral dome to 9.5–12.2 μm in the proximal portion of the rostrum, from 3.5 to 4.3 μm in the midpart of the rostrum, and from 4.7 to 5.4 μm in the distal portion of the rostrum. Usually 4–6 first-order growth increments were observed within each second-order increment in the inner portion of the dark zone, and 3 or 4 increments within the peripheral zone (if they were present). In both the middle and distal portion of the rostrum, second-order increments were grouped within third-order increments: 4–7 second-order growth increments in each third-order increment. These third-order growth increments were not noted in Natsukari et al. (1993).

Validation of statolith growth increments

The presence of three different types of growth increments within statoliths prevented us from assuming that any of them were deposited daily. Therefore, we attempted to validate the periodicity of growth-increment deposition on the basis of two independent and indirect methods.

Comparison of growth increment numbers in statoliths and gladii We investigated statoliths and gladii within the entire size range of *B. magister* sampled from early juveniles (35–40 mm ML) to large mature adults (280–330 mm ML). The total number of laminae within the inner layer of the gladius corresponded well with the total number of second-order growth increments within the statoliths (Fig. 8A). The estimated value of the slope was close to 1 (Table 2), which indicates that growth increments in statoliths and laminae within the inner layer of gladii were laid down synchronously. The results of increment validation from the first method were checked by the following second method.

Growth-increment analysis of successive modal classes The method of comparison of difference between mean ages of successive modes with elapsed days is relevant when 1) good resolution of the modes is possible, and 2) these modes represent the same cohort of squid, without substantial emigration and immigration (Caddy, 1991). It is known that sexual maturation affects the growth of both sexes and that during maturation squid either slow or cease somatic growth (Forsythe and van Heukelem, 1987). Hence, data on *B. magister* males were inappropriate for our purpose because most of them were mature during the period of our study (Figs. 3 and 4) and, therefore, a mode of male length composition might consist of several cohorts. Length-frequency compositions of females in Olyutorsky Bay were rather complex, especially during the summer (Fig. 3), and thus we were prevented from choosing progressive modal classes. Unfortunately, we had no statoliths from well-distinguished modal classes of females in the Navarin–St. Matthew region (Fig. 5). However, in the Navarin–Olyutorsky region, a clearly distinguishable modal group of females (immature in June–July, gradually maturing in August–September) was traced within the catches from June to September. The modal sizes of these females increased progressively from 180–190 mm in June to 250–270 mm in September, suggesting that these females belonged to the same cohort (Fig. 4). This group of females was analyzed from four successive monthly samples taken from June to September.

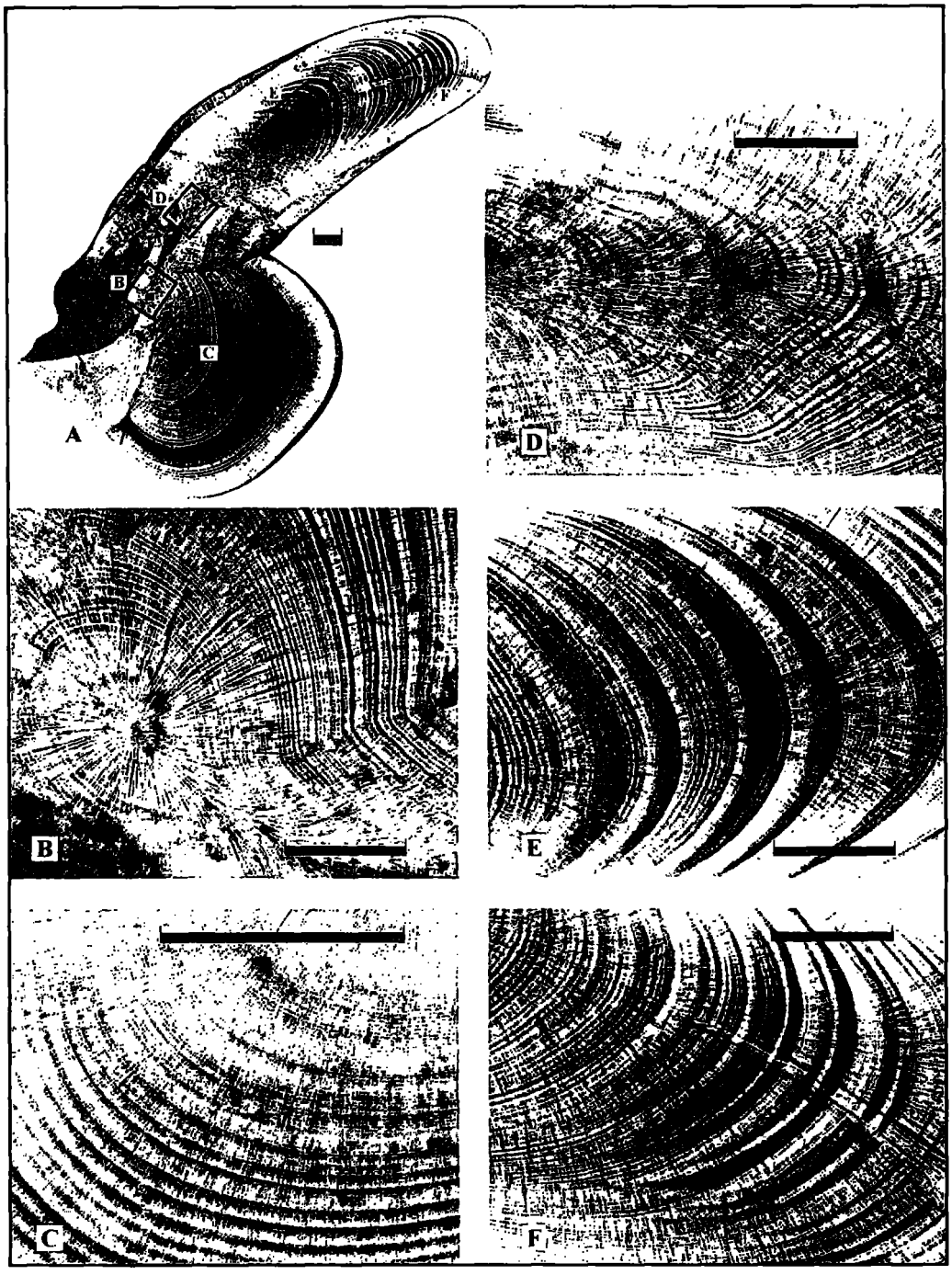

Figure 7

Microstructure of the statolith of *Berryteuthis magister* (light micrographs). (A) General view of a ground statolith (mature male, ML 218 mm); (B–F) magnified views of the areas outlined by rectangles B–F in panel A. (B) Nucleus and postnuclear zone (micrograph taken from statolith of another specimen); (C) first-order increments visible in the lateral dome; (D) second-order increments in the proximal part of the rostrum; (E) second-order increments grouped into well-defined third-order "bands" in the middle part of the rostrum; (F) faint first-order increments appearing within the second-order increments in the distal part of the rostrum. The length of black bars on all panels is 0.1 mm.

Comparison of the difference between the average number of second-order statolith growth increments of females representing the modal size classes in two successive samples with the number of days elapsed between the samples showed that their values were very close (Table 3). This provided further confirmation of daily formation of each second-order increment. The relationship between the number of second-order growth increments of modal-size females and their date of capture was approximated well by linear regression (Fig. 8B; Table 2). The estimated slope value (1.011) was very close to 1, further suggesting that a second-order increment may correspond to one day.

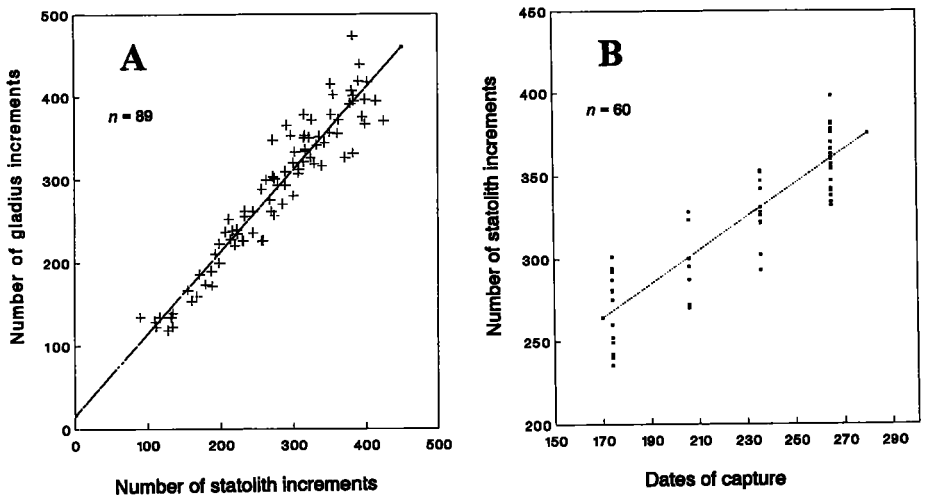

Figure 8

Validation of growth periodicity of statoliths and gladii in *Berryteuthis magister*. (**A**) Relationship between the number of second-order increments in the statoliths and the number of increments in the gladii; (**B**) relationship between the number of second-order increments in statoliths of modal-size females and the dates of their capture (cumulating from 1 January 1993).

Age structure

Minimum age (40 and 47 days) was observed in two juveniles of 26 and 24 mm ML, respectively, caught in the Navarin–Olyutorsky region in July. The oldest male (mature, 295 mm ML) that was aged was 473 days. The two oldest females (276 and 369 mm ML) were also mature and were 479 days old. All these animals were captured in June in the eastern part of the Navarin–Olyutorsky region. During summer and fall, the stock structure of *B. magister* was rather complex. Each month, both in Olyutorsky Bay and the Navarin–Olyutorsky region, we captured squid of 5–12 (usually 7–8) month classes (Figs. 9 and 10).

Olyutorsky Bay In Olyutorsky Bay (Fig. 9), May–July hatched males (age: 310–390 d) and females (age: 325–385 d) were the most abundant mature animals in June. Immature females (age: 300–320 d) of 180–210 mm ML were hatched during July, August (mainly), and September and were not abundant. Immature males of 150–210 mm ML were hatched in August and September.

In August, the stock structure of *B. magister* was considerably different from that observed in June (Table 4). Mature June- and July-hatched squids almost disappeared from catches. Immature and maturing August- and September-hatched squid of 210–270 mm ML (age: 320–350 d) prevailed among females, whereas among males the most abundant were August–October hatched mature individuals of 180–240 mm ML (age: 300–350 d). Small maturing

Table 2

Parameters of the linear function $Y = a + bX$, their standard deviations in parentheses, r-squares, t-statistics, and null hypothesis tests ($b = 1$ at $\alpha = 0.05$) for two relationships between 1) the number of second-order increments in the statoliths (X) and the number of laminae in gladii (Y) and 2) the number of the second-order increments in statoliths of modal-size females and the dates of their capture (cumulating from 1 January 1993).

Relationship	n	a	r^2	b	t-statistic	Results of H_0-test
1	88	13.90 (2.887)	0.8959	0.9949 (0.03655)	0.1396	do not reject
2	60	92.38 (19.94)	0.7904	1.0116 (0.0684)	0.1688	do not reject

males of 150–190 mm ML represented the November month class.

During September, fall-hatched squid still predominated in catches. There were twice as many October-hatched females in September than in August. September- and October-hatched maturing females of 240–270 mm ML (age: 340–370 d) occurred in great numbers. Immature December–January hatched females and males of 150–210 mm ML composed up to 15% of the total catches. Mature males of 210–240 mm belonged mainly to September–October hatched squid. Juveniles of 20–40 mm ML were June-hatched, whereas larger ones (60–120 mm ML) belonged to March–May month classes.

Navarin–Olyutorsky region Age structure of *B. magister* in the Navarin–Olyutorsky region (Fig. 10) in June was somewhat different from that in Olyutorsky Bay (Table 4). During the first half of June, 9 month classes for females and only 5 month classes for males were observed. One-third of females (250–360 mm ML, 380–460 d) had mated and belonged to February–May month classes. The majority of the catches were represented by summer-hatched females (maturing specimens of 210–240 mm ML, 300–320 d) and mature specimens (240–340 mm ML, 330–370 d). Among males, summer-hatched individuals were most abundant (220–250 mm ML, 320–340 d). Immature males, and females (160–190 mm ML, 260–280 d) belonged to the September month class. Juveniles caught in considerable numbers were from late fall (90–120 mm ML), winter (40–80 mm ML), and spring (26–37 mm ML) hatching. In the second half of June, maturing and mature squids from the summer hatch still predominated for catches of both males and females. However, the proportion of fall-hatched squid approximately doubled.

Table 3

Results of growth-increment validation in *B. magister* statoliths, obtained by the method of comparison of difference between average numbers of the second-order increments (mean age in d) of two successive modes of females with the number of days elapsed between the samples.

Sample no. (i)	Sampling date (T)	Modal ML (mm)	Mean age, d (A)	SD of mean age	Number of squid in sample	Elapsed days $T_{i+1}-T_i$	Differences between means $A_{i+1}-A_i$
1	23 June	170–190	265.3	22.8	13	—	—
2	25 Jul	230–260	296.4	21.1	6	32	31.1
3	24 Aug	240–260	330.8	18.9	22	30	34.4
4	22 Sep	250–270	361.0	17.1	24	29	30.2

Table 4

Coefficients of similarity (CS, according to Shorygin, 1952) of *B. magister* age structures in Olyutorsky Bay (O) and the Navarin–Olyutorsky region (N) in different months. (1) and (2) = first and second halves of a given month, respectively. Above right — CS's of age structures of males; below left — CS's of age structures of females.

			A	B	C	D	E	F	G	H	I	J
O	Jun	A	**100**	45.7	26	68.7	55.4	37	35.9	31.7	23.2	4.9
O	Aug	B	34.9	**100**	56.8	33.2	54.9	71.5	56.2	65.4	56.8	34.3
O	Sep	C	9.4	59	**100**	21.5	36.5	74.7	72.8	68.8	67.2	66.1
N	Jun/1	D	76	42.2	15.1	**100**	55.2	32.1	28.3	19.4	18.3	0.4
N	Jun/2	E	64.5	54.4	41.7	63.9	**100**	47.5	41.3	32.1	34.2	19.3
N	Jul	F	27.3	73.9	74.5	34.2	50.5	**100**	81	72.9	72.9	62.7
N	Aug	G	27.7	77.2	76.9	36	54.3	86.9	**100**	68.1	61.9	67.5
N	Sep	H	11.8	56	74.8	19.3	44.1	63.9	66.2	**100**	79.7	58.3
N	Oct/1	I	7.1	43.5	66.7	15.5	33.3	63.3	57.2	55.2	**100**	52
N	Oct/2	J	2.1	34.1	58.4	9.8	22.2	59.6	51.4	45.6	72	**100**

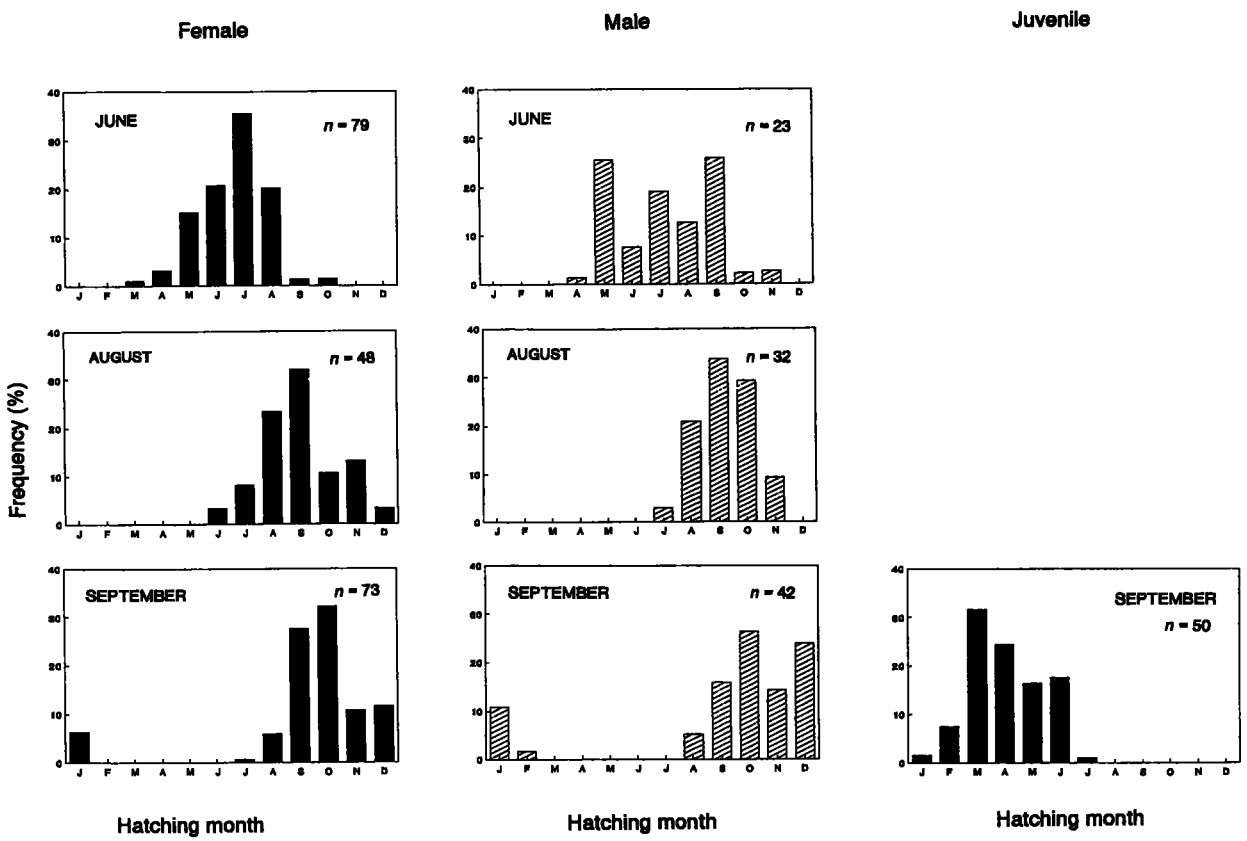

Figure 9

Age structure of *Berryteuthis magister* in Olyutorsky Bay, June–September 1993.

In July, the age composition of *B. magister* changed considerably compared with that for June (Table 4). Among large mature squid (males of 210–240 mm ML, females of 240–300 mm ML), the most abundant group belonged to the August month class (age: 320–340 d), whereas the May and June month classes almost vanished. September- and October-hatched females, which were immature in June, began maturing and a great majority of them attained maturity stage 3. Immature squid of 150–210 mm ML were represented by October and November month classes. Along with grown winter-hatched juveniles (up to 80–120 mm ML) were small juveniles (30–60 mm ML) of April and May month classes.

In August, age composition remained almost the same as that in July (Table 4). Maturing August–October females of 240–300 mm ML and mature September–October males were predominant. Spent females belonged to the summer hatch (age 360–410 d). Immature *B. magister* of 180–240 mm ML were of November and December hatching months. A proportion of January- and May-hatched juveniles decreased, and March- and April-hatched individuals increased.

In September, mature and spent summer-hatched squid almost disappeared from the region. As in August, fall-hatched squids (mainly September and October month classes) predominated, particularly maturing females (230–280 mm ML, 330–370 d) and mature males (210–240 mm ML, 325–380 d). Immature females and immature, maturing, and mature males of 150–210 mm ML were from November–January month classes. Juveniles (70–120 mm ML) belonged to the spring hatch (March and April).

September- and October-hatched females at maturity stages 4 and 5 (240–290 mm ML, 330–390 d) predominated in catches during the first half of October, but, in contrast with September catches, the proportion of mature females increased sharply. The proportion of September-hatched males decreased, but the October-hatched ones increased. All these males were mature (200–235 mm ML, 340–385 d). Immature females of 130–140 mm ML belonged to the March class. In the second half of October, the

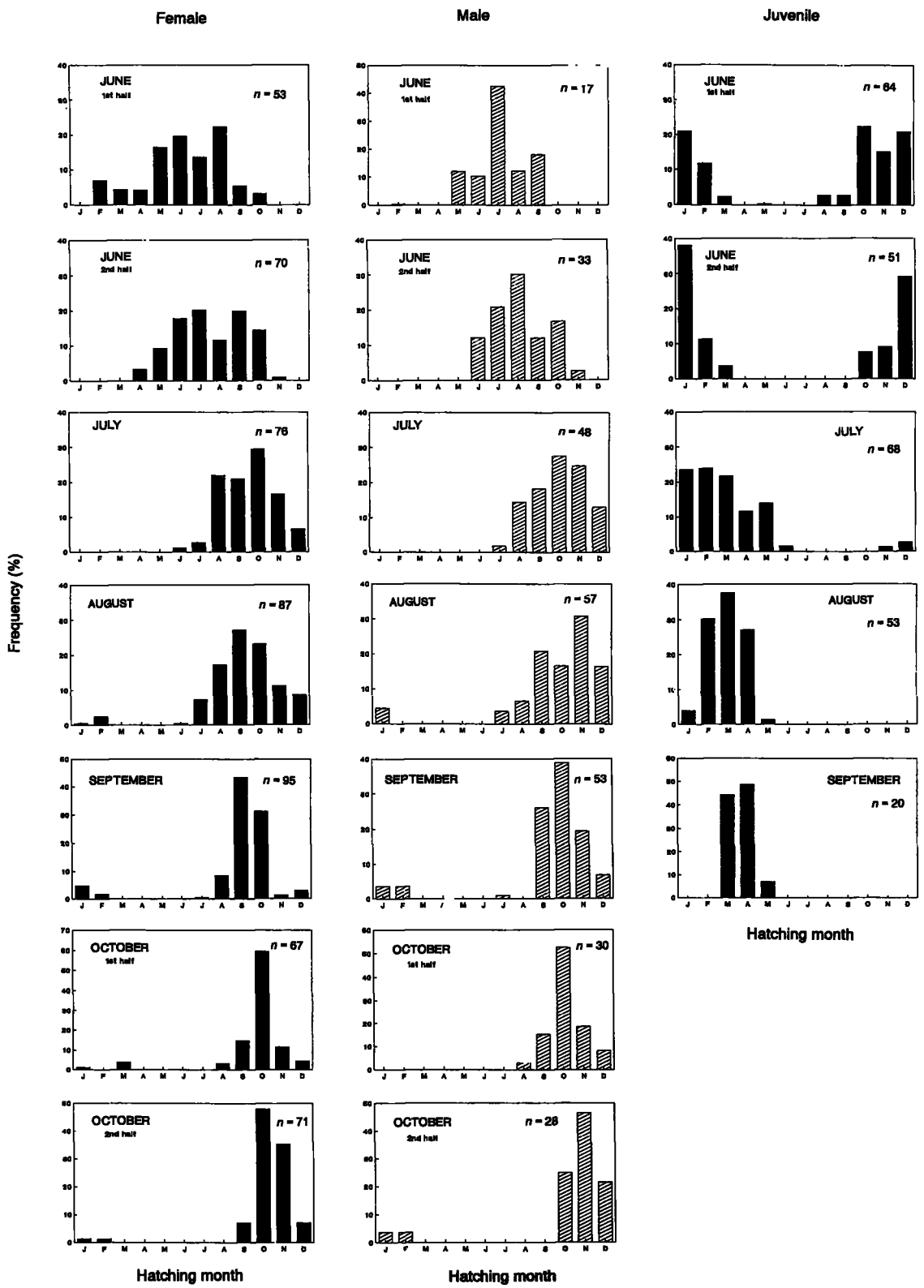

Figure 10

Age structure of *Berryteuthis magister* in the Navarin–Olyutorsky region, June–October 1993.

number of November-hatched squid increased three times for females and twice for males. Almost all fall-hatched females (240–290 mm ML, 350–380 d) were mature and had already mated. Fall-hatched males were 205–238 mm ML (352–385 d).

Analysis of coefficients of similarity (CS) (Table 4) revealed considerable differences in stock structures of *B. magister* observed in different months in Olyutorsky Bay. However, high values of CS (more than 70%) were noted (in both sexes) between the samples taken in June from Olyutorsky Bay (OB) and from the Navarin–Olyutorsky region (NOR); between OB in August and NOR in July; and between OB in September and NOR in July, October, and September. The CS's between the samples taken in different months within the NOR were generally low. However, there was a high resemblance of the stock structure for both sexes between July and August: for females between the first and the second half of October and for males between September and the first half of October. Samples taken in July and September to the first half of October also showed a high CS in males (Table 4).

Growth and maturation

Statolith growth Statoliths of early juveniles (24–32 mm ML) were unusually large; their total length (STL) ranged from 0.9 to 1.35 mm (3.8–4.2% ML, respectively). During ontogenesis, they grew rather slowly and by age 450–470 d increased 2.5–3 times in length. In both sexes, statolith growth was best fitted by a power function and did not reveal sexual dimorphism (Fig. 11, A and B). Allometric growth of the total statolith length (STL) versus mantle length (ML) was negative with a high value of allometric coefficient (>0.38) (Fig. 11, C and D; Table 5). STL allometric growth rates were higher in males than in females, resulting in larger sizes for male statoliths among the same-size animals.

Squid growth Length-at age data assigned for each hatching month demonstrated that *B. magister* be-

Table 5

Parameters of the power function $Y = aX^b$ and logistic growth function $Y_t = K/(1+((K-Y_0)/Y_0)(\exp(rt)))$, their asymptotic standard errors and r-squares of different relationships of *B. magister*. STL = total statolith length (mm); ML = mantle length (mm); Age = age (d); BW = body weight (g).

Parameter	Estimate	Asymptotic standard error	R^2
Allometric growth curve: STL versus ML			
Females			
a	0.3330	0.009229	0.938
b	0.3851	0.005190	
Males			
a	0.2929	0.009551	0.943
b	0.4144	0.006487	
Power growth curve: STL versus Age			
Females			
a	0.09859	0.004572	0.931
b	0.5732	0.008117	
Males			
a	0.1061	0.005687	0.930
b	0.5591	0.008664	
Power curve: BW versus ML			
a	0.0001765	0.00003462	0.907
b	2.6743	0.5214	
Logistic growth curve: ML versus Age			
Females			
r	0.01266	0.0007469	0.919
K	343.8	11.29	
Y_0	13.25	1.936	
Males			
r	0.01358	0.0006863	0.946
K	271.4	6.242	
Y_0	12.98	1.502	

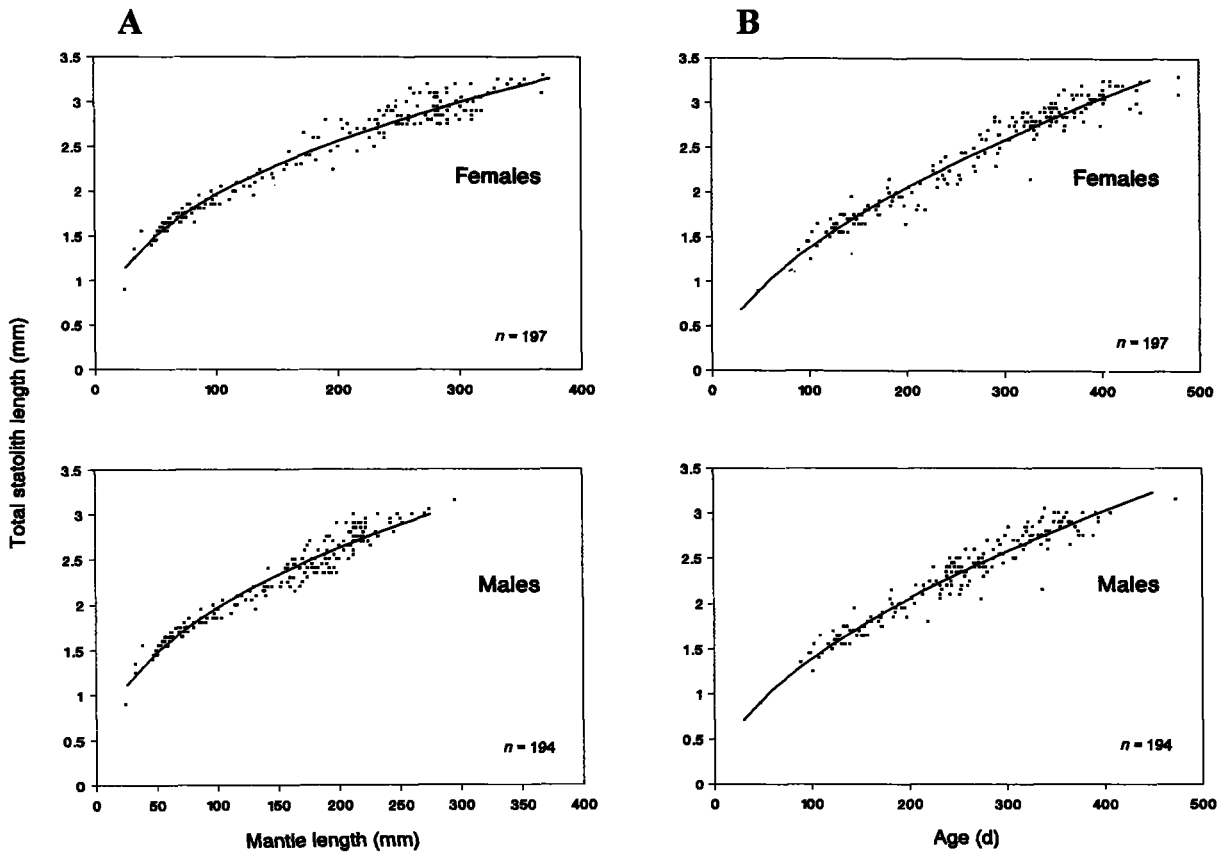

Figure 11

Statolith growth in *Berryteuthis magister*. Relationship between (**A**) total length and mantle length and (**B**) total statolith length and number of second-order increments on the statolith (age in days).

longed to different month classes, differed in size, and represented different sections of the group growth curves. There were only a few data on spring-hatched *B. magister*, especially for males (Figs. 12 and 13). This prevented the comparison of growth rates of the same-age squids from, for example, winter- and summer-hatched animals.

The growth curve of mantle length versus age was best fitted with a logistic growth curve (Table 5). Males and females grew at the same growth rate until 210–240 d (Fig. 14, A and B). Thereafter, males grew more slowly than females and at age 390 d their mean ML was approximately 50 mm less than that of females.

The relationship of mantle length to body length did not show any pattern of sexual dimorphism (Fig. 14C). The power coefficient was less than 3 (2.62), demonstrating the relative slenderness of the body of large-size squid. According to calculated weight growth curves, females began to exceed males in body weight later than in mantle length (at age 270 d) (Fig. 14D).

Berryteuthis magister is a rather slow-growing squid. Daily growth rates (DGR) in ML were low in juveniles (0.27–0.35 $mm \cdot d^{-1}$), reached their maximum values in males at ages 180–210 d (ca. 0.9 $mm \cdot d^{-1}$) and in females at ages 210–270 d (1.05–1.08 $mm \cdot d^{-1}$), then gradually decreased to juvenile levels for females and fell even lower for males (Fig. 14E). Juvenile DGR in BW were very low (0.02–0.06 $g \cdot d^{-1}$). However, they quickly increased with age and attained maximum values at older ages in both males and females, 270–300 d and 300–330 d, respectively (Fig. 14F). The instantaneous rate of growth (G) in ML was maximum in early juveniles (0.0118–0.0124), then gradually decreased to the age of 420 days, in males to a greater extent than in females (0.0007 and 0.0012, respectively). Calculated values of *G* in *BW* were similar to the trend in *ML* (Fig. 14, G and H).

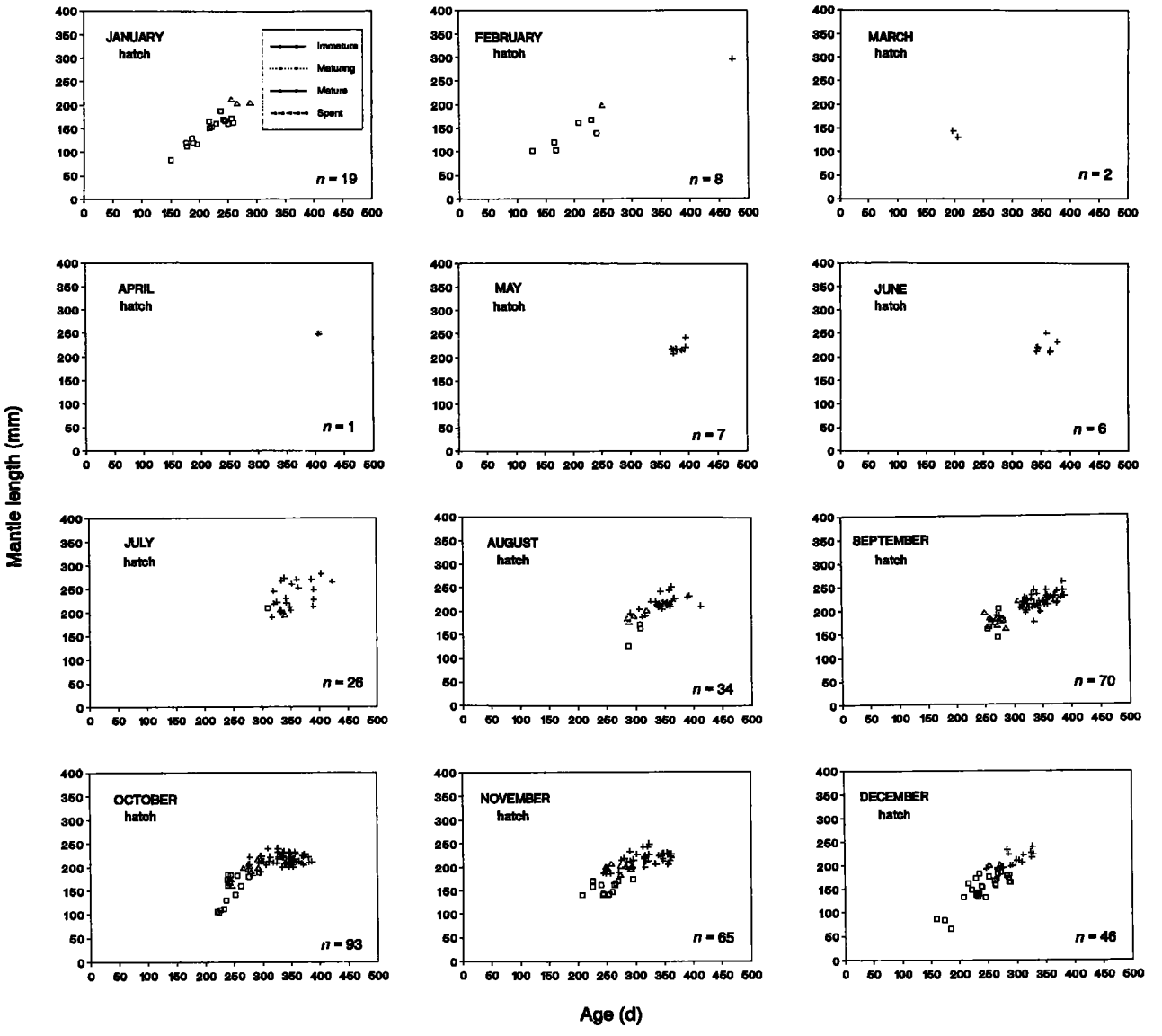

Figure 12

Length-at-age data for males of *Berryteuthis magister* in the western Bering Sea.

Maturation with growth Males and females of various month classes matured at different sizes and ages (Figs. 12 and 13). In our samples, juveniles were mainly from a winter-hatched group, mature specimens at different substages of maturity stage 5 were from a summer-hatched group, and squid of various stages of maturation and maturity were from a fall-hatched group. Thus, it was reasonable to analyze group rates of *B. magister* maturation by using the data on both sexes from the fall-hatched group and females from the summer-hatched group (because all summer-hatched males were already mature during the period studied).

Ages at various maturity stages (maturity rates) differed between the sexes (Fig. 15). Males began maturing earlier than females. All males were at maturity stage 1 at 210 days. However, at 240 days almost half of them reached maturity stage 2 (a few specimens already being mature). By 300 d, the proportion of immature and maturing males (maturity stages 3 and 4) was greatly reduced, with most of the males already mature. At ages older than 310 d,

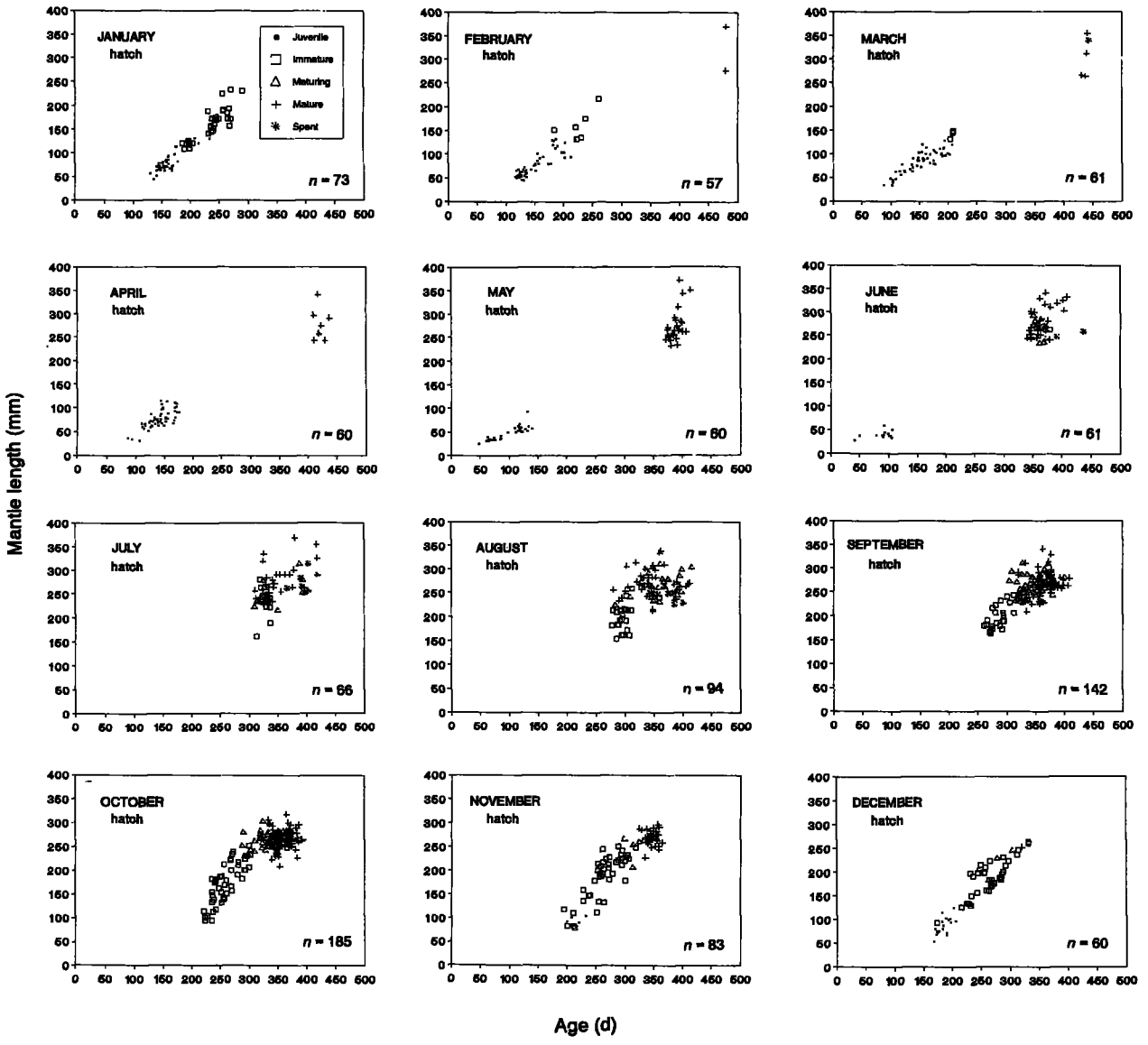

Figure 13

Length-at-age data for females of *Berryteuthis magister* in the western Bering Sea.

there were only mature and occasionally spent specimens (we caught only two spent fall-hatched males at 330 and 340 d). All males at 370–380 d were mature and showed many spermatophores in the Needham sac and no apparent gonad degeneration. An extensive transition of males into the spawning and spent conditions (maturity stage 6) would have to occur far later than age 380 d.

Between 210 and 280 d, all fall-hatched females were immature, with an increasing proportion of females at maturity stage 2. Females started maturing (maturity stage 3) at 290 d. At 330 d, there were still some immature animals, but most of the females were maturing (maturity stages 3 and 4). At this age, there were already a small number of mature and even four spent females. The proportion of females at maturity stage 3 decreased from 330 d to 360 d, and disappeared at 390 d. Between 330 and 390 d, the proportion of females at maturity stage 4 remained approximately constant, whereas mature females gradually increased. Mature females began mating between 300 and 320 d, most of them mating by 350–370 d. There was evidence for both early and late-maturing females, with the bimodal distribution

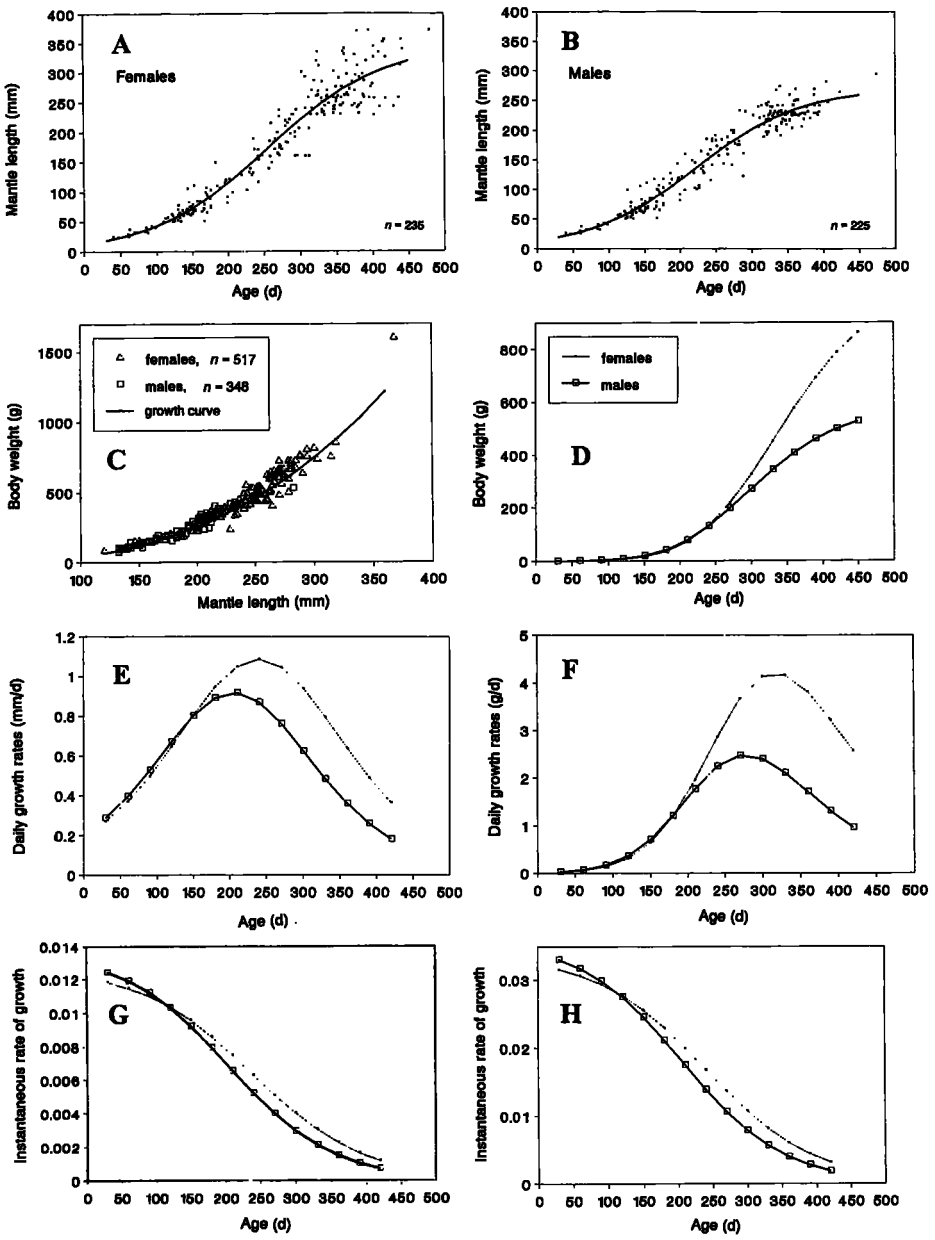

Figure 14

Growth curves and parameters of *Berryteuthis magister*. Relationships between (**A**) mantle length and age for females; (**B**) mantle length and age for males; (**C**) body weight and mantle length; (**D**) body weight and age; (**E**) daily length-growth rates and age; (**F**) daily weight-growth rates and age; (**G**) instantaneous rate of mantle length growth and age; (**H**) instantaneous rate of body-weight growth and age. Lines with dots in panels D–H show females; lines with open squares show males.

obvious at all maturity stages except for spent-stage animals. The difference between these modes was 30–40 d. Like the fall-hatched males, almost all fall-hatched mature females were in good condition, without any pattern of reduction of the gonad, liver, and mantle. Early maturing and late-maturing groups were observed also among summer-hatched females, with a bimodal distribution for spent females (Fig. 15).

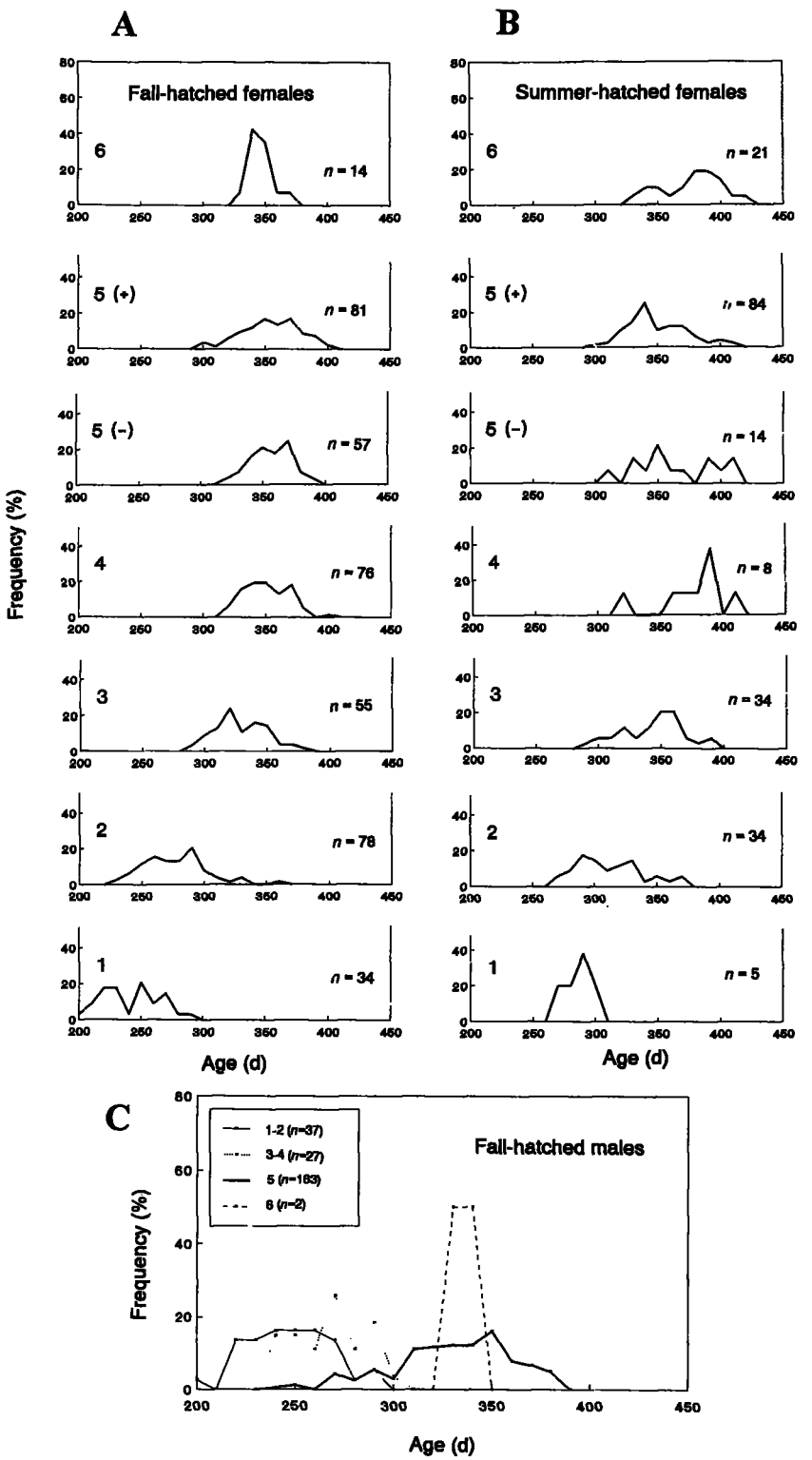

Figure 15

Maturity-at-age data for (**A–B**) two seasonal groups of females and for (**C**) fall-hatched males of *Berryteuthis magister*. 1–6 = maturity stages; 5– = mature females without evidence of mating; 5+ = mature females with evidence of mating.

Discussion

Statolith and gladius microstructure with validation of growth increments

Statoliths of all previously investigated species usually had one or two kinds of growth increments, usually referred to as first- and second-order growth increments. Growth increments of only one kind occur in ommastrephids: *Illex illecebrosus* (Dawe et al., 1985), *Illex argentinus* (Rodhouse and Hatfield, 1990; Arkhipkin, 1993), and *Nototodarus sloanii* (Uozumi and Ohara, 1993). Growth increments of two types were found mainly in loliginids: *Loligo opalescens* (Spratt, 1978), *Photololigo edulis* (Natsukari et al., 1988), and *Loligo vulgaris* (Natsukari and Komine, 1992); and in gonatids: *Gonatus fabricii* (Kristensen, 1980). The first-order growth increments or "rings" in loliginids and gonatids and the growth increments in ommastrephids have been validated as daily increments, whereas an interpretation of the second-order growth increments has not been consistent in different studies. Some authors (Spratt, 1978; Kristensen, 1980) have assumed them to be of fortnightly or monthly origin; others have not been able to find any definite pattern in their deposition and have treated them like first-order increments (Natsukari et al., 1988; Natsukari and Komine, 1992). In this investigation, it was revealed that unlike statoliths of loliginids and ommastrephids, ground statoliths of *B. magister* exhibit three kinds of growth increments: namely, of the first, second, and third orders. Previously, Natsukari et al. (1993) noted only two kinds of growth increments in *B. magister* statoliths. We revealed that the "second-order growth increments" were grouped into distinct "bands" of the third order, very similar in structure and appearance to loliginid "second-order bands."

Natsukari et al. (1993) hypothesized that the first-order growth increments ("fine low contrast rings") in *B. magister* were deposited daily. However, the authors did not validate the periodicity of "fine rings" directly. Their suggestion that there were two different modes of year classes for *B. magister* encountered in the southwestern part of the Sea of Japan, as assumed earlier (Yuuki and Kitazawa, 1986), seemed to be rather speculative without some direct verification (e.g. by statolith ageing techniques).

Squid, like fishes, have physiological processes that are related to diel rhythms (Campana and Neilson, 1985) reflected in periodical changes in metabolic processes and resulting in different rates of deposition onto various hard structures (e.g. gladius and statolith). We found that within the inner layer of the gladius there were regular well-defined laminae that were not grouped into any other growth zones or bands. The similarity in the number of growth increments observed within the gladius with the number of "second-order growth increments" in statoliths corresponded to the same internal rhythm in the squid organism. Previous research on gladii (e.g. *Sthenoteuthis oualaniensis* [Arkhipkin and Bizikov, 1991]) has suggested that this kind of internal rhythm is diel, and therefore we consider the "second-order growth increments" of *B. magister* statoliths as deposited daily. However, this method could not be applied to some cold-water species (e.g. *Moroteuthis ingens* [Arkhipkin and Bizikov, 1991]); therefore it had to be confirmed by another independent validation method. As in the studies by Uozumi and Ohara (1993) and Uozumi and Shiba (1993), we compared differences between mean ages of successive well-defined modes of frequency compositions with elapsed days between samples and found a good correspondence between them. Therefore, the nature of the "second-order growth increments" within *B. magister* statoliths and consequently that of increments within the inner layer of their gladii were confirmed. The statolith ageing technique, however, was found to be more effective because its actual productivity (about 120 ground statoliths per week by one skilled technician) was far higher than that of the gladius technique (40–50 cross sections, respectively). Thus, statoliths were more efficient tools in investigations of age, growth, and stock dynamics of *B. magister*.

It is noteworthy that the "second-order" growth increments observed in *B. magister* statoliths ("heavy rings" of Natsukari et al., 1993) correspond to the first-order daily increments of other squid species, whereas the distinct "third-order" bands that we found in *B. magister* statoliths correspond to the second-order bands of loliginids and other gonatids. "Fine rings" or "first-order increments" revealed in *B. magister* statoliths obviously were of a subdaily nature like those observed earlier in *Sepioteuthis lessoniana* (Jackson, 1990) and in other fish species (Campana and Neilson, 1985).

The starting point for increment counts remains unclear. In ommastrephids, growth increments are deposited after hatching (Balch et al., 1988), whereas loliginid hatchlings have a few dozen growth increments within their statoliths at hatching, with a prominent check occurring outside the nucleus (Natsukari et al., 1988). Statolith size at hatching for *B. magister* is unknown, therefore we assumed (after Natsukari et al., 1993) that the first prominent check lying outside the nucleus was the "natal" ring. If this assumption turns out to be incorrect, and the nucleus in *B. magister* appears at hatching as in

ommastrephids, then the actual age of squids in this study should be corrected by adding the number of increments between the nucleus and "natal" ring (10–12 rings). However, in relation to the longevity of *B. magister*, this bias appears negligible.

Seasonal dynamics in distribution, length-frequency composition, and stock structure

We found three main seasonal groups of *B. magister* in the western Bering Sea: winter-hatched, summer-hatched, and fall-hatched groups. Winter-hatched squids were caught in great numbers during the summer as juveniles ranging from 40 to 100 mm ML. From June to September, these squids increased in size over the slope of the Navarin–Olyutorsky region, growing up to 110–150 mm ML. Later these squids disappeared from catches.

The summer-hatched group predominated catches in Olyutorsky Bay and the Navarin–Olyutorsky region from June to August. About 80% of females and 85% of males from this group were mature in June; their modal length was 250–260 mm and 200–210 mm, respectively. Spawning for this group began in June and was encountered along the slope (400–600 m) between 165°E and 177°E. The average age of spawning squid in June was 330–370 d for females and 320–340 d for males. Spawning intensified in August and finished by the middle of September. Summer spawning of *B. magister* in the western Bering Sea was identified by the pronounced predominance of mature males and mature females that had mated and by relatively large numbers of spent squid in August. Average age of spent males and females was 11–12 months. Aggregations of summer-hatched squid were not dense; catches on their spawning shoals never exceeded 300–400 $kg \cdot h^{-1}$. By October these squid vanished from catches.

Squid of the fall-hatched group occurred in the western Bering Sea during the entire period of study, representing the bulk of catches from August until November. In June, these squid were immature (maturity stages 1–2) and of modal size 170–180 mm ML and were not abundant in catches (ca. 20% of total catch) in all three regions. The abundance of fall-hatched squid increased in the Navarin–Olyutorsky region during summer, apparently because of their continuing immigration along the slope from the eastern Bering Sea shelf. Several factors indicated the presence of a westward migration. First, fall-hatched juveniles appeared in Olyutorsky Bay only in July, whereas in the Navarin–Olyutorsky region they occurred from June onwards. Second, size-frequency composition of squid in the Navarin–St. Matthew region was rather stable from June to September; juveniles and immature squid predominated in catches. The latter observation, together with the observed growth of squid, strongly indicated that this region was transient for shoals of juveniles and immature adults migrating from the east to the Navarin–Olyutorsky region.

Growth and maturation of the fall-hatched squid were observed on the slope of the Navarin–Olyutorsky region and within Olyutorsky Bay from June to August. By September, 90% of the fall-hatched males achieved full maturity at modal length 200–210 mm, whereas a majority of females (about 60%) were still maturing (stage 3), attaining 250–260 mm ML. Maturation of the fall-hatched females began in October at modal length 270 mm ML. By November, about 75% of females were mature and ca. 70% of them had mated. Maturation of the fall-hatched squid in September–October was accompanied by their aggregation into dense shoals at depths ranging from 350 to 450 m along the slope of the Navarin–Olyutorsky region and in Olyutorsky Bay with average catches >1 $t \cdot h^{-1}$. Thus, fall-hatched squid represented the bulk of *B. magister* stock in the western Bering Sea, with the highest fishery potential of all seasonal groups.

The population of fall-hatched squid in the Navarin–Olyutorsky region successively changed in structure during September and October. This shift demonstrated the ongoing emigration of mature squid from the Navarin–Olyutorsky region. Squid possibly moved in a southwest direction along the slope during October–November. Dense shoals of *B. magister* disappeared, first in the Navarin–Olyutorsky region, and only later in Olyutorsky Bay.

During summer and fall, seasonal groups of *B. magister* used the continental slope of the western Bering Sea in somewhat different ways. Summer-hatched squid used the slope during June–August as spawning grounds, mainly at depths of 350–450 m. For the fall-hatched squid, the slope was a feeding ground and, at least for a number of them, a spawning ground. During summer, the fall-hatched squid increased in size rapidly at depths of 350–500 m. In September–October, they formed dense aggregations and after spawning, rather quickly disappeared from the region. As for the winter-hatched group, its migratory behavior remained unclear, and we cannot say whether or not this group used the slope as a feeding ground only or as a spawning area as well. With respect to spawning seasons of different groups, it is obvious that the time lag between summer spawning and fall spawning is much greater than that between fall- and winter-spawning groups. Unfortunately, we do not have enough data on the winter season, and it is possible that there are not three

but two seasonal spawning groups: summer-spawning and fall-winter spawning, the latter with two spawning peaks, during fall and winter. It is interesting that Natsukari et al. (1993) found the same two spawning peaks (summer and fall-winter), although of different intensity, for *B. magister* occurring in the Rebun Bank (Sea of Japan) and Kitami-yamato Bank (Sea of Okhotsk).

Age, growth, maturation, and possible life cycle

Until now, investigations of squid life cycles by any direct method have shown that tropical species are characterized mainly by a half-year life cycle (small- and medium-size loliginids [Jackson and Choat, 1992]) and a one-year life cycle (medium-size and large ommastrephids [Arkhipkin and Bizikov, 1991; Arkhipkin and Mikheev, 1992]), whereas subtropical and temperate species generally have a one-year life cycle (Natsukari et al., 1988; Arkhipkin, 1990; Natsukari and Komine, 1992). The maximum age of cold-water subarctic, Arctic, and Antarctic species has not been determined directly yet. However, studies of length-composition dynamics through various years as well as growth data obtained from the hard structures of squid have suggested that cold-water species may live two years or more (i.e. *B. magister* [Fedorets, 1986a]; *Kondakovia longimana* [Bizikov, 1991; Jarre et al., 1991]; *Martialia hyadesi* [Rodhouse, 1991]). Natsukari et al. (1993) suggested that *B. magister* live four years, but we have produced different estimates which reflect different criteria for increment counting.

According to our data, *B. magister* in waters of the western Bering Sea live more than one year, with the oldest specimens about 16 months old, and the bulk of fall-hatched squid 13–14 months old and far from being in a spent condition. However, summer-hatched squid matured earlier, with the majority of spent animals being 12–14 months old.

Berryteuthis magister is a nektonic species resembling active oceanic ommastrephids in body shape and muscle strength (Nesis, 1985). It showed the same growth and maturation features as many middle- and large-size ommastrephids, namely 1) an earlier decrease in growth rates for males, which results in smaller sizes at maturation for males in comparison with females of the same age; 2) maximum daily growth rates in the middle of ontogenesis with a gradual decrease by the end of life; 3) a constant reduction of instantaneous growth rates from maximum values in early juveniles to minimum values in mature specimens; 4) the achievement of maximum DGR in body weight at older ages than those attained for maximum DGR in ML; 5) a wide length-weight range for squid of the same age; and 6) the presence of early and late-maturing animals within the same seasonal group of females. As expected, cold-water *B. magister* grew and matured slower than large species of ommastrephids, had a smaller body size, and lived longer.

Growth curves of seasonal groups of squid would probably differ, as has been shown before for ommastrephid (Arkhipkin, 1990; Uozumi and Ohara, 1993) and loliginid squid (Natsukari et al., 1988; Jackson and Choat, 1992). This was confirmed indirectly for *B. magister* in comparing the smaller sizes of mature summer-hatched females (250–260 mm ML) with mature fall-hatched females (270–280 mm ML).

Taking into account our data with those of several previous studies (Fedorets, 1986a; Okiyama, 1993), we were able to suggest an approximate scheme for the life cycle of *B. magister* in the Bering sea for the most fully investigated, abundant fall-hatched group. The direction of ontogenetic migrations of *B. magister* is expected to coincide with the general scheme of water circulation in the Bering Sea (Hughes et al., 1974; Favorite et al., 1976; Shuntov et al., 1993). In the deepwater southern part of the Bering Sea there are three main counterclockwise circulations: that which lies westward from Shirshov Ridge, that between Shirshov and Bowers Ridges, and that between Bowers Ridge and the shelf of Bristol Bay. There are many lesser circulations (Shuntov et al., 1993). Immature fall-hatched squid (180–200 mm ML) in early summer appeared in the Navarin–St. Matthew region and began migrating southwestward along the continental slope of the Navarin–Olyutorsky region. During summer, these squid fed actively over the slope and grew quickly. In August–September, maturing females attained 260–270 mm ML. In October, the majority of them were mature and, by the end of the month, had mated. In November they vanished, first from the Navarin–Olyutorsky region and later from Olyutorsky Bay. One group of these squid spawns and dies in the two regions just mentioned. Another group of these squid, however, may migrate actively in a southwest direction onto the slope of the Commander Islands. There are two possible migration routes from the main feeding grounds in the Navarin–Olyutorsky region to the area around the Commander Islands: 1) along the slopes of Olyutorsky Bay and North Kamchatka (total distance about 1,800 km); and 2) south of Cape Olyutorsky along the Shirshov Ridge (ca. 1,000 km). Both routes include sections with great depths (>1,500 m); the first route having an approximately 100-km section and the second route an approximately 500-km section. It is known that not only immature squid but even mature males and maturing females of *B. magister* may occur in pelagic wa-

ters (Fedorets and Kozlova, 1988; Shevtsov, 1990). However, because *B. magister* adults occur mainly at and over the slope, the first route seems more likely. Taking into account the similarity of body shape of *B. magister* and *I. argentinus*, as well as the depths and water temperatures of their spawning migrations, we assume that migratory swimming rates of *B. magister* may resemble those of *I. argentinus:* 0.46 of absolute length (including mantle length, length of head and arms, AL) per sec (Arkhipkin, 1993). As the modal AL values in *B. magister* are 350–390 mm for mature males and 440–490 mm for mature females (our data), their average migratory rates may be estimated as 0.1–0.18 $m \cdot sec^{-1}$ and 0.20–0.23 $m \cdot sec^{-1}$, respectively. At this speed *B. magister* females may reach spawning grounds near the Commander Islands in 66–73 days and males in 80–92 days. But, in fact, *B. magister* cannot migrate at this speed, because its mantle is more watery and less muscular than that of ommastrephids: the protein content of *B. magister* mantle muscles is 13.5% compared with 20% which is typical for ommastrephids (Shevtsov and Dolbnina, 1975). Nevertheless, the data of Fedorets (1986a), who found dense aggregations of *B. magister* near the Commander Islands in November–January, support our suggestion of a squid migration to the Commander Islands. During this period, aggregations of *B. magister* near the Commander Islands consisted entirely of mature males and females of quite constant sizes (210–220 mm and 270–280 mm ML, respectively). However, these aggregations were observed at depths of 150–250 m, whereas *B. magister* migrates to much greater depths to spawn (1,000–1,100 m [Okiyama, 1993]). Thus, it is possible that mature squid of the fall-hatched group spawned one-two months later (in January–March) at mean ages around 18 months. It is hardly possible that *B. magister* from the western Bering Sea should reach even the Near Islands, the westernmost of the Aleutian Islands, because the northward current in the deep and wide Near Strait is very strong and may cross the squid migratory route. Kovalev (1990) has shown by the substrate-specific properties of cholinesterases that squid from the Pribilov–Alaska region (eastern Bering Sea) are different from those of the Navarin–Olyutorsky region, suggesting some degree of genetic isolation.

To estimate the total longevity of cold-water squid, it is important to consider the duration of their embryonic phase. Recently, Laptikhovsky (1991) modeled longevity of the embryonic phase in squid by using two independent variables: water temperature and average egg diameter. Taking into account the large egg size of *B. magister* (3.5 mm [Fedorets and Kozlova, 1986]; our data) and the extremely cold water over its spawning grounds (1.5–2.5°C [Fedorets, 1986a]), we believe the duration of the embryonic phase for *B. magister* could be from 4 to 6 months. This estimation corresponds well with data of von Boletzky (1994), who considered the duration of embryonic development in decapods as ranging from 6 to 12 months at water temperature 2–5°C. Thus, the life cycle of the fall-hatched group of *B. magister* could last about two years (6 months of embryonic phase and 18 months of postembryonic development). The life cycles of other seasonal groups require further investigations.

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Stock discrimination among European anchovies, *Engraulis encrasicolus*, by means of PCR-amplified mitochondrial DNA analysis

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Abstract.—A study of mitochondrial DNA (mtDNA) variation in European anchovies, *Engraulis encrasicolus* L., in the northwestern Mediterranean area was carried out with samples from Trieste, Ancona, and Vieste in the Adriatic Sea, from the Ionian, Tyrrhenian, and Aegean seas, and the from the Sicilian Channel. Restriction fragment length polymorphisms (RFLP's) in genes of the NADH dehydrogenase complex (ND genes) were investigated by using the polymerase chain reaction (PCR). Restriction of a 2.5 Kb PCR product coding for ND5 and ND6 revealed 53 composite haplotypes in 140 fish, 39 of which were unique. Mean haplotype diversity was 0.88; hence levels of variation were notably high. Pairwise values of nucleotide divergence ranged between 0.00001 and 0.01375, and gene diversity analysis indicated that an average of 7.6% of variation was partitioned between samples (G_{ST}). There was significant geographic heterogeneity, and Monte Carlo χ^2 simulations showed that Aegean Sea fish differed significantly from most other samples. Significant differences in the distribution of restriction patterns for one enzyme (*Sau* 96I) indicated that a degree of heterogeneity may also exist between anchovy populations in the Adriatic Sea and adjacent waters, although there was no intersample variation within the Adriatic Sea. Overall, the data were in accordance with the results of previous work using allozyme electrophoresis and meristics.

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The European anchovy, *Engraulis encrasicolus* L., a shoaling clupeoid fish, is distributed along the eastern Atlantic coast from Scandinavia to West Africa, and is also found in the Mediterranean, Black, and Azov seas (Whitehead et al., 1988). A commercially important species, the anchovy represented around 25% of the Italian pelagic catch in the early 1980's (Bombace, 1992). However, the Adriatic Sea anchovy stock, an important contributor to the Italian harvest, suffered a collapse from environmental causes in 1986–87, and catches have not returned to former levels. As a consequence, market values of anchovies have increased tenfold (Cingolani et al.[1]).

The paucity of data on the stock structure of *E. encrasicolus* in the Mediterranean area belies the economic significance of the species. The majority of studies have been executed by using phenotypic characters, and Levi et al. (1994) have described two putative stocks in the Adriatic Sea that have different growth rates, as measured by otolith reading. Recently, Garcia et al.[2] reported no genetic structuring

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[1] Cingolani, N., G. Kirkwood, G. Giannetti, E. Arneri, and D. Levi. 1994. Note on the stock assessment of *Engraulis encrasicolus* (L.) and *Sardina pilchardus* (Walb.) of the Northern and Central Adriatic Sea. Unpubl. manuscr. submitted to FAO-CGPM: third technical consultation on stock assessment in the Central Mediterranean; Tunis, 8–12 November 1994. Available from FAO, Viale delle Terme di Caracalla, 00100 Rome, Italy.

[2] Garcia, A., I. Palomera, B. Liorzou, O. Giovanardi, and C. Pla. 1994. Northwestern Mediterranean anchovy: distribution, biology, fisheries and biomass estimation by different methods. Final Project Report to the European Community MA.3.730. Available from European Commission, Directorate-General XIV Fisheries, internal resources, Conservation Policy and Environmental Questions, Rue de la Loi 200, B-1049 Brussels, Belgium.

of anchovies after an allozyme study that covered a large area of the western Mediterranean. In contrast, Spanakis et al. (1989) were able to distinguish stocks from the Ionian and Aegean seas by morphometrics and allozyme electrophoresis, noting that a degree of migration between these areas was probable.

The application of DNA technology to stock discrimination in *E. encrasicolus* is an obvious step, given the limited success of allozyme analysis, and mitochondrial DNA (mtDNA) has several distinctive properties which commend it to such investigations. Its inheritance is essentially clonal, reducing the effective population size to 1/4 of that for nuclear genes; mtDNA variation is hence more susceptible to the effects of stochastic processes (genetic drift and partial extinctions), and interpopulation variation accumulates more rapidly. This process is perhaps accelerated by the higher mutation rates often reported for mtDNA (Brown et al., 1979). Several studies have demonstrated stock differentiation in teleosts using mtDNA where none was detected at the allozyme level (see Ward and Grewe, 1994), although Ward and Grewe (1994) pointed out that the reverse is also sometimes true. It should be noted, however, that, since mtDNA acts as a single locus, the ability to screen a number of independent loci is an advantage of allozyme and nuclear DNA (nDNA) methods.

Despite their economic importance, relatively few studies of mtDNA variation in clupeoid fish have been published. Tringali and Wilson (1993) reported no significant spatial variation in the distribution of *Sardinella aurita* Val. mtDNA haplotypes in the eastern Gulf of Mexico but found that these fish were distinct from a sample taken in waters off southern Brazil. Kornfield and Bogdanowicz (1987) described geographic heterogeneity in Atlantic herring, *Clupea harengus*, although this variation has subsequently been shown to be nonsignificant (Roff and Bentzen, 1989). Other clupeoid species studied include American shad, *Alosa sapidissima* (Bentzen et al., 1988; Nolan et al., 1991; Chapman et al., 1994) and menhaden, *Brevoortia tyrannus* and *Brevoortia patronus* (Bowen and Avise, 1990), three species whose life history strategies include estuarine or freshwater components. The only published study on *E. encrasicolus* mtDNA variation concentrated on the occurrence of heteroplasmy (multiple forms of mtDNA within an individual), attributed to "paternal leakage" (Magoulas and Zouros, 1993).

Until recently, analysis of mtDNA involved laborious extraction protocols (e.g. Lansman et al., 1981) or hybridization of mtDNA probes with Southern-blotted digests of total DNA, but the revolution in molecular biology due to the discovery of polymerase chain reaction (PCR) amplification of DNA (Saiki et al., 1988) has largely removed these obstacles. Researchers may now apply the technique to concentrate efforts on mtDNA regions of particular interest, whether for species identification or for the detection of intraspecific variation and stock markers (Chow et al., 1993; Cronin et al., 1993; Chapman et al., 1994).

The genes of the NADH dehydrogenase complex (ND genes) have been the subject of a number of recent investigations, usually exhibiting sufficient variation to provide useful genetic markers (Cronin et al, 1993; Hall, 1993; Park et al., 1993). In this study we have investigated the utility of restriction fragment length polymorphism (RFLP) analysis of PCR-amplified mtDNA ND genes in the study of population structure in anchovies from the Adriatic Sea and surrounding waters. Our sampling strategy has enabled the comparison of results from this rapid, state-of-the-art approach with those previously obtained by allozyme analysis.

Materials and methods

The anchovy samples used for analysis were from the ports of Trieste, Ancona, and Vieste in the Adriatic Sea, from the Sicilian Channel, and from the Ionian, Tyrrhenian, and Aegean seas (Fig. 1). Each sample comprised 20 individuals. Fish were captured by commercial vessels with technology typical of the fishing grounds, i.e. light seine (*lampara*) and pair trawl (*volante*), and immediately placed on solid CO_2 (dry ice). Fish were later stored at –80°C until laboratory analysis.

DNA extraction

Further details on the preparation of solutions may be found in Sambrook et al. (1989). A piece of muscle tissue approximately 5×3×3 mm was added to 300 μL extraction solution (0.1 M Tris, 0.01 M EDTA, 0.1 M NaCl, 2% SDS, proteinase K 0.8 mgmL^{-1}, pH 8.0), mixed, and incubated at 55°C for 1 hour. After digestion and phenol extraction, 2.5 volumes of ice-cold 99% ethanol were added, the tube was inverted several times, and spun for 5 minutes in a microcentrifuge to pellet the precipitated DNA. The pellet was washed with 70% ethanol, air-dried for 30 minutes, and dissolved in 100 μL TE buffer (0.01 M Tris, 0.02 M EDTA, pH 7.5).

PCR amplification of mtDNA

The main set of PCR primers employed were "universal" vertebrate sequences which amplified a 2.5

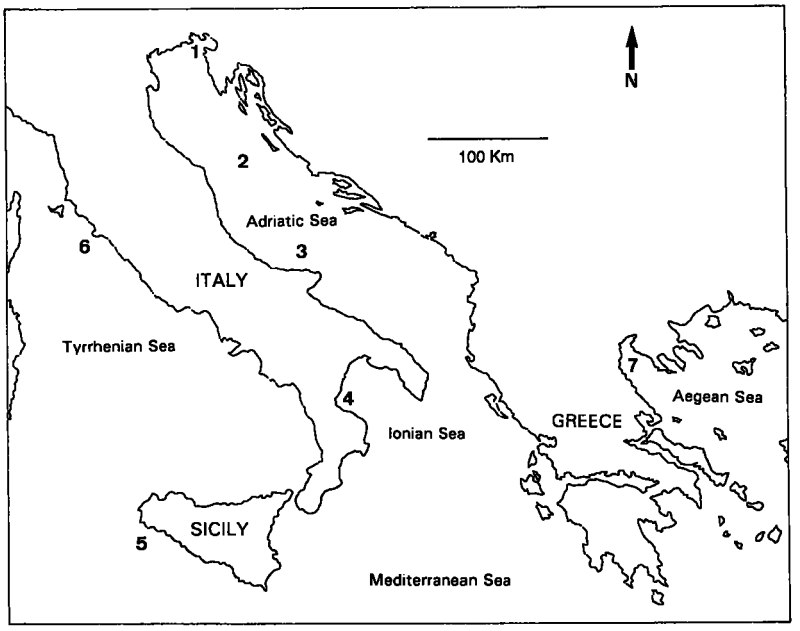

Figure 1

Map of the northern Mediterranean showing sample locations for European anchovy, *Engraulis encrasicolus*. Samples referred to in the text were Trieste (1), Ancona (2), Vieste, (3), Ionian Sea (4), Sicilian Channel (5), Tyrrhenian Sea (6), and Aegean Sea (7).

Kb region containing the ND5 and ND6 genes of the NADH dehydrogenase complex (Cronin et al., 1993).

ND 5/6
5'- AAT AGT TTA TCC AGT TGG TCT TAG -3' 24 mer
5'- TTA CAA CGA TGG TTT TTC ATA GTC A -3' 25 mer

Other mtDNA primers assayed amplified a 2.3 Kb region coding for the ND3/ND4 genes (Cronin et al., 1993) and a 2.0 Kb fragment coding for ND1 and 16s RNA (Hall, 1992[3]).

ND 3/4
5'- TAA (C/T)TA GTA CAG (C/T)TG ACT TCC AA -3' 23 mer
5'- TTT TGG TTC CTA AGA CCA A(C/T)G GAT -3' 24 mer

ND1/16s
5'- ACC CCG CCT GTT TAC CAA AAA CAT -3' 24 mer
5'- GGT ATG AGC CCG ATA GCT TA -3' 20 mer

The amount of template DNA for the PCR reaction was usually 1 μL of the 100 μL volume extraction described above (approximately 50 ng), but occasionally a 1/10 dilution was required for efficient amplification. The reaction cocktail (per 50 μL reaction) contained 5 μL 10× PCR buffer (0.5 M KCl, 0.1 M Tris, 2.5 mM $MgCl_2$, pH 8.3), 5μL dNTP mix (at 2 mM with respect to each dNTP), 1 μL of each primer (approximately 25 pmol), 1 u Boehringer *Taq* polymerase, 1 μL template DNA and 37 μL sterile filtered dH_20. This was overlaid with two drops of sterile mineral oil. Amplification cycle conditions for the ND5/6 primers, with the use of a Hybaid Omni-Gene thermal cycler, were 1) 95°C, 5 min; 1 cycle; 2) 49°C, 1 min 30 s; 72°C, 1 min 30 s; 94°C, 30 s; 25 cycles; 3) 49°C, 1 min 30 s; 72°C, 10 min; 1 cycle. Conditions for amplifying ND1/16s and ND3/4 were identical, except that, for ND1/16s, annealing took place at 51°C.

DNA restriction and data collection

From 3 to 5 μL of PCR product were restricted with a range of endonucleases recognizing four, five, and six nucleotide sequences: *Aat* II, *Alu* I, *Ava* I, *Ava* II, *Cfo* I, *Eco* RI, *Hae* III (*Pal* I), *Hind* III, *Hinf* I, *Msp* I, *Nci* I, *Pvu* I, *Rsa* I, *Sau* 3AI, *Sau* 96I, and *Taq* I. Restriction products were resolved on agarose and polyacrylamide gels by using a TBE buffer system (Sambrook et al., 1989) and visualized by ethidium bromide and silver nitrate staining, respectively. Restriction fragment data were recorded from all gels, and fragment sizes estimated from their mobilities relative to lambda-phage DNA-marker frag-

[3] Hall, H. 1992. Zoological Society of London, Regent's Park, London, U.K. Personal commun.

ments. For each enzyme, the various restriction patterns were named alphabetically ("A" being the most common), and the resultant composite haplotypes were assigned numerically. Within-sample variation was estimated as nucleotide diversity (Nei and Tajima, 1981; Nei, 1987), as the average number of nucleotide substitutions per site for the sequences sampled, and as haplotype diversity, which is related to allozyme heterozygosity. Nucleotide divergence (Nei, 1987) was used to measure between-sample variation. The significance of geographic heterogeneity in haplotype distribution was tested by using a Monte Carlo χ^2 approach (Roff and Bentzen, 1989), and this method was also used to test the distribution of banding patterns produced by single restriction enzymes. Partitioning of mtDNA variation was accomplished by gene diversity analysis (Nei, 1973; Chakraborty, 1980). Between-sample variation (G_{ST}) was subdivided into variation between seas (G_{SEA}) and between sampling ports within seas (G_{PS}). Data were analysed by using REAP v4.1 (McElroy et al., 1992), PHYLIP v3.5c (Felsenstein, 1993), and spreadsheet macros were written for Lotus 1-2-3.

Results

DNA amplification

Of the three primer pairs assayed, only those for the ND5/6 and ND1/16s regions produced amplification products consistently. No products were obtained from anchovy DNA templates with the ND3/4 primer set. We estimated the sizes of the unrestricted ND5/6 and ND1/16s PCR products to be 2.5 Kb and 2.0 Kb, respectively.

Levels of variability

In a preliminary study of 15 fish, 10 ND5/6 composite haplotypes were revealed by using 12 restriction enzymes (***Alu* I**, *Ava* II, ***Cfo* I**, ***Eco* RI**, ***Hinf* I**, *Msp* I, *Nci* I, *Pal* I, *Rsa* I, ***Sau* 96I** and ***Taq* I**). Only one enzyme, *Sau* 3AI, was monomorphic for all samples; all other enzymes revealed variation. The same number of haplotypes revealed by these eleven enzymes could also be differentiated by using a subset of six (those in bold type); hence these six were chosen to analyze the entire sample set.

Initial studies indicated that levels of diversity in ND1/16s were of a similar order to those in ND5/6. Sixteen endonucleases were used (*Aat* II, ***Alu* I**, *Ava* I, ***Ava* II**, ***Cfo* I**, *Eco* RI, ***Hae* III**, *Hin*d III, *Hinf* I, ***Msp* I**, ***Nci* I**, *Pvu* I, ***Rsa* I**, *Sau* 3AI, ***Sau* 96I**, *Taq* I), five of which did not cut the fragment (*Aat* II, *Ava* I, *Eco* RI, *Hin*d III, and *Pvu* I), three of which produced monomorphic profiles (*Hinf* I, *Sau* 3AI, and *Taq* I), and another eight of which revealed polymorphism (bold type). Ten composite haplotypes were detected in 15 individuals. Because of logistic considerations, further work on the ND1/16s region was sacrificed in favor of increasing sample numbers in the study of ND5/6 variation; hence all subsequent results refer solely to the latter region.

A total of 77 ND5/6 restriction fragments were scored for the entire data set of 140 fish, revealing 53 composite haplotypes (Table 1). Of these, 14 haplotypes occurred at least twice, and the remaining 39 were encountered in a single fish only. Only haplotype 3 was found at all sample locations. Mean within-sample haplotype diversity was 0.8816 (±0.0004), and mean nucleotide diversity was 0.0164 ($\pm 3\times10^{-6}$) (Table 2). According to both measures, the lowest level of variation was found in the Aegean Sea sample, where 45% of the fish were of genotype 3.

Inter-sample variation

Nucleotide divergence between samples varied between 0.0005 and 0.0137, the mean figure being 0.0031 (Table 3). The greatest values of nucleotide divergence were in comparisons involving the Aegean Sea sample.

Monte Carlo χ^2 analysis of geographic heterogeneity was, in each case, carried out with 1,000 randomizations of the data set. When all samples and all 53 haplotypes were included, there was significant geographic heterogeneity (Table 4(i); P=0.011), and this was also true of the distribution of restriction morphs for all enzymes except *Eco* RI (data not shown). Removing the Aegean Sea group resulted in a probability of geographic homogeneity of haplotypes of 0.337 (Table 4(ii)). Indeed, out of 21 pairwise comparisons between all seven samples (Table 5), only five were significant at P<0.05, and these all involved the Aegean sample (only the Aegean–Sicilian-Channel comparison was nonsignificant; P=0.23). Sequential Bonferroni testing (Rice, 1989) rejected all but the two most significant of these results, however (Table 5).

A comparison of the distribution of 28 composite haplotypes between the three Adriatic samples was nonsignificant (P=0.689; Table 4(iii)), hence the Adriatic samples were pooled (n=60). Although there was no significant heterogeneity in haplotype distribution between the pooled Adriatic and outlying samples (omitting the Aegean Sea) (P=0.488; Table 4(iv)), there was significant heterogeneity in the distribution of forms revealed by one out of the six enzymes (Table 4(v); *Sau* 96I, P=0.007). There was thus an indication of genetic heterogeneity between Adriatic fish and those from adjacent waters.

Table 1

European anchovy, *Engraulis encrasicolus*, mtDNA composite haplotypes, and their distribution across samples. Enzymes used to constuct composite haplotypes were (left to right): *Alu* I, *Cfo* I, *Eco* RI, *Hinf* I, *Sau* 96I and *Taq* I. Sample locations were Trieste (Tr), Ancona (An), Vieste (Vi), Ionian Sea (Io), Sicily (Si), Tyrrhenian Sea (Ty) and Aegean Sea (Aeg).

		Number of each haplotype per sample						
	Haplotype	Tr	An	Vi	Io	Si	Ty	Aeg
1	AAAAAB	4	2	1	2	1	5	—
2	AAAABA	1	3	2	2	1	2	—
3	BBABCC	3	2	2	6	7	5	9
4	ACAABA	3	1	1	—	—	—	—
5	AAAADB	1	1	3	1	2	3	—
6	AAAABC	—	1	1	—	—	—	—
7	DABAAB	2	1	—	—	—	—	—
8	EABAAB	—	3	1	1	—	—	—
9	DABFAB	1	—	—	1	—	—	—
10	AAACAB	—	1	1	1	—	—	—
11	CDBDAB	—	1	—	2	1	—	—
12	IBABCC	—	—	—	—	—	—	2
13	BGABEC	—	—	—	—	1	—	1
14	BBABKC	—	—	—	—	—	2	—
15	DABAAA	1	—	—	—	—	—	—
16	FABAAB	1	—	—	—	—	—	—
17	GCAABA	1	—	—	—	—	—	—
18	AFAABA	1	—	—	—	—	—	—
19	BBAGCA	1	—	—	—	—	—	—
20	BCAABA	—	1	—	—	—	—	—
21	AHABCC	—	1	—	—	—	—	—
22	DABAAC	—	1	—	—	—	—	—
23	ACCABA	—	1	—	—	—	—	—
24	HBABCC	—	—	1	—	—	—	—
25	CDBAAB	—	—	1	—	—	—	—
26	IBABCC	—	—	1	—	—	—	—
27	AEACAB	—	—	1	—	—	—	—
28	AAACAG	—	—	1	—	—	—	—
29	EAAABA	—	—	1	—	—	—	—
30	AAAHAB	—	—	1	—	—	—	—
31	BCABCC	—	—	1	—	—	—	—
32	BBABCF	—	—	—	1	—	—	—
33	BBABEC	—	—	—	1	—	—	—
34	AAAAIC	—	—	—	1	—	—	—
35	BBABJC	—	—	—	1	—	—	—
36	AEBIAB	—	—	—	—	1	—	—
37	BAAADB	—	—	—	—	1	—	—
38	AAAAHD	—	—	—	—	1	—	—
39	AAAAGB	—	—	—	—	1	—	—
40	AAAAFA	—	—	—	—	1	—	—
41	BBAECE	—	—	—	—	1	—	—
42	DCBAAB	—	—	—	—	1	—	—
43	BBABCE	—	—	—	—	—	1	—
44	IBABCC	—	—	—	—	—	1	—
45	BBABIE	—	—	—	—	—	1	—
46	BBAICC	—	—	—	—	—	—	1
47	BHABKC	—	—	—	—	—	—	1
48	BBABCA	—	—	—	—	—	—	1
49	IIABCC	—	—	—	—	—	—	1
50	IABAAB	—	—	—	—	—	—	1
51	BBBBCC	—	—	—	—	—	—	1
52	BJABCC	—	—	—	—	—	—	1
53	BHABCC	—	—	—	—	—	—	1

Gene diversity analysis of all seven samples (Table 6) indicated that over 92.4% of the mtDNA variation detected was within samples, hence 7.6% was partitioned between samples (G_{ST}). Jackknifed estimates of G_{ST} were in the 5.8–8.3% range, and the mean estimate was significantly different from zero (t_s=22.51, df=6, P<0.001). G_{ST} values for pairwise comparisons of samples were in the 2.6–19.4% range, the highest values from comparisons involving the Aegean Sea group (Table 7). G_{ST} was subdivided into variation between seas (G_{SEA}) and between sampling ports within seas (for G_{PS}, in the Adriatic only). G_{SEA} accounted for 77% of inter-sample variation, leaving 23% partitioned between Adriatic ports (Table 6). The indication was that the degree of genetic differentiation was greater on a larger geographic scale.

Discussion

Restriction analysis of PCR-amplified mtDNA is a relatively simple technique which enables the rapid screening of large numbers of fish for DNA-level polymorphism. The wide range of "universal" and teleost-specific primer sequences in the literature (e.g. Avise, 1994) means that one or more fragments that amplify successfully should be obtainable for most species. Additionally, the production of μg quantities of DNA by PCR and the silver-staining technique remove the necessity for isotopic labelling of restriction fragments, an improvement both in terms of cost and safety.

Our results show that variability in anchovy ND5/6 genes is notably high: 53 haplotypes were detected in only 140 fish, with a mean nucleotide diversity of 0.0164. Hauser et al. (in press) have reported similar levels of variation for the ND5/6 region in kapenta, *Limnothrissa miodon,* a freshwater clupeoid. Using the same primers as those in this study and a set of six enzymes, they reported 85 haplotypes in 362 fish, with nucleotide diversities of 0.0137 and 0.0098 for Lake Tanganyika and Lake Kivu fish, respectively, and commented that the order Clupeiformes may show generally high levels of mtDNA variation. These figures contrast with a restriction study that showed the ND5/6 region to be monomorphic in Atlantic salmon, *Salmo salar* (O'Connell, 1993), while work on brown trout, *Salmo trutta* (Hall, 1993), has demonstrated intermediate levels of variation (19 haplotypes in 219 fish with the use of seven enzymes). Recent work on the ND5/6 genes of Trinidadian guppies, *Poecilia reticulata,* has also shown low levels of intrapopulation diversity, attributed to the effects of local extinctions and founder events (Shaw[4]). We believe that the relatively high level of variation described here may be representative of the entire anchovy mtDNA genome because our pilot study of the ND1/16s region showed that variability was of a similar order to ND5/6. Chapman et al. (1994), in a recent study of the genus *Alosa*, noted that the ND1/16s region evolved more quickly than cy-

Table 2

Levels of mtDNA variation within samples of European anchovy, *Engraulis encrasicolus,* measured as haplotype and nucleotide diversity.

Sample	Haplotype diversity	Nucleotide diversity
Trieste	0.9077 ±0.02177	0.017130
Ancona	0.9333 ±0.01703	0.017974
Vieste	0.9487 ±0.01493	0.019318
Ionian	0.8821 ±0.03557	0.020577
Sicily	0.8615 ±0.04568	0.017546
Tyrrhenian	0.8462 ±0.02839	0.015874
Aegean	0.7846 ±0.06273	0.006370
Mean	0.8806 ±0.00045	0.016399

[4] Shaw, P. W. 1994. School of Biological Sciences, Univ. Wales Swansea, Singleton Park, Swansea, U.K. Personal commun.

Table 3

Nucleotide divergence (Nei, 1987 [Eq. 10.21]) between samples of European anchovy, *Engraulis encrasicolus.*

	Nucleotide divergence					
Sample	Trieste	Ancona	Vieste	Ionian	Sicily	Tyrrhenian
Ancona	0.00040					
Vieste	0.00053	0.00032				
Ionian	0.00001	0.00011	0.00042			
Sicily	0.00302	0.00333	0.00160	0.00060		
Tyrrhenian	0.00216	0.00247	0.00105	0.00031	0.00046	
Aegean	0.01281	0.01375	0.01032	0.00799	0.00286	0.00423

Table 4

Monte Carlo χ^2 simulation analyses of the geographical distribution of mtDNA variation in European anchovy, *Engraulis encrasicolus*. For all samples n=20. For all analyses, 1,000 iterations were performed. * = those comparisons that were still significant at P<0.05 after sequential Bonferroni testing.

i) Comparing all seven samples; 53 composite haplotypes
χ^2 from original matrix = 323.3, exceeded by 11/1,000 simulations; P=0.011*;

ii) Comparing all samples except Aegean Sea; 44 composite haplotypes
χ^2 from original matrix = 224.5, exceeded by 337/1,000 simulations; P=0.337;

iii) Comparing the three Adriatic Sea samples only; 28 composite haplotypes
χ^2 from original matrix = 51.99, exceeded by 689/1,000 simulations; P=0.689;

iv) Comparing all samples except the Aegean Sea after pooling Adriatic Sea samples (i.e. four sample groups); 44 composite haplotypes
χ^2 from original matrix = 130.41, exceeded by 488/1,000 simulations; P=0.488;

v) Comparisons of the distribution of restriction patterns for individual endonucleases between a pooled Adriatic sample (n=60) and all other groups except the Aegean Sea.

Enzyme	No. patterns	Original χ^2	Exceeded by n simulations	P
Alu I	9	22.5	588/1,000	P=0.588
Cfo I	8	23.5	321/1,000	P=0.321
Eco RI	3	10.1	100/1,000	P=0.100
Hinf I	9	31.7	111/1,000	P=0.111
Sau 96I	11	49.4	7/1,000	P=0.007*
Taq I	8	31.3	48/1,000	P=0.048

Table 5

Probability values for pairwise Monte Carlo χ^2 comparisons of ND5/6 composite haplotype distribution in samples of European anchovy, *Engraulis encrasicolus*. All comparisons employed 1,000 iterations. * = those comparisons that were still significant at P<0.05 after sequential Bonferroni testing.

Sample	Trieste	Ancona	Vieste	Ionian	Sicily	Tyrrhenian
Ancona	0.463					
Vieste	0.347	0.952				
Ionian	0.282	0.815	0.620			
Sicily	0.116	0.248	0.474	0.807		
Tyrrhenian	0.151	0.100	0.242	0.302	0.272	
Aegean	<0.001*	<0.001*	0.003	0.022	0.231	0.003

tochrome *b*, and an alternative view is that the genes of the NADH dehydrogenase system have a uniformly high rate of evolution. Magoulas (1993), however, has reported over 30 composite haplotypes in RFLP analysis of the entire *E. encrasicolus* mtDNA molecule, and, because his results were obtained by using five enzymes which recognized hexanucleotide sites only, his observations lend support to our hypothesis.

The distribution of both composite haplotypes and restriction forms for individual restriction enzymes differed between the Aegean Sea anchovy population and the other areas sampled. When the same samples were studied with allozyme electrophoresis, the greatest estimates of genetic divergence were also found in comparisons involving Aegean Sea fish; hence both techniques confirm the distinctness of this group (Carvalho et al.[5]). Magoulas (1993) found two

[5] Carvalho, G. R., D. G. Bembo, A. Carone, G. Giesbrecht, N. Cingolani, and T. J. Pitcher. 1994. Stock discrimination in relation to the assessment of Adriatic anchovy and sardine fisheries. Final Report to the European Community EC XIV-1/MED/91/001/A. Available from European Commission, Directorate-General XIV Fisheries, internal resources, Conservation Policy and Environmental Questions, Rue de la Loi 200, B-1049, Brussels, Belgium.

Table 6

Gene diversity analysis of ND5/6 haplotypes in European anchovy, *Engraulis encrasicolus*. Minima and maxima were derived by jackknife deletion of samples (i.e. seven recalculations).

Gene diversity		Mean	Minimum	Maximum
Total	H_T	0.9327	0.9247	0.9377
Within samples	H_S	0.8615	0.8475	0.8750
Between samples	D_{ST}	0.0712	0.0541	0.0782
Coefficients				
Within samples	G_S	0.9236	0.9164	0.9412
Between samples	G_{ST}	0.0763	0.0583	0.0836
Between seas	G_{SEA}	0.0584	0.0395	0.0687
Between ports within seas	G_{PS}	0.0178	0.0148	0.0241

Mean G_{SEA}/G_{ST} =76.6%
Mean G_{PS}/G_{ST} =23.4%

Table 7

G_{ST} values for pairwise comparisons of samples of European anchovy, *Engraulis encrasicolus*.

	Coefficient of between-sample variation G_{ST}					
Sample	Trieste	Ancona	Vieste	Ionian	Sicily	Tyrrhenian
Ancona	0.0966					
Vieste	0.0261	0.0774				
Ionian	0.1202	0.1081	0.1014			
Sicily	0.1301	0.1185	0.1111	0.1403		
Tyrrhenian	0.1363	0.1251	0.1179	0.1479	0.1576	
Aegean	0.1667	0.1553	0.1480	0.1766	0.1856	0.1945

main anchovy mtDNA phylads (groups of related haplotypes) in the Mediterranean: phylad *A* dominated the Black and Aegean seas, and phylad *B* was more numerous in western waters. More extensive sampling in the Aegean and Black seas would allow us to test whether the same groupings are supported by analysis of the ND5/6 genes only.

The effective number of female migrants between populations, N_eM, may be estimated from mtDNA data by using the term $N_eM = (1/G_{ST}-1)/2$ (Nei, 1973; Ward and Grewe, 1994). On the basis of our data from pairwise comparisons, between 2 and 20 migrant females per generation could account for observed levels of interpopulation diversity. The former figure was calculated for the comparison between Aegean Sea and Tyrrhenian Sea fish, the two most spatially isolated samples. Such data should always be interpreted with caution, however (Ferguson, 1994), because small (and nonsignificant) values of G_{ST} will still generate estimates of numbers of effective migrants that will appear low relative to estimates of stock size for pelagic species. For example, the higher figure of 20 quoted above was derived from a G_{ST} value of 0.0261, although Monte Carlo χ^2 analysis had not demonstrated significant heterogeneity between the samples.

All Monte Carlo comparisons of haplotype distribution that omitted the Aegean Sea sample were nonsignificant, although, after pooling the three Adriatic samples, a comparison of restriction pattern distribution was significant for one enzyme (*Sau* 96I). There was thus some indication of genetic differentiation between fish from the Adriatic Sea and adjacent waters, as has already been suggested by allozyme analysis (Carvalho[5]). The discreteness of the Adriatic stock has also been demonstrated with more traditional methods, and meristic studies have shown that these anchovies are highly distinct from those found in the neighboring Ionian Sea (Carvalho[5]). The large number of unique, composite haplotypes found in the ND5/6 genes undoubtedly confounded analysis, and further work on *E. encrasicolus*

ND5/6 genes will require greater sample sizes (probably around 40–50 fish). Alternatively, another region such as ND1/16s or the cytochrome oxidase (CO) genes might be a source of complementary mtDNA markers. In revealing spatial trends in accordance with those recorded in previous allozyme and mtDNA studies, our results underline the power, sensitivity, and speed of this genetic approach to stock discrimination in such a highly mobile marine teleost.

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Effects of temperature on the development and survival of eggs of four coastal California fishes

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Abstract.—Laboratory experiments were conducted to determine the effects of temperature on egg development and survival of four fish species found off southern California. Our objectives were to further understanding of natural spawning patterns and to aid in identifying and ageing field-collected specimens. An egg-staging procedure was devised and eggs were observed every two hours during development at a range of temperatures (8–28°C). Barred sand bass, *Paralabrax nebulifer*, eggs survived to hatching and produced viable embryos at the highest temperature range (16–28°C), reflecting this species' summer spawning season. Fantail sole, *Xystreurys liolepis*, eggs also hatched at a higher temperature range (16–24°C). This species spawns primarily from summer through fall. Eggs of the two species with winter-spring spawning peaks, white croaker, *Genyonemus lineatus*, and California halibut, *Paralichthys californicus*, had lower temperature-tolerance ranges (12–20°C). Developmental rate at a specific temperature did not significantly differ between species, whereas within tolerance limits, temperature strongly affected rate of development for all species. Time to hatching for all species was inversely related to temperature, and the relationship was approximately exponential. Species-specific differences in egg-stage sequence were observed; embryonic organogenesis in relation to germ-ring migration and blastopore closure was faster for barred sand bass and fantail sole than for white croaker and California halibut.

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Many studies have examined the influence of temperature on the development and survival of fish during early life history stages (see reviews by Pauly and Pullin, 1988; Pepin, 1991). Since the strength of a year class may be established during early stages (Hjort, 1914; May, 1974), it is important to understand possible causes of mortality during this period. For high egg viability, the timing and location of spawning must coincide with favorable environmental conditions including sea temperature (Alderdice and Forrester, 1968; Riley, 1974; Thompson and Riley, 1981). Additionally, detailed information on the relationship between temperature and the rate of egg development has been used to age field-collected eggs and to backcalculate spawning time (Ferraro, 1980; Thompson and Riley, 1981; Haynes and Ignell, 1983).

We determined the effects of temperature on egg development and survival of four fish species found off southern California: barred sand bass, *Paralabrax nebulifer* (Serranidae); white croaker, *Genyonemus lineatus* (Sciaenidae); California halibut, *Paralichthys californicus* (Paralichthyidae); and fantail sole, *Xystreurys liolepis* (Paralichthyidae). The first three species are important sport and commercial fishes in this area (Lavenberg et al., 1986). The larvae of these species are relatively abundant in the nearshore zone, where white croaker and California halibut spawn most intensely in winter–spring, and barred sand bass in summer (Love et al., 1984; Lavenberg et al., 1986; Walker et al., 1987; Moser and Watson, 1990; McGowen, 1993). Fantail sole larvae are less common off southern California where peaks in abundance occur during late summer and fall (Moser and Watson, 1990). Our primary objective in examining the eggs of these four species was to understand how temperature affects development and survival during the critical early life history period and thus contribute to a better understanding of temporal and spatial spawning patterns in the wild. A secondary objective was to gather information to aid in identifying and ageing field-collected specimens.

Materials and methods

Brood stocks of 5–12 adult fish were held in the laboratory in tanks rang-

ing from 1.8 to 7.6 m diameter and supplied with flow-through coastal seawater at a salinity of 34–35‰. Temperature and photoperiod were maintained at ambient levels simulating natural conditions in nearshore southern California waters (Caddell et al., 1990). Experiments generally began during the spawning season and at a temperature at which spawning would naturally occur for each species (Table 1). The hormones gonadotropin and carp pituitary were used to induce ovarian development of white croaker and fantail sole, respectively, following the methods of Caddell et al. (1990). California halibut brood stock ripened naturally. For each of these three species, eggs were stripped from one female and sperm from 2 or 3 males and these were combined to obtain a single batch of newly fertilized eggs. Barred sand bass spawned naturally in captivity, and newly fertilized eggs floating at the water's surface were collected. The number of individual sand bass participating in a spawning event was unknown. Egg development was initially monitored for each species at five temperatures: 8°, 12°, 16°, 20°, and 24°C. Barred sand bass eggs were also exposed to 28°C water because of their warmer (summer) spawning season. Since fantail sole eggs exhibited high survival at 24°C during the initial experiment, an additional trial was conducted at 28°C in order to establish the upper temperature tolerance limit of sole eggs. This trial was conducted approximately one year later, with incoming water heated to a typical summer–fall temperature (18.5°C) to facilitate gonad maturation.

For each species, an experiment began immediately after egg fertilization. Eggs were stocked in 3-L glass jars at a density of about 100 per liter. The jars contained filtered, UV-light–sterilized seawater at the ambient spawning temperature (Table 1). Jars were placed in temperature-controlled water baths, and jar temperatures were raised or lowered 1°C every 15 minutes until the desired treatment temperatures (see above paragraph) were reached. In order to incubate adequate numbers of eggs, two jars were maintained at each treatment temperature (±0.5°C) for the duration of the experiment. Each jar was mildly aerated to avoid the formation of temperature gradients. Light cycles were maintained at 12L:12D. Every 2 hours until hatching, at least five buoyant eggs per jar were sampled and preserved in 4% formalin. Water in the jars was not exchanged with fresh seawater during the experiments other than as necessary to siphon out dead eggs that accumulated on the bottom.

Eggs were examined with a dissecting microscope to characterize development. We did not illustrate stages of development; eggs of California halibut and fantail sole are illustrated in Oda (1991), and white croaker eggs are illustrated in Watson (1982). We devised a staging classification system based on Ahlstrom (1943) and Walsh et al. (1991) (Table 2). Because the rate of embryonic development in relation to germ-ring migration and blastopore closure varied by species, we could not develop a sequential staging system incorporating all developmental events that could be used for all species. We formulated, therefore, a staging system where some events of embryonic development (stages E, O, and S) were separate from general egg developmental stages I–IX (Table 2).

For each temperature-by-species treatment, a sample size of at least ten eggs per 2-hour time pe-

Table 1

Egg measurements and details of experimental protocol for four southern California fish species spawned in the laboratory. Dates experiments were initiated and water temperatures (T) at which fish were spawned are presented. Thirty laboratory-reared eggs of each species were measured after preservation in 4% formalin for at least one year. Superscripts indicate chorion, yolk, and oil globule mean diameters that differed significantly between species using the Tukey multiple-range test ($P<0.05$).

	Spawning		Egg mean diameter (mm)		
Species	Date	T (°C)	Chorion (SD)	Yolk (SD)	Oil (SD)
Barred sand bass *Paralabrax nebulifer*	17 Aug 1986	18.0	0.85 (0.02)[1]	0.64 (0.03)[1]	0.17 (0.01)[1]
White croaker *Genyonemus lineatus*	19 Apr 1985	15.0	0.81 (0.02)[2]	0.63 (0.02)[1]	0.22 (0.02)[2]
California halibut *Paralichthys californicus*	10 May 1985	16.0	0.75 (0.02)[3]	0.58 (0.02)[2]	0.12 (0.01)[3]
Fantail sole *Xystreurys liolepis*	6 Nov 1985	16.5	0.76 (0.02)[4]	0.61 (0.03)[1]	0.20 (0.01)[4]
2nd trial (28°C)	13 Jan 1987	18.5			

Table 2

Stages of development for laboratory-reared eggs of four California fishes. Each stage begins with the described developmental event. Because the sequence of three embryonic developmental events (stages E, O, and S) differed by species in relation to stages V and VI, they are presented separately.

Stage	Description
I	Cell division; 2–128 celled eggs
II	Multicelled (>128 celled) blastodermal cap evident
III	Segmentation cavity developed
IV	Germ ring formed and embryonic shield visible
V	Germ ring encloses >1/2 of the yolk mass
VI	Blastopore closure
VII	Embryo tail separated from yolk ≤ head length
VIII	Embryo tail separated from yolk > head length
IX	Eggs hatched
Stage	**Description**
E	Thickening of embryonic axis visible
O	Optic vesicles present
S	Somites visible

riod was obtained by combining eggs sampled from the two jars held at each temperature. A sample was determined to be at an egg stage when ≥50% of the eggs in that sample met the stage criteria. Because the duration of each stage differed, we standardized our presentation of egg development in accordance with Ketchen (1956), by spacing egg stages on the vertical axis proportional to the rate of development at a median survival temperature: 20°C for barred sand bass and fantail sole (Figs. 1 and 2), and 16°C for white croaker and California halibut (Figs. 3 and 4).

For each species at each temperature, the rate of egg development was quantified as the slope (β) of age regressed on stage, where age is time (in hours) from fertilization to the nine developmental stages (I–IX). Embryonic developmental stages E, O, and S were not considered in this analysis. Lines were fitted by using least-squares regression forced through the origin. Multiple regression equations were also fitted for each of the four species to estimate age (in hours) of an egg, given developmental temperature and egg stage (I–VIII). Stage IX (hatched) was not included in these predictive equations because this would not be a recognizable stage in field-collected eggs.

Chorion, yolk mass, and oil globule diameters were measured for 30 eggs of each species over a range of developmental stages. To allow for shrinkage, measurements were made after eggs had remained in 4% formalin for at least one year.

Results

Eggs of all four species were buoyant and spherical and had a smooth chorion, unsegmented yolk, and a single oil globule. Mean chorion diameter was significantly different between all species ranging from 0.75 mm (California halibut) to 0.85 mm (barred sand bass) (Table 1; one-way analysis of variance (ANOVA), $F_{3,116}$=184.6; P<0.001). Only the mean yolk diameter of California halibut differed significantly from mean yolk diameters of the other species (Table 1; one-way ANOVA, $F_{3,108}$=29.3; P<0.001). Mean oil globule diameter varied from 0.12 mm (California halibut) to 0.22 mm (white croaker) and was significantly different between all species (Table 1; one-way ANOVA, $F_{3,108}$=320.2; P<0.001).

Embryonic development in relation to germ-ring migration and blastopore closure occurred sooner for

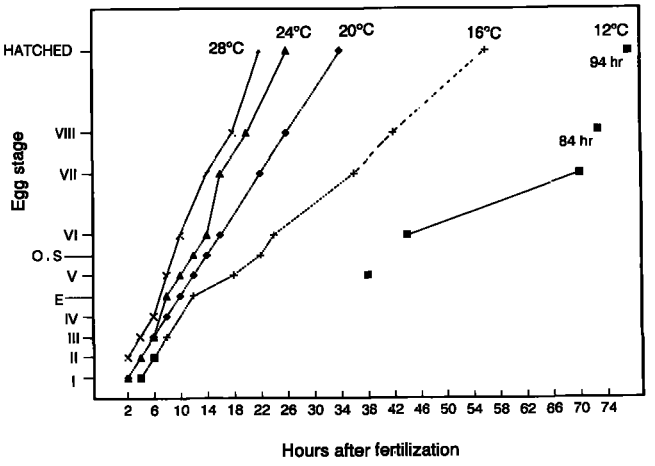

Figure 1

Development of eggs of barred sand bass, *Paralabrax nebulifer*, at five temperatures. Eggs died at 8°C with no cell division evident. At 12°C, many eggs sampled were dead, resulting in a lack of egg-stage observations for some time periods (unconnected points). Hatched larvae from eggs at 12°C were abnormal and soon died. Descriptions of egg stages are presented in Table 2.

barred sand bass and fantail sole eggs than for white croaker and California halibut eggs. For both bass and sole, optic vesicles and somites (stages O and S) were visible in the embryo by the time of blastopore closure, stage VI (Table 2, Figs. 1 and 2). Embryonic development of bass was particularly rapid; the embryonic axis was evident by the time the germ ring enclosed half the yolk mass. In contrast, for both croaker and halibut the embryonic axis was visible just prior to blastopore closure, and optic vesicles and somites appeared after closure (Figs. 3 and 4).

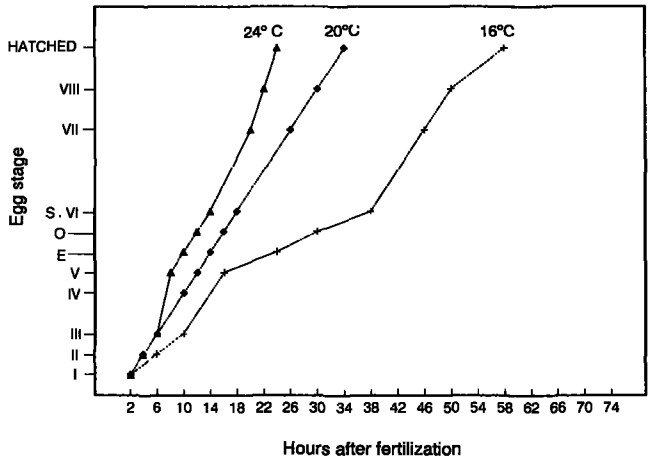

Figure 2

Development of eggs of fantail sole, *Xystreurys liolepis*, at three temperatures. Eggs died at 8°, 12°, and 28°C during stage II. Descriptions of egg stages are presented in Table 2.

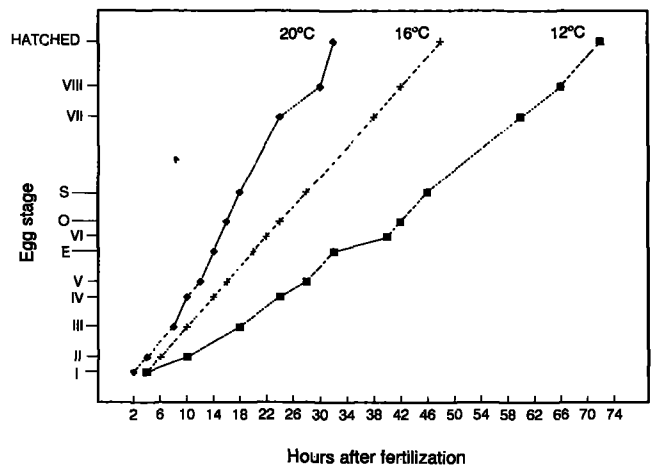

Figure 3

Development of eggs of white croaker, *Genyonemus lineatus*, at three temperatures. Eggs died at 8°C during stage I and at 24°C with no cell division evident. Descriptions of egg stages are presented in Table 2.

Eggs of barred sand bass hatched at a wider range of temperatures, 12–28°C, than did those of the other three species. However, at 12°C bass eggs took much longer to hatch (94 hours) than at higher temperatures, and many sampled eggs were dead (Fig. 1). Bass larvae that hatched at 12°C appeared to be abnormally developed, swam weakly, and soon died. Thus, successful hatching of viable embryos occurred only at 16–28°C for barred sand bass. Fantail sole eggs hatched at 16–24°C (Fig. 2), whereas both white croaker and California halibut eggs hatched at a lower temperature range, 12–20°C (Figs. 3 and 4). Although not quantified, in each treatment most eggs that remained after sampling hatched and all larvae in the samples (except barred sand bass at 12°C) appeared normal and viable. At temperatures where hatching did not occur (8°C for sand bass; 8°, 12° and 28°C for fantail sole; and 8° and 24°C for both white croaker and California halibut), eggs died with little development, reaching at most stage II.

Within survival ranges, eggs of all species developed faster at higher temperatures (Figs. 1–4). The relationship between age and stage was best fitted by a linear function ($Age=\beta\, stage$; $r^2>0.95$; Table 3). One-way ANOVA was used to test effects of species and temperature on rate of development (β); we could not test interactions between species and temperature with a two-way ANOVA because of missing values due to egg mortalities at temperature extremes. Species had no effect on rate of development (one-way ANOVA, $F_{3,10}=0.20$; $P=0.89$). Pooling across species showed that temperature had a strong effect on rate of development (one-way ANOVA, $F_{4,9}=33.72$; $P<0.001$). A multiple-range analysis (the Tukey test) for the temperature effect showed rates of development at 12°, 16°, and 20°C to be significantly different ($P<0.05$; Table 3).

Because developmental rate at a specific temperature did not significantly differ between species, we examined the general relationship between temperature and age at hatching by pooling data from all species (Fig. 5). This relationship was best fit by an exponential function:

$$\mathrm{Ln}(Age) = 5.395 - 0.090\,(T), \qquad [r^2=0.94, n=14]$$

where Age is the time in hours from fertilization to hatching and T is the incubation temperature (°C). Similarly, equations derived for each species to determine egg age at stage and

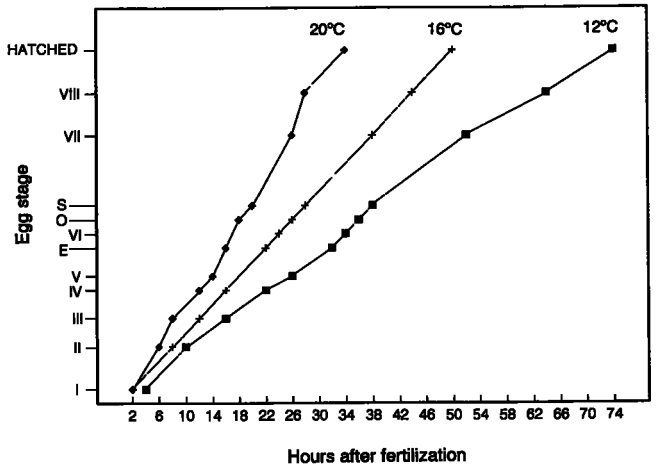

Figure 4

Development of eggs of California halibut, *Paralichthys californicus*, at three temperatures. Eggs died at 8°C during stage I and at 24°C during stage II. Descriptions of egg stages are presented in Table 2.

incubation temperature were best fit by exponential functions (Table 4).

Discussion

Many egg-staging systems have been developed for fishes (Ahlstrom, 1943; Colby and Brooke, 1973; Riley, 1974; Laurence and Rogers, 1976; Ferraro, 1980; Thompson and Riley, 1981; Haynes and Ignell, 1983; Walsh et al., 1991). We found it difficult to devise a system that could be used for all four species because the embryonic development of barred sand bass and fantail sole was faster in relation to germ-ring migration than that of white croaker and California halibut. Species-specific rates of embryonic organogenesis relative to blastopore closure were also noted by Ahlstrom and Moser (1980). Although not commonly considered, these developmental differences could be useful traits in identifying field-collected fish eggs.

Absolute temperature ranges tolerated by eggs of the four species reflect temperatures encountered owing to seasonal spawning patterns off southern California (Love et al., 1984; Lavenberg et al., 1986; Walker et al., 1987; Moser and Watson, 1990; McGowen, 1993). High temperatures successfully tolerated by barred sand bass (16–28°C) and fantail sole (16–24°C) eggs coincide with their summer and late summer–fall spawning seasons. Surface temperatures in the nearshore zone of southern California are generally highest in August, reaching peaks of 20–22°C, and lowest in January or February with temperatures of 13–15°C (Petersen et al., 1986), although unseasonably low temperatures, caused by upwelling, can occur during spring or summer. Both white croaker and California halibut eggs survived only at lower temperatures (12–20°C); peak spawn-

Table 3

Rates of development for eggs of four California fishes reared at five temperatures in the laboratory. Rates are expressed as the slopes (β) of age regressed on stage (Age=β stage). Age is time (hours) from fertilization to the nine egg developmental stages (I–IX); embryonic developmental stages E, O, and S were not considered in this analysis. Dashed lines are temperatures where eggs of that species did not survive. For all regression equations, r^2>0.95. Superscripts indicate means that were significantly different from each other in using the Tukey multiple-range test (P<0.05).

	Temperature (°C)				
Species	12	16	20	24	28
Barred sand bass	9.53	4.95	3.12	2.46	2.04
White croaker	7.54	4.73	3.25	—	
California halibut	7.14	4.98	3.42	—	
Fantail sole	—	5.78	3.38	2.51	—
Mean β	8.07[1]	5.11[2]	3.29[3]	2.49[3]	2.04

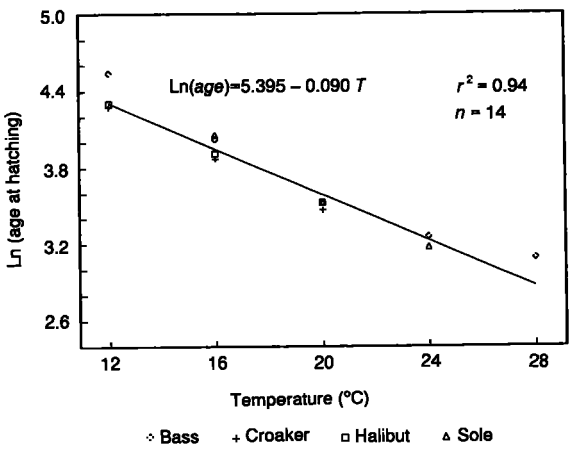

Figure 5

Relationship between egg age at hatching (hours from fertilization to hatching) and temperature (T) for barred sand bass, *Paralabrax nebulifer*, white croaker, *Genyonemus lineatus*, California halibut, *Paralichthys californicus*, and fantail sole, *Xystreurys liolepis*.

Table 4

Regression equations for estimating age (hours) of eggs of four California fishes reared in the laboratory over a range of temperatures. Parameters were calculated for temperatures (T) where eggs survived, producing viable embryos: 16–28°C for sand bass; 12–20°C for croaker and halibut; and 16–24°C for fantail sole. Equations are valid for egg developmental stages (S) I–VIII (1–8 in equations).

Species	Regression equation	R^2
Barred sand bass	$\text{Ln}(age) = 2.039 - 0.062\,T + 0.328\,S$	0.95
White croaker	$\text{Ln}(age) = 2.876 - 0.105\,T + 0.327\,S$	0.95
California halibut	$\text{Ln}(age) = 2.542 - 0.084\,T + 0.330\,S$	0.91
Fantail sole	$\text{Ln}(age) = 2.363 - 0.080\,T + 0.348\,S$	0.93

ing of these species occurs in winter–spring when nearshore sea surface temperatures off southern California usually are 13–17°C (Petersen et al., 1986).

Although seasonal spawning peaks of the four species coincide with their temperature tolerance ranges, all species, except sand bass, spawn to some degree thoughout the year. Moser and Watson (1990) examined abundances of California halibut and fantail sole larvae using a 30-year (1951–81) data set with stations from central California to southern Baja California. Densities of sole larvae during the nonpeak winter–spring season were very low; spawning occurred primarily off Baja California where mean sea temperatures were somewhat warmer than off southern California (Moser and Watson, 1990). Halibut displayed a more complex spawning pattern, which varied with location. Halibut were reported to spawn off southern California primarily when water temperatures were lowest (February–March) and to spawn secondarily in July–October (Moser and Watson, 1990). In contrast, off central and southern Baja California, a second spawning stock of California halibut occurred with peak spawning in June–August when temperatures are highest. Since we conducted our experiments with halibut collected off southern California and acclimated to 16°C, it is possible that experiments with eggs from fish collected in other localities or acclimated to other temperatures could result in a different range of survival temperatures.

Like the spawning patterns of California halibut, temporal spawning patterns of white croaker varied with location in a study conducted during 1978–81 by Love et al. (1984). Off southern California, most spawning occurred from November to April, with a peak in February–March; whereas off central California spawning occurred throughout the year, with greatest activity from July through February. Because croaker spawn off southern California during winter when temperatures are lowest, Love et al. (1984) suggested that the colder waters off central California allowed for a longer spawning season. Off Monterey, mean temperatures during June–October (the warmest months) are only 13–14°C; thus, the lower temperature tolerance range observed for croaker eggs probably reflects seasonal spawning conditions in both southern and central California.

Although the absolute temperature ranges that were tolerated differed between species, rates of egg development at a specific temperature did not significantly differ between species (Table 3). However, temperature strongly affected rates of development when data were pooled across species. Hatching times for all four species were inversely proportional to temperature, and the relationship was best fitted by an exponential function. This result is consistent with previous work on eggs of fishes such as Dover sole, *Microstomus pacificus*, cod, *Gadus morhua*, and walleye pollock, *Theragra chalcogramma* (Fonds, 1979; Thompson and Riley, 1981; Haynes and Ignell, 1983). Although these and many studies present results of single species experiments, reviews by Pauly and Pullin (1988) and Pepin (1991) pooled 84 and 124 species, respectively, and they similarly found an exponential relationship between incubation time and temperature. Both reviews also found developmental time to be significantly related to egg diameter. Although in our study mean chorion diameter differed significantly between species, these differences were not great (0.1 mm between the smallest and largest mean chorion diameters; Table 1) and evidently were not large enough to result in significant differences in developmental rate between species. The two reviews had somewhat conflicting conclusions concerning the importance of species-specific differences in developmental rates. Pauly and Pullin (1988) felt that after considering differences in developmental rate due to egg diameter and temperature, taxonomic differences were not important, whereas Pepin (1991) found some evidence for rate differences between groups of similar species.

The temperature range over which eggs hatched was at least eight degrees for fantail sole, white croaker, and California halibut, and possibly more if range endpoints fell outside the extreme temperatures survived. An eight-degree range is typical of other species such as English sole, *Pleuronectes vetulus*, Dover sole, and cod (Alderdice and Forrester, 1968; Irvin, 1974; Fonds, 1979; Thompson and Riley, 1981). Eggs of fantail sole might have tolerated the highest temperature tested (28°C), if we had been able to induce spawning during the more natural summer-fall season instead of winter (Table 1). However, sole brood stock were held at a warmer temperature (18.5°C) typical of their spawning season.

Barred sand bass hatched at a much wider range of temperatures, 12–28°C, although at 12°C embryos were not viable. The adaptive significance of the wider temperature tolerance of barred sand bass is not readily apparent. Field-collected barred sand bass larvae cannot be separated from larvae of two similar sea basses, the kelp bass, *Paralabrax clathratus*, and the spotted sand bass, *P. maculatofasciatus*; thus reports of bass abundance are based on a complex of these three species. Nonetheless, larval abundance of sea basses is the most seasonal of the species we studied, beginning in early summer and peaking in August, and thus bass eggs in the ocean are probably exposed to a narrower range of temperatures (Lavenberg et al., 1986). Perhaps because sea bass have a limited spawning season when waters are warmest, reaching 20–22°C nearshore (Petersen et al., 1986), a broad tolerance to high temperatures results in enhanced bass egg survival. Unseasonally cool temperatures or extended periods of upwelling could result in reduced survival; Lavenberg et al. (1986) reported that fewer sea bass larvae were collected during June and July 1980 when temperatures were anomalously low (Petersen et al., 1986).

Temperature ranges tolerated by fish eggs and larvae are also related to adult geographic distribution. In a study of the nearshore southern California Bight, Walker et al. (1987) found that larvae collected in cooler months were generally of species whose adult northern ranges extend to Canada, whereas larvae abundant during warmer months were species whose ranges extended primarily to Point Conception or northern California. The four species we studied follow this pattern: adults of barred sand bass and fantail sole range to Santa Cruz and Monterey Bay, respectively, whereas white croaker and California halibut both range farther north to British Columbia (Miller and Lea, 1972). All species have been collected as far south as Baja California. Thus, species-specific temperature tolerance ranges for early life history stages of fish may reflect a variety of interrelated factors such as the timing and duration of a species' spawning season, spatial spawning patterns, and adult geographic distributions.

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Metabolism, body composition, and energy budget of the mesopelagic fish *Maurolicus muelleri* in the Sea of Japan

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Abstract.—Metabolic activity (=oxygen consumption), chemical composition (water, ash, carbon [C], hydrogen [H], nitrogen [N]), and caloric content were determined for various developmental stages of the mesopelagic fish *Maurolicus muelleri* from the Sea of Japan. Oxygen consumption rates were estimated from enzyme activity involved in the respiratory electron transport system (ETS). Body composition varied with development of the fish, ranging from 68.3 to 78.3% of wet weight (WW) for water, 10.7 to 25.7% of dry weight (DW) for ash, 34.1 to 54.4% of DW for C, 5.1 to 8.4% of DW for H, 7.2 to 12.2% of DW for N, and 1.02 to 1.98 Kcal/g WW or 3.51 to 6.33 Kcal/g DW for caloric content. Condition factor index (CFI) ranged from 5.2 to 9.5 (mg WW×10^3/(mm TL)^3). Caloric content, C, H, and CFI increased with development, but the reverse was the case for water, ash, and N. Age-to-age and lifetime energy budgets were established, i.e. metabolic data from ETS assay and caloric data from body composition analyses, combined with natural growth data. The results indicated that higher age-specific net growth efficiency was associated with younger ages, decreasing toward the end of life, with a lifetime average of 17%. Estimated age-specific daily ration followed the same pattern, with a lifetime average of 2.9%/day. From the gonad index and caloric contents of gonads, energy invested in reproduction was calculated as 1.3% of the lifetime sum of assimilated energy for females and as 0.6% for males. Because the number of iterative spawnings during the lifetime of *M. muelleri* is unknown, this energy partition to reproduction is a conservative estimate. From the comparison of the present results with those for other mesopelagic fishes off southern California, it is suggested that *M. muelleri* is a more efficient mediator of energy flow and matter cycling in the pelagic ecosystem because of its smaller size and shorter life span.

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Maurolicus muelleri (Gmelin) is a small, short-lived sternoptychid fish distributed in the mesopelagic zone of tropical, subtropical, subarctic, and subantarctic waters of the Pacific and Atlantic Oceans (Kawaguchi and Mauchline, 1987). Gjøsaeter (1981) and Kawaguchi and Mauchline (1987) have reviewed the biology and ecology of *M. muelleri* and have pointed out the geographical variability in the life mode of this fish.

Maurolicus muelleri is the only micronektonic fish in the Sea of Japan, yet its stock size has been estimated as 3.3 × 10^6 metric tons (Okiyama, 1981). It is reported to mature at age 1 yr in the Sea of Japan, and to grow to 60 mm SL (Yuuki, 1982, 1984; Ikeda, 1994). The estimated life span of the fish is 20–22 months. Spawning is aseasonal with two peaks in spring and autumn or only one peak in autumn (Yuuki, 1982; Ikeda, 1994). Possible iterative spawnings have been suggested (Okiyama, 1971; Yuuki, 1982), and migrations up to a 50-m depth at night and down to below a 150-m depth during the day have been reported (Hamano et al., 1992). Copepods are numerically the most important dietary component of this species, with euphausiids second (Ikeda et al., 1994).

In order to evaluate the quantitative roles of *M. muelleri* in the pelagic ecosystem of the Sea of Japan, information about partitioning of materials or energy for various processes is required. However, little information about material and energy budget is available for this fish because of the lack of appropriate physiological data. A major problem inherent in an experimental study of *M. muelleri* is the difficulty in maintaining them under laboratory conditions. This problem is not limited only to *M. muelleri* but is also seen in other mesopelagic fishes (cf. Robinson, 1973). Along with this difficulty, direct measurement of the respiratory oxygen consumption rate of mesopelagic fishes is currently limited to those living for a short period of time in the laboratory after capture (Torres et al., 1979; Donnelly and Torres, 1988). Since "metabolism," estimated from respiratory oxygen consumption, is of central importance in estimating the energy budget of fishes (Winberg, 1956), the lack of adequate techniques for maintaining mesopelagic fishes makes it difficult to calculate energy used for metabolism.

Because of this difficulty in measuring respiratory oxygen consumption directly, Ikeda (1989) used the enzyme activity of the respiratory electron transport system (ETS) as an indirect measure of routine metabolism of myctophid fishes in the field. The energy-producing process

through oxygen consumption in cells is mediated mostly by the formation of adenosine triphosphate (ATP), and this oxidative phosphorylation is driven by ETS that is embedded in the inner membrane of eukaryotic mitochondria and in the cell membrane of prokaryotes (cf. Packard, 1985). The ETS assay was first introduced for the study of plankton respiration (Packard et al., 1971, 1975), and additional data have been accumulated (Packard, 1985). Although application of this assay to fish respiration is currently limited to only a few studies (Ikeda, 1989; Yamashita and Bailey, 1990), this method is advantageous in that incubation of live specimens is not necessary, and it is almost free from the effect of physiological stress incurred during capture of fish in the field. The ETS activity represents a potential rather than an actual oxygen consumption rate. In this respect, the ratio of ETS activity to respiratory oxygen consumption is known to be quite constant across various systematic groups of animals (King and Packard, 1975). The biochemical basis of the ETS assay and the rationale for the estimation of respiratory oxygen consumption rates are detailed in Packard (1985).

In the present study, ETS activity was determined and used as a basis to estimate respiratory oxygen consumption rates of *M. muelleri* from the Sea of Japan. The chemical composition of fish and gonads at various developmental stages was determined. These metabolic and chemical composition data were combined with natural growth rate data to establish an energy budget pattern for *M. muelleri* over its lifetime.

Materials and methods

Fish

Fishes were collected from Toyama Bay and Sado Strait (both within the southern Sea of Japan) and from waters around Yamato Rise (central Sea of Japan) aboard the RV *Mizuho-Maru* from September 1988 through September 1992. Collections were made at night with a 2-m Isaacs-Kidd midwater trawl (1.5 mm mesh) which was towed obliquely from 100–250 m depths to the surface. Fish-larvae nets (0.5 mm mesh) were used to collect larvae and small juveniles. For the collection of specimens used for the ETS assay, the trawl and nets were towed slowly (1.5 knots) for a short time period (10 min) to avoid damage to the specimens. Immediately following net retrieval, fishes in the codend were transferred to a bucket filled with seawater. For body composition analyses and ETS assay, specimens were placed on filter paper to remove excess water on the body surface, measured for body length, and were frozen (<–20°C). Total length (TL: from tip of the snout to end of the tail), instead of standard length (SL), was used throughout this study to facilitate work on shipboard. For conversion of TL to SL the equation $SL = 0.822TL + 0.161$ may be used (Ikeda, 1994).

Metabolism

ETS activity was measured in individual fish within two weeks after collection by the modified tetrazolium reduction method (Owens and King, 1975). The general procedure of ETS assay for fish samples is described elsewhere (Ikeda, 1989). No significant loss of ETS activity during storage for 36 days at –20°C has been reported for two fish species (Ikeda, 1989). The homogenates were incubated at 12°C, the estimated daily mean temperature encountered by *M. muelleri* during their diel vertical migration. In a separate test, the effect of temperature on ETS activity was assessed at six temperatures (0.5°, 4°, 8°, 12°, 16°, and 20°C).

For the conversion of ETS activity to actual respiratory oxygen consumption (R), $ETS/R = 2$ was proposed on the assumption that Michaelis-Menten kinetics could be applied to respiratory chemistry and that the concentration of the respiratory regulator (i.e. ADP) was maintained near the Km (cf. Packard, 1985). The ETS:R ratios obtained directly from crustacean plankton and fishes are close to this theoretical value (Table 1). Hence, $ETS/R = 2$ was used to convert ETS to R in this study.

Oxygen consumption was converted to caloric units by using the equivalent of 4.80 cal/mL O_2 (Gnaiger, 1983).

Condition factor index and body composition

Condition factor index (CFI) was defined as wet weight $(WW) \times 10^3/(TL)^3$ for this study.

Frozen specimens were weighed (WW in mg) and then freeze-dried, dried further at 60°C for 5 hours to remove residual water, and then weighed (DW in mg). Dried specimens were pooled on the basis of TL into eight size groups (<10, 10 to <15, 15 to <20, 20 to <30, 30 to <40, 40 to <50, 50 to <60, and ≥60 mm TL) and were ground into a fine powder with a ceramic mortar and pestle. No separation by sex was made. However, adult males are known to be 35 to 55 mm TL in the Sea of Japan (Ikeda, 1994), therefore some males may have been included in the 30 to <40 mm, 40 to <50 mm, and 50 to <60 mm TL groups but none in the ≥60 mm TL group. Powdered samples were used for elemental analyses and ash determinations.

Table 1

The ETS:R ratio for zooplankton and fishes. Note that the ratio is dimensionless.

Animal	*n*	ETS:R Mean ±SD	Reference
Zooplankton			
Calanoides carinatus	13	1.74 ±0.62[1]	Packard et al. (1975)
Calanus pacificus	48	2.02 ±0.29	Owens and King (1975)
Acartia tonsa	13	1.91 ±0.21	Bamstedt (1980)
"Antarctic zooplankton"	12	1.86 ±0.74	Ikeda and Hing Fay (1981)
Fish			
Pomacentrus popeii	5	1.54 ±0.53	Ikeda (1989)
Gobiidae sp.	12	1.63 ±0.28	Ikeda (1989)
Theragra chalcogramma (feeding larvae)	27	2.13 ±0.72	Yamashita and Bailey (1990)

[1] Recalculated by Packard (1985).

Gonads (ovaries and testes) were removed from frozen specimens >36 mm TL and weighed (WW). Prior to freeze-drying and grinding, the diameter of oocytes was measured by using a microscope, and ovaries with oocytes >0.5 mm diameter were defined as "mature" (Ikeda, 1994). For some mature ovaries, the individual oocytes were dissected after freeze-drying. These gonads and isolated oocytes were used in subsequent analyses.

Carbon (C), hydrogen (H), and nitrogen (N) were analyzed with an elemental analyzer (Yanaco CHN Corder MT-5, Yanagimoto Co., Ltd., Kyoto) with antipyrine as a standard. A weighed fraction of each sample was incinerated at 480°C for 5 hours and reweighed for ash determination. All measurements were made in duplicate for each sample. From replicated determinations (n=10) on the same sample, the precision of these analyses, as expressed by the coefficient of variations (SD/mean, %), were 1% for C and H, 2% for N, and 7% for ash. The elemental composition data were expressed as the percentage of DW, or as the percentage of ash-free dry weight (AFDW). The caloric content was calculated by using a formula given by Gnaiger (1983), amended by Gnaiger and Shick (1985): $(4.436W_N + 66.265W_c - 11.2)/4.18$, where W_N and W_c are fractions of N and C, respectively, on an AFDW basis.

Energy budget

Calculation of the energy budget is based on the basic balanced equation of Winberg (1956), i.e.

$$0.8 \times F = M + G,$$

and

$$K_2 = 100 \times G/(G + M),$$

where 0.8 is the generalized assimilation efficiency, F is the daily food ingestion, M is the daily metabolism, G is the daily growth, and K_2 is the net growth efficiency (note that some symbols were changed from those used by Winberg [1956]). Energy associated with loss in scales, mucus secretion, excretion, etc. were considered to be negligible and were omitted. Energy use for reproduction was estimated from calorific data of isolated gonads. F is often expressed as the percentage of body energy (=daily ration, F').

The growth in length of *M. muelleri* has been shown to fit well to the von Bertalanffy curve (Gjøsaeter, 1981; Yuuki, 1984; Ikeda, 1994): $TL = TL_\infty (1 - e^{-K(t-t_0)})$, where TL_∞ is the theoretical maximum size, K is a growth factor, and t_0 is the time (yr) at which growth starts. In the calculation of the energy budget, the curve of *M. muelleri* in Toyama Bay, southern Sea of Japan, established by Ikeda (1994) was used: i.e. TL_∞= 59.5 mm, K = 1.19, and t_0 = 0.65 (yr). On the basis of the hatching size (ca. 3 mm) of *M. muelleri*, t=0.7 (TL=3.6 mm) was assumed as the start of growth for this fish, and the growth calculation was made in 0.1 yr (=36.5 d) increments. Total length at a given age of the fish was converted to wet weight (WW in mg) by using the allometric equation established in the present study (WW=0.00211$TL^{3.346}$ [r=0.997, n=312]), then to caloric units by multiplying with the appropriate conversion factor (Kcal/g WW) obtained from chemical composition analyses. For the calculation of between-age metabolic expenditure, a mean value, multiplied by 36.5 d, was used. Between-age values thus obtained were also used to compute age-specific net growth efficiency (K_2) and daily ration (F').

Results

Metabolism

A total of 49 fishes (57–1,327 mg WW) were used for the ETS assay. A scatter diagram showing the relationship between specific oxygen consumption rates (R/WW: μL O_2/(mg WW·h)) and WW is presented in Figure 1. The effect of WW on oxygen consumption rates (R: μL O_2/(fish·h)) was examined by using a GM regression model (Ricker, 1973), $\log_{10}R = v \log_{10}WW + \log_{10}u$, where v and u are constants. Estimates were v = 0.987 (95% CI: 0.917–1.053) and $\log_{10}u$ = –0.609 for the data derived from the ETS assay. The v did not differ significantly from unity (v=1). On this basis, a mean specific oxygen consumption rate (R/WW) was calculated as 0.225 (±0.038 SD).

The relationship between ETS activity (ETS: μL O_2/(mg WW·h)) and temperature (°C) was linear over the temperature tested (0.5 to 20°C) on a semilog graph (Fig. 2). The relationship was expressed as

$$\log_{10}ETS = 0.0541\ (95\%\ \text{CI: } 0.0472 - 0.0610)T - 1.0440, \text{ for fish 1}$$

and

$$\log_{10}ETS = 0.0554\ (95\%\ \text{CI: } 0.0490 - 0.0618)T - 1.0038, \text{ for fish 2.}$$

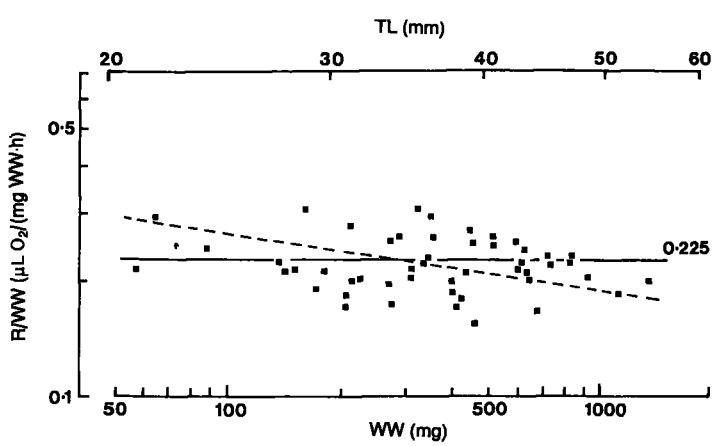

Figure 1

Relationship between specific oxygen consumption rates (R/WW, μL O_2/(mg WW·h) at 12°C) and wet weight (mg WW) obtained from ETS assay (ETS activity × 0.5) for *Maurolicus muelleri*. Because statistical analysis indicated no effect of WW, a mean was calculated and superimposed. The broken line is the relationship expected when size-dependent metabolism is assumed for ETS data (i.e. $R \propto WW^{0.85}$ or $R/WW \propto WW^{-0.15}$, see text for details). Top abscissa denotes body length (mm TL) equivalent to mg WW of bottom abscissa.

The slope of these two regression lines did not differ significantly. From a common slope (0.0547) that was computed, a Q_{10} = 3.52 was derived.

Condition factor index, body composition, and caloric content

Over all size groups (<10 to >60 mm TL), the ranges recorded were 5.23 to 9.53 for CFI, 68.8 to 78.8 (% WW) for water, 10.7 to 25.7 (% DW) for ash, 34.1 to 54.4 (% DW) for C, 7.2 to 12.2 (% DW) for N, 5.1 to 8.4 (% DW) for H, and 1.02 to 1.98 (Kcal/g WW) or 3.51 to 6.33 (Kcal/g DW) for caloric content (Table 2).

Changes in these variables with increasing TL were examined by using three regression models: linear ($Y = aX + b$), power ($Y = aX^b$) and exponential ($Y = ae^{bX}$). In these analyses, X was represented by the mid-range value for each size group except that 10 was used for the <10 mm TL group and 60 for the ≥60 mm TL group. Among these three regression models, the best was selected, as judged by the highest correlation coefficient. The analyses revealed two opposite patterns, i.e. an increase (CFI, C, H, and caloric contents) or a decrease (water, ash, and N) with the growth of *M. muelleri*. All regressions were significant (Table 2) except for N. The decrease of N with an increase in TL, however, was significant if data from the <10 mm TL group were removed (r=–0.947, P<0.01).

The results of analyses on gonads are summarized in Table 3. Among mature ovaries, oocytes, and testes, the oocytes exhibited the highest caloric content (5.61 Kcal/g DW), followed by mature ovaries (4.88 Kcal/g DW). The lowest caloric content (4.66 and 4.79 Kcal/g DW) was recorded on two testicular samples.

Energy budget

The patterns of energy utilization for cumulative growth (G) and cumulative metabolic expenditure (M), and changes in age-specific net growth efficiency (K_2) and age-specific daily ration (F') of 0-yr-old through 1.8-yr-old *M. muelleri* are shown in Figure 3. K_2 and F' were the highest at the beginning of life and decreased progressively toward the end of life at 1.8 years. Irregularities in the pattern, which are most pronounced for K_2, reflect the change of multiplier (Kcal/g WW) to convert WW to calories. The overall ranges of K_2 and F' were 7.6 to 61.6% (lifetime average: 16.7%) and 2.4 to 10.4% (2.9%), respectively.

Table 2

Condition factor index (CFI), water and ash contents, elemental composition (C, N, H), and calculated caloric content (per WW and per DW bases) of eight size groups of *Maurolicus muelleri*. Mean ± SD. *n* denotes the number of samples from different sampling dates (replicates for ash, elemental composition, and calorific content), and the total number of fishes is in parentheses (replicates for CFI and water). The changing pattern with the increase of size was examined by using three regression models (linear, power, exponential) and its significance was judged by the correlation coefficients. Models indicated had the highest correlation coefficient. ND = not determined.

					Elemental composition			Calorific content	
TL (mm)	*n*	CFI	Water (%WW)	Ash (%DW)	C (%DW)	N (%DW)	H (%DW)	(Kcal/g WW)	(Kcal/g DW)
<10	1(14)	ND	ND	25.7	34.1	8.5	5.1	ND	3.51
10 to <15	2(31)	5.23 ±0.52	77.0 ±0.9	16.0 ±0.5	42.3 ±0.5	11.9 ±0.1	6.4 ±0.1	1.05 ±0.03	4.83 ±0.29
15 to <20	2(34)	5.51 ±0.55	77.0 ±1.8	15.8 ±0.2	42.1 ±0.2	12.1 ±0.3	6.1 ±0.1	1.05 ±0.08	4.74 ± 0.31
20 to <30	3(40)	6.91 ±0.43	78.8 ±0.2	14.0 ±0.9	43.8 ±0.2	12.2 ±0.5	6.4 ±0.1	1.02 ±0.02	4.91 ±0.24
30 to <40	4(52)	7.35 ±0.46	77.7 ±2.2	13.7 ±1.9	45.3 ±2.8	11.1 ±1.3	6.8 ±0.7	1.13 ±0.20	4.95 ±0.34
40 to <50	6(59)	7.69 ±0.73	75.5 ±2.6	13.4 ± 4.0	48.0 ±3.4	9.5 ±1.1	7.1 ±0.5	1.33 ±0.24	5.51 ±0.61
50 to <60	5(46)	7.99 ±0.98	74.1 ±3.2	10.7 ±2.0	50.0 ±2.7	8.8 ±1.2	7.5 ±0.4	1.47 ±0.27	5.43 ±0.62
≥60	2(6)	9.53 ±0.78	68.8 ±1.1	11.4 ±5.4	54.4 ±2.3	7.2 ±0.1	8.4 ±0.4	1.98 ±0.13	6.33 ±0.22
Correlation to TL (*r*)		0.966**	–0.782*	–0.892**	0.926**	–0.620	0.925**	0.908**	0.864**
Regression model		Power	Linear	Power	Linear	Exponen	Linear	Exponen	Linear

*$P<0.05$, **$P<0.01$.

Energy invested in reproduction is partly included in *G* in the present calculation (e.g. *G* is derived from intact fishes including gonads, but neither eggs nor sperm already released were included). The greatest proportional weight of gonads for *M. muelleri* in Toyama Bay has been reported as 10% of WW for females and 6% of WW for males (recalculated from gonad index data in Ikeda, 1994). From the caloric content of adults given in Table 2 (1.47 Kcal/g WW) and those of ovaries (1.12 Kcal/g WW) and testes (0.93 Kcal/g WW) in Table 3, the proportions of energy in the form of ovaries and testes were computed as 7.6% (10 × 1.12/1.47) and 3.8% (8.6 × 0.93/1.47), respectively, of *G* (1,820 cal) in 1.8-yr-old fish (53 mm TL). When *M* is combined with *G* (i.e. assimilated energy: 1,820 + 9,075 cal), the fraction of energy stored in gonads becomes 1.3% for females and 0.6 % for males. Alternatively, energy invested in egg production in females may be estimated by knowing the number of mature oocytes. The DW of single mature oocytes is 34 μg (±1.76, *n*=5), and the maximum number counted for *M. muelleri* in Toyama Bay is 283 (Ikeda, 1994). These figures, combined with calorific content of the oocytes (5.61 Kcal/g WW, Table 4) yield 54.0 cal ($34 \times 10^{-6} \times 5.61 \times 10^{3} \times 283$), which corresponds to 0.5% of energy assimilated (1,820 + 9,075 cal) by 1.8-yr-old fish.

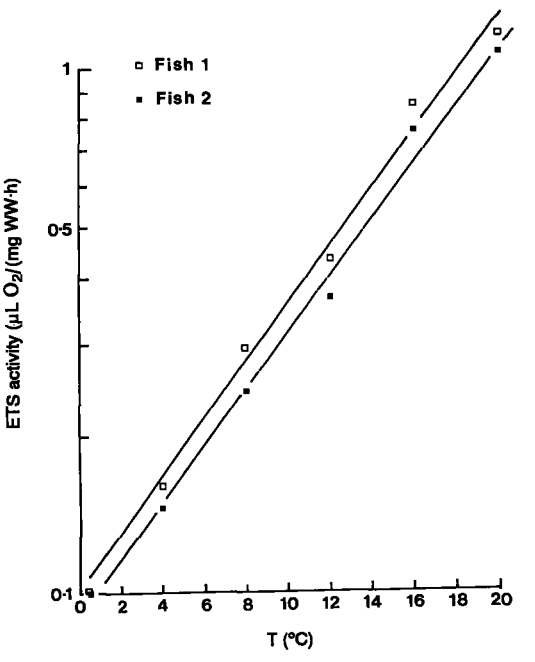

Figure 2

Relationship between ETS activity (ETS: μL O_2/(mg WW·h)) and temperature (°C)(fish 1: 442 mg WW, and fish 2: 472 mg WW) for *Maurolicus muelleri*. Slopes are not significantly different (*t*-test, $P>0.05$).

Table 3

Water and ash contents, elemental composition (C, N, H), and calculated caloric content (per WW and per DW bases) of gonads in *Maurolicus muelleri*. Mean ±SD. The number of ovaries and testes combined for the analysis is in parentheses. Ovaries with oocytes >0.5 mm in diameter are designated as mature ones. ND = not determined.

	Sampling date	Water (%WW)	Ash (%DW)	C (%DW)	N (%DW)	H (%DW)	Kcal/g WW	Kcal/g DW
♀ mature ovaries (9)	Apr 1989	77.0 ±2.3	9.0 ±0.2	45.5 ±0.1	10.7 ±0.4	6.6 ±0.0	1.12 ±0.00	4.89 ±0.01
♀ oocytes	Apr 1989	ND	5.6 ±0.1	50.7 ±0.8	10.0 ±0.1	7.6 ±0.1	ND	5.61 ±0.12
♂ testes (2)	Apr 1989	83.0 ±1.4	9.7 ±0.1	43.9 ±0.1	11.5 ±0.1	6.2 ±0.1	0.79 ±0.00	4.66 ±0.01
♂ testes (4)	Sep 1992	80.5 ±0.3	17.5 ±0.4	43.0 ±0.0	12.8 ±0.2	6.2 ±0.0	0.93 ±0.00	4.79 ±0.00

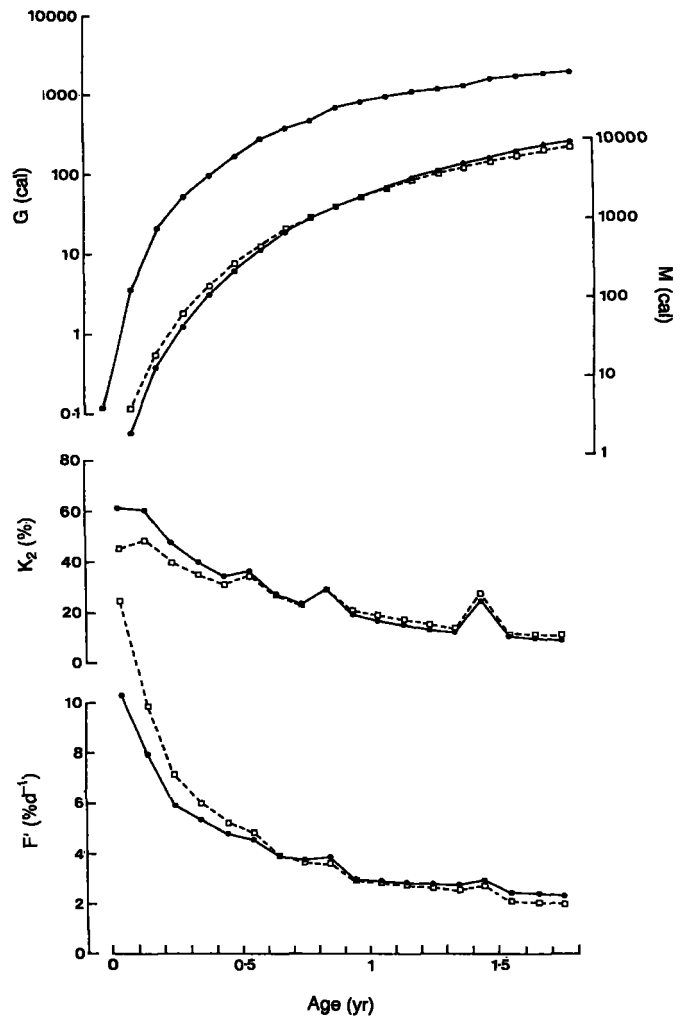

Figure 3

Changes with age of cumulative energy utilized for growth (G) and metabolism (M)(top), age-specific net growth efficiency (K_2)(middle); and daily ration (F')(bottom) for *Maurolicus muelleri*. For M, K_2, and F', solid line represents size-independent metabolism, and broken line size-dependent metabolism.

Discussion

The decrease of specific oxygen consumption rates (R/WW) with the increase of body size is a widespread phenomenon in animals (Zeuthen, 1953; Hemmingsen, 1960) but is often masked by narrow size coverage and the scatter of data (Hemmingsen, 1960). From this view, R/WW independent of size of specimens obtained in this study may be an artifact due to incomplete coverage of the entire body-size range of *M. muelleri* (specimens less than 57mg WW or 20 mm TL were not used in the ETS assay). If a general body weight exponent of $v = 0.85$ given for fishes (Winberg, 1956; modified by Ricker, 1973) is adopted, $R = 0.534WW^{0.85}$ is obtained from the same ETS assay data (cf. Fig. 1). In the present study, differences in the energy budget calculations due to the use of size-dependent M, instead of size-independent M, were also examined (Fig. 3; Table 4).

The differences due to the use of size-dependent M, instead of size-independent M, were most pronounced at younger stages, in which the size-dependent M yielded lower age-specific K_2 and higher age-specific F' (Fig. 3). However, choice of size-independent M or size-dependent M had little effect on the results of lifetime averages of K_2 (16.7% vs. 18.5%) and F' (2.9% vs. 2.6%)(Table 4). The choice of size-dependent M, instead of size-independent M, again had little effect on calculations of the fraction of energy stored in gonads (the former added only 0.1% to figures derived from size-independent M).

Information about metabolic rate of micronektonic fishes is currently limited. Whole-animal respirometry data of typical epipelagic fish were obtained by Lasker (1970), who successfully maintained Pacific sardine (*Sardinops caerulea*) in the laboratory and measured

Table 4

Energy budget parameters and calculated lifetime sums of energy expenditure for metabolism (M) and growth (G), and lifetime averages of net growth efficiency (K_2) and daily ration (F') for *Maurolicus muelleri*. Both size-independent (v=1) and size-dependent metabolism (v=0.85) were assumed for the calculation of M and parameters including M. Note that 0.9 yr is the mid-lifetime of this fish.

Life span (yr)	1.8	
Body size at 0 and 1.8 yr (0.9 yr)		
Length (TL in mm)	3.6, 53.0 (36.0)	
Wet weight (WW in mg)	0.15, 1,238 (537)	
Energy (cal)	0.12, 1,820 (722)	
Lifetime sum		
Metabolism (M, cal)	when v=1	9,075
	when v=0.85	7,998
Growth (G, cal)		1,820
Lifetime average		
Net growth efficiency (K_2, %)	when v=1	(1,820 × 100)/(1,820 + 9,075) = 16.7
	when v=0.85	(1,820 × 100)/(1,820 + 7,998) = 18.5
Daily ration (F', %)	when v=1	((1,820 + 9,075) × 100)/(0.8 × 1.8 × 365 × 722) = 2.9
	when v=0.85	((1,820 + 7,998) × 100)/(0.8 × 1.8 × 365 × 722) = 2.6

0.3 μL O_2/(mg WW·h) at 16.5–22°C (median 19°C) for specimens weighing 25–189 g WW (median 48.5 g WW). For mesopelagic fishes off southern California, Torres et al. (1979) reported 0.059–0.095 μL O_2/(mg WW·h) (mean 0.073 μL O_2/(mg WW·h)) at 10°C on four species weighing 2.1–9.3 g WW (mean 6.1 g WW). Because body size and temperature are two dominant factors affecting oxygen consumption, direct comparison with the present data on *M. muelleri* is not possible. To overcome this problem, the specific oxygen consumption data given by these previous workers were extrapolated to the mean size of *M. muelleri* (429 mg WW) used for ETS assay, assuming size-dependent metabolism as mentioned above ($R \propto WW^{0.85}$), and adjusted to the rates at 12°C by using a factor for temperature adjustment in Winberg (1956). As a result, we obtain 0.31 μL O_2/(mg WW·h) for the Pacific sardine, and 0.11 μL O_2/(mg WW·h) for four mesopelagic fishes off southern California. Specific oxygen consumption rates for *M. muelleri* (0.225 μL O_2/(mg WW·h)) estimated from ETS activity in this study fall near the center of the range of these high epipelagic and low mesopelagic rates. Lower specific oxygen consumption rates of deeper living fishes are attributed to their greatly reduced locomotion (Torres et al., 1979). From this view, the results of this comparison suggest differential activity levels for each fish. The activity of *M. muelleri* is relatively lower than that of the Pacific sardine but higher than those of its mesopelagic counterparts off southern California.

The Q_{10} = 3.52 derived from the relationship between the ETS activity and temperature for *M. muelleri* (Fig. 2) in the present study appears rather anomalous (i.e. Q_{10}=2 to 3 for various biological processes, cf. Prosser, 1961) but is close to Q_{10} = 3.90 and 3.24 for myctophid and nonmyctophid (*Anoplogaster cornuta*, *Gonostoma elongatum*) fishes, respectively, from the eastern Gulf of Mexico (Donnelly and Torres, 1988). Because *M. muelleri* and both myctophid and nonmyctophid fishes studied by Donnelly and Torres (1988) are diel vertical migrators, these greater Q_{10} values suggest that diel fluctuations in metabolic rates are associated with daily vertical movements in stratified water. Diel fluctuation in metabolic activity associated with diel vertical migration was ignored in this study on the premise that daily metabolism of *M. muelleri* was determined by integrated daily mean temperature (12°C), as has been demonstrated experimentally on the hyperiid amphipod *Themisto japonica*, which exhibits an extensive diel vertical migration (Ikeda, 1992).

With regard to the developmental changes in body condition and composition, there are no published data available for comparison with the present data on *M. muelleri*. However, studies on nonmesopelagic fishes, including red sea bream (*Chrysophrys major*) by Anraku and Azeta (1973) and walleye pollock (*Theragra chalcogramma*) by Harris et al. (1986), have demonstrated increases of CFI, C, and caloric contents and decreases in water, ash, and N in asso-

ciation with growth of these fishes. Although neither of these previous studies on nonmesopelagic fishes included adult individuals, the general patterns of change in body condition and composition over the course of growth are consistent with those observed in *M. muelleri*. Progressive accumulation of lipid in the body is thought to be the cause of these developmental changes in CFI, elemental composition, and caloric content (Anraku and Azeta, 1973; Harris et al., 1986). Accumulation of lipid around the digestive tract, gonads, and liver was confirmed for mature adults of *M. muelleri* in the present study, supporting the idea that accumulation of body lipid results in the other changes noted.

On the basis of analyses of 37 fish species of mixed ages and living at various depths off southern California, Childress and Nygaard (1973) concluded that deeper living fishes are characterized by higher water and lower caloric contents. Compared with the results of Childress and Nygaard (1973), the present data on water and caloric contents of *M. muelleri* fall somewhere between those living in epipelagic and mesopelagic zones off southern California. Thus, the general bathymetric level at which the population of *M. muelleri* lives, extrapolated from body composition data, is in general agreement with direct field observation (50 to >150 m depth, Hamano et al., 1992).

Childress et al. (1980) compared life history patterns among epipelagic, mesopelagic, and bathypelagic fishes off southern California and indicated that epipelagic species had the highest growth rates, mesopelagic species the lowest, and bathypelagic species were intermediate. In terms of energy budget, deeper living species are characterized by higher lifetime averages of K_2. In calculating energy budgets, Childress et al. (1980) assumed size-independent M, so that the present results of size-independent M for *M. muelleri* can be compared directly with their results. This comparison revealed that K_2 of *M. muelleri* (17%) is much higher than that of epipelagic fishes (3%) but falls within the range of mesopelagic fishes (15–26%) off southern California. The lifetime average of daily ration F' estimated by Childress et al. (1980) is 3.3 for epipelagic, 0.79 for mesopelagic, and 0.62% for bathypelagic fishes (recalculated by using the assimilation efficiency of 80%, instead of 73%). The present estimated lifetime average of F' (2.9%) for *M. muelleri* is higher than mesopelagic F', and closer to the epipelagic F' given by Childress et al. (1980). Greater F' in *M. muelleri* is a result expected from higher metabolic activities of this fish compared with mesopelagic fishes off southern California. As a mesopelagic fish in the Sea of Japan, *M. muelleri* is different from mesopelagic fishes off southern California in that the former is much smaller in size (53 mm TL or 44 mm SL vs. 72–118 mm SL) and shorter lived (1.8 yr vs. 5–7.5 yr) than the latter. Energy budget comparison indicates that *M. muelleri* is a more active swimmer (has a higher metabolic activity), thereby consuming more food than those off California, although net growth efficiency is identical between the two. A general implication gained from these comparisons is that *M. muelleri* in the Sea of Japan are more efficient mediators in energy flow and matter cycling in the pelagic ecosystem than are mesopelagic fishes off southern California.

Caloric contents of ovaries and testes of the Pacific sardine (*Sardinops caerulea*) have been reported as 5.43 and 4.85 Kcal/g DW (Lasker, 1970), both of which are greater than the respective values for *M. muelleri* (4.89 and 4.79 Kcal/g DW, cf. Table 3). Caloric content of mature oocytes, instead of intact ovaries, of *M. muelleri* is comparable to that of the Pacific sardine. Lasker (1970) estimated the energy investment in reproduction to be only 2% of assimilated energy. The energy partitioned for reproduction in *M. muelleri*, on the basis of the maximum gonad index, is 1.3% of the assimilated energy of 1.8-yr-old fish for females and 0.6% for males in this study. The presence of different size groups of yolked oocytes in the ovaries has been observed for *M. muelleri* from various geographical locations including the Sea of Japan, and is considered to be evidence of multiple or serial spawning (Okiyama, 1971; Gjøsaeter, 1981; Yuuki, 1982; Melo and Armstrong, 1991; Prosch, 1991). From this view, the present estimations of energy partition to reproduction in this fish are conservative ones, but the lack of information about spawning frequency prevents quantitative calculation at present. When the spawning frequency and the number of eggs released at each spawning become known for *M. muelleri* in future studies, the reproductive effort of the females will be better defined with the data for caloric content of oocytes given in this study.

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Variation in size and age at maturity in *Photololigo* (Mollusca: Cephalopoda) from the northwest shelf of Australia

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Abstract.—Individuals of the tropical loliginid squid *Photololigo* sp. 1 were collected from the tropical waters of the northwest continental shelf of Australia. Both males and females exhibited pronounced phenotypic variation in size at maturity. Statolith increment analysis was carried out to determine individual age. On the basis of the assumption that statolith increments were deposited daily, counts revealed that this species had a short life-span and that all individuals were younger than 160 d and exhibited linear growth over the size range sampled. All of the longest squid collected were females, which achieved this size disparity predominantly by being older than males rather than by growing at a faster rate. Age analysis revealed that small mature individuals were considerably younger than large mature individuals. A large size distribution of mature individuals was therefore achieved by variation in age at maturity. Possible causal mechanisms are considered.

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Pelagic cephalopods are characterized by fast growth, early maturity, and predominantly indeterminate growth (Rodhouse and Hatfield, 1990; Alford and Jackson, 1993). This is especially pronounced in tropical species (Jackson and Choat, 1992). Cephalopods also show considerable variation in individual growth rates (e.g. Natsukari et al., 1988; Jackson, 1989; Arkhipkin and Mikheev, 1992; Villanueva, 1992). Furthermore, a marked plasticity has been noted in size at maturity for a number of cephalopods (e.g. *Lolliguncula brevis*, Hixon, 1980; *Loligo opalescens*, Hixon, 1983; *L. pealei*, Macy, 1982; *Alloteuthis subulata*, Rodhouse et al., 1988; *Dosidicus gigas*, Nesis, 1983; *Sepia officinalis*, Boletzky, 1983; and *Sepia pharaonis*, Dunning et al., 1994). However, whether the variation in size at maturity noted in the above studies reflected age differences or differences in individual growth rate could not be determined because individual age was not known.

Mangold (1983) was able to document not only variation in size at maturity but also variation in age at maturity in the octopus *Eledone moschata* by raising known-age siblings from hatching to maturity. She found marked differences in sibling growth rates, some siblings showing a tenfold difference in weight after two months. She was also able to document that the differences in size at maturity resulted from some individuals delaying maturation to a greater size and age. Using statolith ageing techniques, Jackson (1993) was able to delineate seasonal differences in trends in gonad growth and age at maturity for field populations of *Loligo chinensis*[1] and *Idiosepius pygmaeus*.

By following the growth of cephalopods of known age in captivity, it is possible to determine whether variation in size at maturity is attributed to differences in individual age or to differences in individual growth and maturity rates or to a combination of both of these factors.

[1] It is now becoming more common to refer to *Loligo* in Australia as *Photololigo* (see Yeatman and Benzie, 1994). The species previously referred to as *Loligo chinensis* (Jackson, 1990b, 1993, 1994; Jackson and Choat, 1992) is now known to be a distinct species inhabiting shallow water in tropical Australia and has been referred to as *Photololigo* sp. 3 (Yeatman and Benzie, 1994) and *Photololigo* cf. *chinensis* (east coast form) in Dunning et al. (1994). Because this species has not yet been named, and to avoid confusion, this species will be referred to by its previously published name.

However, culture conditions do not reflect the natural environment, and although benthic octopods can be raised relatively easily in captivity, this is not true for the pelagic squids. The use of statolith increments to age individual squids is providing a means both to disentangle the size-age question and to determine the reproductive tactics of squid.

During the summer of 1990, collections were made of *Photololigo* sp. 1 from the northwest shelf, western Australia, as part of a population genetic study of Australian loliginids (see Yeatman and Benzie, 1994). This species, which was first identified by using genetic markers, showed marked variation in size at maturity, some individuals maturing at less than half the size of their counterparts. *Photololigo* sp. 1, so named because of the presence of light organs on the ink sac (see Natsukari, 1984), is one of two species identified that fits the gross morphology of *Photololigo edulis* documented from these northern tropical waters (Dunning, 1982). After establishing that the small and large mature individuals do not represent different species (Yeatman and Benzie, 1994), we used statolith ageing techniques on a subsample of these individuals to explore how age is related to the observed plasticity in size at maturity.

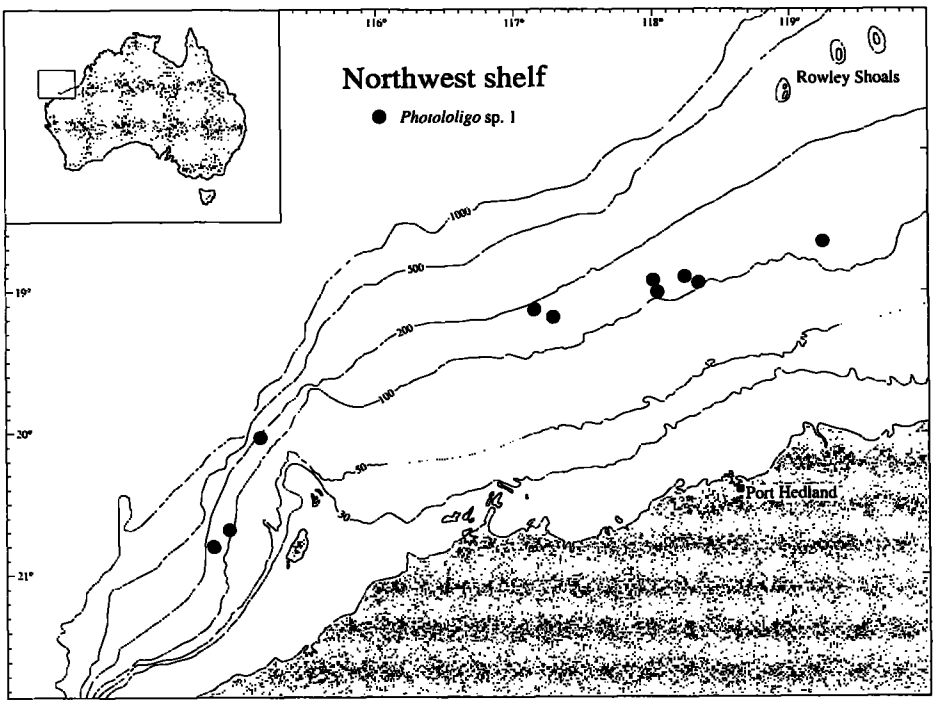

Figure 1
Capture localities for *Photololigo* sp. 1 from the northwest shelf of Australia.

Materials and methods

Sample collection

Individuals of *Photololigo* sp. 1 (37 males, 42 females) were collected by bottom trawl during the 1990 September–October cruise of the RV *Southern Surveyor* on the northwest shelf (Fig. 1). After the removal and subsequent freezing of tentacular tissue for electrophoresis, a random subsample (n=32) of squid heads was taken from the 79 specimens and fixed in 70% ethyl alcohol. Statoliths were removed from the fixed specimens of *Photololigo* sp. 1 after a period of nearly two years in ethanol. Statoliths of thirteen male squid and nineteen female squid, captured at water depths between 102 and 178 meters, were examined.

Maturity status

Each squid was assigned a maturity status according to Lipinski's universal scale (see Juanico, 1983; Sauer and Lipinski, 1990) which recognizes six macroscopic stages: 1 = juvenile; 2 = immature; 3 = preparatory; 4 = maturing; 5 = mature; and 6 = spent. For males, the definitions of the various categories are the following: 1 = spermatophoric complex (SC) visible as a spot only; 2 = testes and parts of the SC visible; 3 = spermatophoric organ visible with white streak on vas deferens; 4 = vas deferens extended and spermatophoric sac (SS) contains white particles, testis structure present; 5 = SS contains tightly packed spermatophores; and 6 = degenerating spermatophores and SC, and loss of testis structure.

The categories (stages) in females are distinguished by the following criteria: 1 = nidamental glands (NG) appear as fine transparent strips; 2 = sexual organs translucent or whitish, oviduct meander visible, ovary visible as homogenous structure; 3 = sexual organs not translucent, oviduct meander extended, immature ova visible, NG enlarged; 4 = NG large, covering most internal organs, mature ova in ovary; 5 = same as 4 but mature eggs in oviduct; 6 = few, if any, eggs in the oviduct and ovary.

Lipinski's maturity scale was used because it can easily be used in the field. However, recently stages 1 through 4 have been validated by histological cri-

teria; the differences between stages 4 and 5 were found to be mostly morphological for both sexes (Sauer and Lipinski, 1990). Dorsal mantle length (ML), measured on fresh material, was used as the standard squid length.

Statolith preparation and ageing

Statoliths were stored dry in a plastic cavity block. For increment analysis, statoliths were mounted in the thermoplastic cement Crystal Bond. Increments in statoliths, from small individuals, could be counted directly without any further preparation. The statoliths from larger individuals needed grinding and polishing (see Jackson, 1990a) to reveal all the increments from the nucleus to the edge. The increments within the statolith microstructure were very clear and easy to count. All counts were carried out in the dorsal or lateral region of the dorsal dome by following the increments with a camera lucida attached to an Olympus BH microscope (×400). Total increment number was taken as the mean of three replicate counts that differed less than 10% from the mean.

The periodicity of the increments was not determined in this study. However, the increments were very similar in appearance to validated daily statolith increments of other tropical loliginids—*Loligo chinensis* and *Loliolus noctiluca* (Jackson, 1990b). Daily periodicity in statolith increments was also validated for the tropical loliginid *Sepioteuthis lessoniana* (Jackson, 1990a; Jackson et al., 1993). The increments within the statolith microstructure of *Photololigo* sp. 1 in this study were therefore assumed to be daily. However, there is a need for validation of increment periodicity in this species.

Results

Photololigo edulis is distinguished from other *Photololigo* species primarily by its sucker dentition, which usually requires detailed morphological inspection. However, previous genetic analysis has revealed two cryptic species exhibiting "*edulis*-like" teeth in northern Australia (Yeatman and Benzie, 1993).

All of the individuals of *Photololigo* sp. 1 from the northwest shelf in this study were also used in a population genetic study, each for eleven (five polymorphic) loci (Yeatman and Benzie, 1994). Genotypic frequencies for all loci showed good conformance to Hardy-Weinberg expectations for random mating, and the F_{IS} value was not significant, thus demonstrating a lack of within-population structure.

Size at age

The length-at-age data for the *Photololigo* sp. 1 population were linear over the size range sampled. This species appears to have a short life-span; the oldest individual is estimated to be less than 160 d (Fig. 2). The regression equations were $y = 1.12x - 57.46$ [r^2=0.77], and $y = 1.02x - 45.57$ [r^2=0.90], (where x is age in days and y is ML in mm) for males and females, respectively. Both regressions were highly significant ($P \leq 0.0001$), and there was no significant difference between males and females in the slopes or elevations in the Age:ML relationships (ANCOVA, $P > 0.05$). Males that were aged ranged in size from 38 mm to 87 mm ML, and females that were aged ranged from 32 mm to 115 mm ML.

Maturation

Males All males sampled (n=37) were between maturity stages 2 and 5. Stage-5 males showed a large range in mantle length (48 to 126 mm ML). Some mature stage-5 males were smaller than immature stage-3 and stage-4 males (Fig. 3A).

On the basis of the subsample of aged males (n=13), the largest male aged was over twice as long as the smallest male aged (Fig. 4A), whereas the oldest male (119 d) was only 31 d older than the youngest male (88 d). The age data (Fig. 4B) confirmed that some males were maturing at not only a smaller size but also at a younger age.

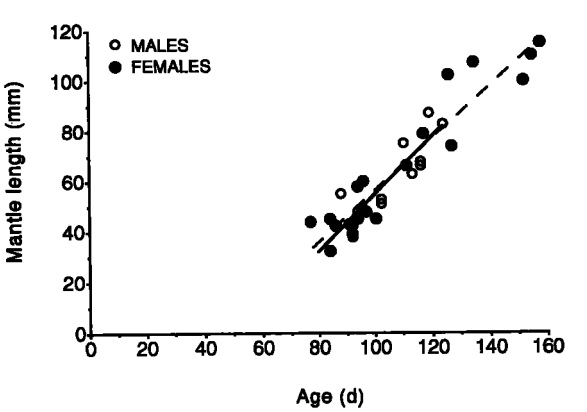

Figure 2

The relationship between age and mantle length for male (n=13) and female (n=19) individuals of *Photololigo* sp. 1. Solid regression line represents males, dashed regression line represents females.

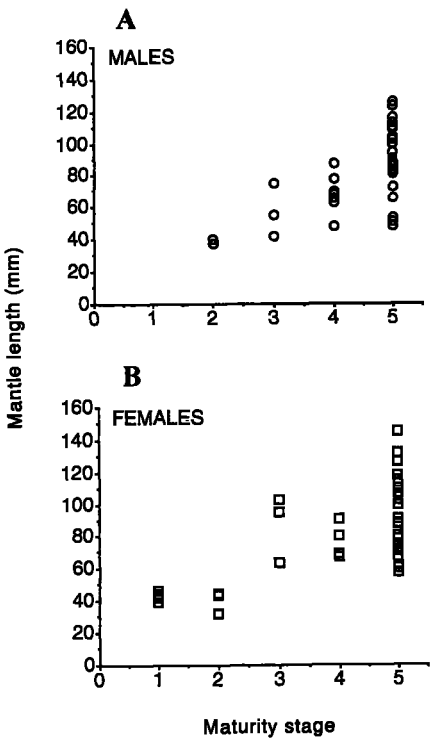

Figure 3

The relationship between maturity stage and mantle length for all (**A**) male (n=37) and (**B**) female (n=42) individuals of *Photololigo* sp. 1.

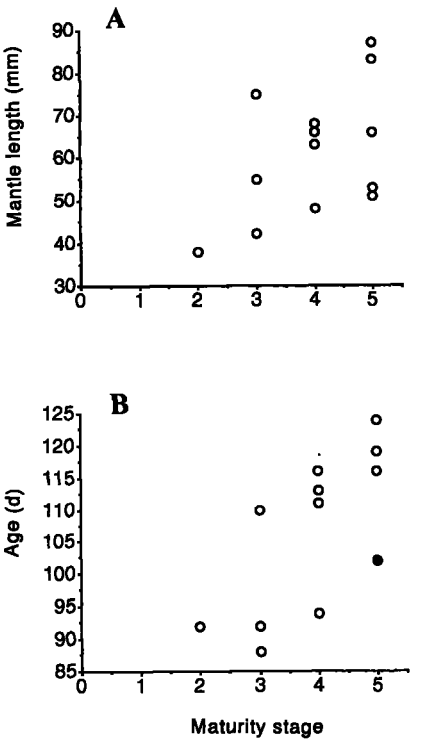

Figure 4

The relationship between (**A**) maturity stage and mantle length and (**B**) maturity stage and age for all aged male individuals of *Photololigo* sp. 1 (n=13). The filled circle represents two data points.

Females There were representatives of all maturity stages in the female sample (n=42), with considerable variation in the size of stage-5 females (Fig. 3B). The subsample of aged females (n=19) showed pronounced variation in size and age (Fig. 5, A and B) due to the greater size and age of the female sample (age range= 77–158 d). The majority of aged females were mature (stage 5) and only eight immature (stage-1 and stage-2) females were available for age analysis. Mature females ranged from 58 mm to 145 mm ML and from 94 to 158 d in age (Fig. 5, A and B). Although all immature females were smaller than the smallest mature female, some of the immature females were actually older than some of the younger mature females. As with the males, the small mature females were not only smaller but younger than their larger mature counterparts.

Discussion

Genetic approaches to squid taxonomy and population studies are becoming increasingly important. Electrophoresis has been a successful tool used in the study of population variability within squid species (Carvalho and Pitcher 1989; Garthwaite et al., 1989; Carvalho et al., 1992; Brierley et al., 1993, a and b). Furthermore, genetic techniques are becoming increasingly important as an indispensable tool in taxonomic studies (Brierley and Thorpe, 1994; Yokawa, 1994). Recent work by Yeatman and Benzie (1993, 1994) has demonstrated that electrophoresis can distinguish cryptic species that are difficult to identify morphologically. Continued use of genetic analysis of squid populations is needed and will almost certainly reveal additional cryptic species (e.g. Brierley et al., 1993, a and b).

The short life-span and nonasymptotic growth displayed by *Photololigo* sp. 1 is similar to other tropical cephalopods in northern Australian waters (Jackson and Choat, 1992). This study suggests that there might be sexual dimorphism in *Photololigo* sp. 1, with females obtaining a larger size than males. Other

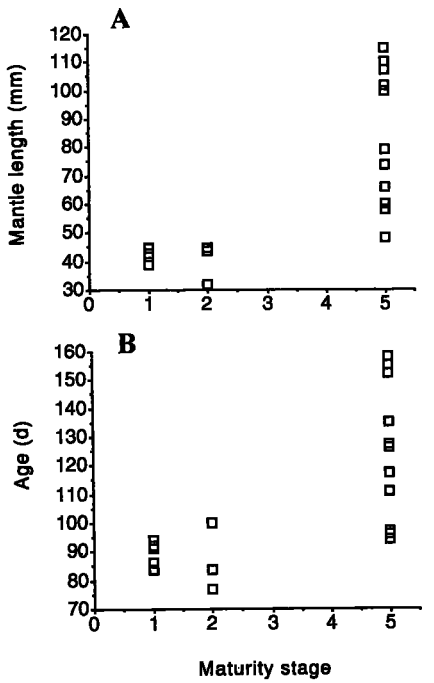

Figure 5

The relationship between (**A**) maturity stage and mantle length and (**B**) maturity stage and age for all aged female individuals of *Photololigo* sp. 1 (n=19).

tropical pelagic cephalopods (e.g. *Idiosepius pygmaeus*, Jackson, 1989; and *Loliolus noctiluca*, Jackson and Choat, 1992) do show sexual dimorphism with females obtaining a larger size and greater age than males. However, this is in contrast to the congener *Loligo chinensis*, males of which obtain a greater length and age (Jackson and Choat, 1992). The ecological or genetic factors contributing to a larger body size in either males or females are currently unclear.

The wide range in age and length at maturity observed in *Photololigo* sp. 1 off northwestern Australia is considerably different from that of the summer population of *L. chinensis* in shallow water off Townsville, North Queensland. Jackson (1993) found that maturation in *L. chinensis* was more closely related to size than age and that individuals reached maturity rapidly over a relatively restricted size range regardless of age. However, Jackson (1993) also found that several of the larger and older females were very immature and thus some individuals did delay maturation. *Photololigo* sp. 1 is a deepwater species captured at depths <100 m whereas *L. chinensis* off Townsville is a shallow water species (generally <20 m and often in <10 m), thus the reproductive tactics of these two squid species may be a response to the two very different environments.

Considerable variation in size at maturity has also been documented in other loliginids. *Photololigo edulis* in Japan shows considerable variability in size at maturity both geographically and seasonally. Natsukari and Tashiro (1991) have reported mature individuals of *P. edulis* as small as 52 and 59 mm ML for males and females, respectively, whereas the more typical size for maturation is between 150 and 200 mm ML, with some individuals remaining immature until >300 mm ML. *Loligo vulgaris reynaudii* off South Africa can mature as small as 90 and 100 mm ML (males and females, respectively) whereas immature males and females can be as large as 250 and 180 mm ML, respectively (Augustyn et al., 1992). *Loligo gahi* also shows a considerable range in size at maturity, with mature males ranging in size from approximately 71 to >300 mm ML and mature females ranging in size from approximately 98 mm to >220 mm ML (Hatfield et al., 1990). An extreme example has also been recorded by Dunning et al. (1994) who found that all males of the cuttlefish *Sepia pharaonis* collected in the Gulf of Carpentaria, Australia, were mature over a length range of 34 mm to 173 mm ML. These examples of phenotypic plasticity are much more extreme than what has been documented for *Photololigo* sp. 1 in this study. However, by attributing age to individuals, one can consider time-specific aspects in variation in size at maturity.

Considerable phenotypic plasticity has also been observed in some freshwater fishes. Mann and McCart (1981) noted the presence of two forms of *Coregonus sardinella* in a small homogenous lake in northern Canada. The presence of two such morphologically distinct forms was somewhat surprising because of the lack of environmental heterogeneity. The reasons for such plasticity were not discerned, although there was some evidence of spatial segregation and temporal segregation in spawning. Mann and McCart (1981) also suggested that such variation may not be genetically fixed but may rather be a result of different environmental conditions during early development. An even more marked degree of phenotypic plasticity has been observed in the arctic char, *Salvelinus alpinus*, in Thingvallavatn, the largest lake in Iceland. Arctic char occurs in four forms, two planktonic feeders and two benthic feeders (Sandlund et al., 1992). The morphological plasticity in this species appears to be predominantly due to niche separation based on habitat and feeding strategies possibly related to ontogenetic or population divergence.

The phenotypic plasticity observed in *Photololigo* sp. 1 does not appear to be displayed in distinct forms

but rather in a continuum in size and age at maturity from very small, precocious individuals to larger, later-maturing individuals. Such variation appears to be similar to phenotypic variation observed in poeciliid fishes. Poeciliids show a large degree of plasticity in size and age at maturity both within and among populations (e.g. Trexler et al., 1992). Variation in size at maturity for male poeciliids has been related to behavioral interactions such as maturation inhibition due to the presence of larger males or due to environmental stresses such as a limited food supply or a decreased probability of survival (Chapman and Chapman, 1992). Genetic control is also thought to play an important role in variation in size and age at maturity in fish species, with certain alleles causing early maturation in some species of poeciliids (Campton and Gall, 1988).

It is not known whether environmental, behavioral, or genetic factors are influencing the variability observed in size and age at maturity in *Photololigo* sp. 1. It might be a combination of all three factors. Squids exhibit complex behavioral communication and courtship displays (Hanlon et al., 1983; Moynihan, 1985) which in many ways may be analogous to mating strategies in the short-lived poeciliid fishes, which have internal fertilization and the ability to store sperm (Haynes, 1993) as do cephalopods.

The statolith age analysis in this study has revealed that the observed differences in size at maturity were predominantly due to larger individuals being older than their smaller counterparts rather than due to profound differences in individual growth rates. Future work incorporating larger sample sizes of aged individuals will, no doubt, make the discernment of size and age-based patterns of maturity clearer in tropical loliginids.

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Ovarian atretic rates and sexual maturity of European horse mackerel, *Trachurus trachurus* (L.), in the Saronikos Gulf (Greece)

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Abstract.—Histological sections of European horse mackerel, *Trachurus trachurus* (L.) ovaries were used to follow oogenesis and to describe the atretic states. Atretic states were used to examine the reproductive cycle during two successive reproductive seasons. During the first season, spawning lasted from December to May, with peak spawning occurring between the end of March and the beginning of April. The duration of the spawning season for the average female was estimated to be about 3 months. Atretic state 1 (yolked oocytes where <50% were in alpha (α) stage atresia) was the most common atretic condition during the spawning season. Atretic states 2 (yolked oocytes where ≥50% were in α-stage atresia) and 3 (no yolked oocytes present but β atresia or later atresia stages) increased near the end of the season, and at the end of the season, females in atretic state 3 were predominant. The mean number of potential and past-spawning stages per female increased throughout the spawning season, indicating an increase in spawning frequency. During the second season, spawning occurred from January to May. High numbers of females in atretic states 2 and 3 were noted during the period considered to be the middle of the season, followed by an increase of females classified in atretic state 0 (yolked oocytes with no α-atresia stage), indicating a species flexibility to different conditions. The use of traditional macroscopic methods, such as gonadosomatic and hepatosomatic indices, revealed a conformity with the histological data concerning the identification of the spawning season. Total body lengths at female maturity (ML_{50}), estimated histologically and macroscopically, were found to be 211 and 220 mm, respectively.

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In the Greek seas, the genus *Trachurus* is represented by three species: European horse mackerel, *T. trachurus* (L.); Mediterranean horse mackerel, *T. mediterraneus* (S.); and blue jack mackerel, *T. picturatus* (B.). The first two species are of commercial value and are very abundant, whereas the third is very scarce. Their average catch over the years 1987–90 constitutes about 10% of the total annual yield of the country and 15% of the total Saronikos Gulf catch (NSSG, 1989–93). Although these species are commercially important fish for the entire Mediterranean region, little is known about their biology, especially their reproduction. The genus *Trachurus* comprises multiple spawners with a prolonged spawning season (Polonsky and Tormosova, 1969; Kaiser, 1973; Macer, 1974; Andrianov, 1985; Eaton, 1989; Lisovenko and Andrianov, 1991; Macewicz and Hunter, 1993; Komarov[1]).

The most convenient method of determining the reproductive cycle in a female is to observe the seasonal developmental changes of the gonads. Until recently these changes for species of *Trachurus* were examined by studying the seasonal variations of maturity stages or the gonadosomatic index, or both (Kaiser, 1973; Macer, 1974; Nazarov, 1977; Arruda, 1984; Andrianov, 1985; Kerstan, 1985; Komarov[1]). However, for multispawners the use of gross anatomical criteria provides a less accurate assessment of fish maturity and reproduction in comparison with that of histological methods (Hunter and Macewicz, 1985a; Dickerson et al., 1992; Eltink[2]). Histological examination is essential for detecting maturing females, partly spawned fish, the postovulatory follicles, and atretic oocytes.

In the present work we used the ovarian atretic states defined by Hunter and Macewicz (1985b) in order to follow the reproductive cycle of European horse mackerel. Specifically, we estimated the rate at which females spawn and pass from the active (when fish are capable of spawning in the current season) to the inactive state (when fish have completed their spawning cycle), the peak period of spawning, and the duration of the spawning

[1] Komarov, J. A. 1964. On the reproduction of horse mackerel (*Trachurus trachurus*) off the southwestern coast of Africa. ICES Council Meeting 94, 5 p. (Mimeo.)

[2] Eltink, A. 1991. Batch fecundity and fraction spawning of horse mackerel (*Trachurus trachurus* L.). European Community Study Contract BO-1990-207, 71 p.

season for the average female. In addition, anatomical maturity stages and the gonadosomatic index were compared to histological results in order to show the extent that these data can provide accurate information concerning the reproductive cycle. Finally, we estimated the length at which 50% of females are mature, using both histological and macroscopic criteria.

Materials and methods

Sampling and macroscopic classification

Samples of European horse mackerel were collected in the Saronikos Gulf (Fig. 1) by a commercial trawler operating from October through May. In the study area, the mean annual temperature and salinity at a depth range of about 100–200 meters were 14°C and 38‰, respectively. At this depth range, which characterizes European horse mackerel distribution (Fischer et al., 1987), there was little monthly temperature variation during the sampling period (Georgopoulos[3]). The samples were taken almost monthly, from October 1989 until May 1991, but they were taken more often during the peak spawning period until the end of the sampling period. Supplementary samples were obtained with a purse seiner during the period closed to trawling (i.e. June–September) (Table 1).

European horse mackerels were randomly selected from the catch, and the total length of the fish was measured to the nearest centimeter. Ten fish from each 1-cm length class (throughout the available range) were retained. These fish were measured (total length) to the nearest millimeter, sexed, and weighed (total weight) to the nearest gram. After gross examination of the gonads, the fish were classified into maturity stages according to Macer (1974). Because some of the stages used by Macer were difficult to distinguish macroscopically, (such as developing virgin (maturing/immature) versus resting, ripe versus running, and spent versus recovering), three pairs of Macer's stages were grouped into single stages. Thus, the maturity scale used consisted of seven stages: I = virgin, II = resting, III = early developing, IV = later developing, V = ripe, VI = partly spent, and VII = spent. Gonads and livers were removed and weighed to the nearest 0.1 gram.

Ovaries classified into maturity stages greater than II (about a third of the length of the body cavity) were preserved in 7% neutral, buffered formalin for histological examination. A number of randomly selected ovaries in maturity stages I and II were also preserved in 7% buffered formalin.

Histological method and classification

A small piece (about 0.5–1 cm long) of each preserved ovary was removed, dehydrated, and embedded in paraffin. Subsequently, 3-μm sections were cut and stained with Harris hematoxylin followed by eosin counterstain (H+E). In each sectioned ovary we recorded the following characters (Wallace and Selman, 1981; Mayer et al., 1988; Macewicz and Hunter, 1993): (a) oocytes that had not begun vitellogenesis; (b) oocytes in early vitellogenic stages; (c) advanced yolked oocytes; (d) migratory-nucleus-stage oocytes; (e) hydrated oocytes; and (f) postovulatory follicles. Postovulatory follicles were aged following the criteria used for *T. symmetricus* (Macewicz and Hunter, 1993; Macewicz[4]). The ovarian sections were also

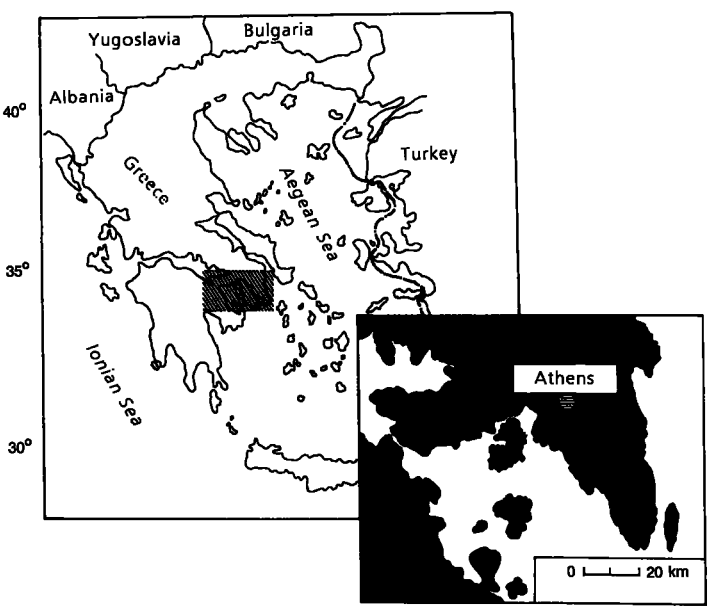

Figure 1
Map of the Saronikos Gulf (Greece).

[3] Georgopoulos, D. 1993–95. National Centre for Marine Research, Aghios Kosmas, 16 604 Hellinikon, Greece. Personal commun.

[4] Macewicz, B. J. 1993. Southwest Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, P. O. Box 271, La Jolla, CA 92038. Personal commun.

Table 1

Sampling data and numbers of horse mackerel, *T. trachurus*, females in various histological subclasses during the sampling period in the Saronikos Gulf (Greece).

Sampling date	Fishing gear[1]	Immature[2]	Mature: Active: Spawning[3]	Mature: Active: Nonspawning[4]	Mature: Inactive: Postspawning[5]	Females sectioned	Total no. females sampled
24 Oct 1989	TR	34	0	1	0	35	68
20 Nov 1989	TR	4	0	9	0	13	32
28 Dec 1989	TR	0	1	12	0	13	27
24 Jan 1990	TR	0	2	14	1	17	53
15 Feb 1990	TR	0	13	12	1	26	30
12 Mar 1990	TR	0	32	8	1	41	79
28 Mar 1990	TR	0	17	0	3	20	48
18 Apr 1990	TR	0	14	0	5	19	67
09 May 1990	TR	0	11	0	5	16	57
29 May 1990	TR	0	6	0	9	15	39
20 Jun 1990	PS						24[6]
05 Jul 1990	PS	0	1	0	14	15	29
12 Sep 1990	PS	25	0	0	0	25	51
19 Oct 1990	TR	8	0	0	0	8	83
20 Nov 1990	TR	7	0	0	0	7	34
18 Dec 1990	TR	7	0	20	0	27	70
24 Jan 1991	TR	0	9	8	0	17	53
13 Mar 1991	TR	0	4	1	19	24	30
31 Mar 1991	TR	0	15	2	4	21	90
14 Apr 1991	TR	0	13	0	15	28	42
07 May 1991	TR	0	5	0	0	5	24
24 May 1991	TR						50[6]
30 May 1991	TR						72[6]
Total		85	143	87	77	392	1,152

[1] TR = Trawler, PS = Purse seiner.
[2] No yolked oocytes and no postovulatory or atretic follicles were present.
[3] Migratory-nucleus-stage oocytes and/or hydrated oocytes were present, or yolked oocytes and postovulatory follicles.
[4] Yolked oocytes were present and no migratory-nucleus-stage or hydrated oocytes, or postovulatory follicles.
[5] Postovulatory or atretic follicles could be detected, but either no yolked oocytes were present or if present, ≥50% were undergoing α-atresia.
[6] Samples of females with were macroscopically classified as immature (virgin or resting) and were not sectioned.

examined for the presence of alpha (α), beta (β), gamma (γ) or delta (δ) stage atresia (Bretschneider and Duyvene de Wit, 1947). Our definition of an atretic follicle, which characterizes an oocyte undergoing atresia in β or subsequent atretic stages, was adopted from Hunter and Macewicz (1985b).

Because females tend to reabsorb their oocytes once the spawning season comes to an end, the criteria of 50% or more of yolked oocytes (not those in early vitellogenic stages) with α-stage atresia, or the absence of yolked oocytes but presence of postovulatory follicles or atretic follicles, or both, were used to indicate that these females had finished their spawning season (Hunter and Macewicz, 1985, a and b; Hunter et al., 1986; Dickerson et al., 1992; Macewicz and Hunter, 1993). It should be mentioned that the occurrence of α-stage atresia in yolked oocytes is the best characteristic to backcalculate the time of past reproductive activity because the type of oocyte undergoing atresia is still discernible, and this atretic oocyte can be easily distinguished from postovulatory follicles (Hunter and Macewicz, 1985b). Hence, all the yolked oocytes (not those in early vitellogenic stages) in each section were counted under the mi-

croscope, and the percentage (< or ≥50%) of oocytes in α-stage atresia was noted.

Females with ovaries containing yolked oocytes were classified as active, i.e. capable of spawning in the current spawning season. Active females were separated into spawning and nonspawning groups. Spawning females contained ovaries with histological characteristics of past spawning (postovulatory follicles) or imminent spawning (hydrated oocytes or migratory-nucleus-stage oocytes). The nonspawning females that displayed no such characteristics were assumed to be capable of spawning in the near future. Females with yolked oocytes where 50% or more were in α-stage atresia, or had no yolked oocytes but only postovulatory or atretic follicles, or both, were classified as postspawning or inactive in the current season. The active and the postspawning females were both considered mature. Females that showed no histological evidence of past, imminent, or future reproductive activity were classified as immature.

Reproductive cycle

Atretic states Description of atresia stages (α, β, γ, and δ) follows Bretschneider and Duyvene de Wit (1947), Hunter and Macewicz (1985, a and b) and Macewicz and Hunter (1993). These stages are common among several species studied including the jack mackerel, *Trachurus symmetricus* (Macewicz and Hunter, 1993).

Classification of ovaries based on oocyte and atresia stages follows Hunter and Macewicz (1985b) and is briefly summarized as follows:

Atretic state 0 No α atresia of yolked oocytes.
Atretic state 1 <50% (1 oocyte to 49%) of yolked oocytes were in α atresia.
Atretic state 2 ≥50% of yolked oocytes were in α atresia.
Atretic state 3 No remaining yolked oocytes, but β atresia or later atresia stages were present.

Atretic state 3 was used to separate immature females from postspawners, because advanced atresia stages indicate the possibility of past spawning. The late postspawning ovary was also characterized by disorganized septa, a condition which indicated that this particular female might have spawned during the latest reproductive season.

We defined the reproductive season for European horse mackerel as the period from the date of first active females with yolked oocytes, not necessarily spawning, until the last active females sampled. The fraction of active females classified as spawning was used to estimate the spawning rate index, while the fraction of the postspawning females was used as an index of the rate at which females passed from the active to the inactive state. These data were fitted to logistic curves ($y=1/(1+e^{a-bx})$, where y is the fraction of the females used and x is the number of days elapsed since the initiation of spawning; Hunter et al., 1992). We calculated the approximate spawning season for individual females by subtracting the days from the 50% spawning point to the 50% postspawning point.

In some females, multiple spawning stages (migratory-nucleus oocytes, hydrated oocytes, 1-d-old postovulatory follicles, 2-d-old postovulatory follicles) occurred within the same ovary indicating different potential or past spawnings. Under the assumption that the stages of advanced yolked oocytes and partially yolked oocytes could represent two potential spawnings, as many as six different spawning stages could be distinguished histologically in the same ovary. Hence, the mean number of stages per sampling date was estimated, providing information about seasonal changes of spawning frequency (Hunter et al., 1992).

Gonadosomatic and hepatosomatic index We also followed the seasonal changes in ovarian development by calculating the mean monthly gonadosomatic (GSI) and hepatosomatic (HSI) indices. The formulae used were the following: GSI= 100 (ovary weight)/(body weight–ovary weight) and HSI= 100 (liver weight)/(body weight–liver weight).

Estimation of length at 50% maturity

Total lengths of all histologically identified females were used to estimate the length at 50% maturity (ML_{50}) of European horse mackerel during the spawning season. We assumed that all females with vitellogenic ovaries would reach sexual maturity, and therefore such females were included in the proportions of mature females. The proportions were estimated at length classes of 10 mm, and the data fitted to a logistic curve. Lengths of females with ovaries classified macroscopically were similarly fitted to a logistic function for comparison of the ML_{50} value. Macroscopically mature females possessed ovaries that were classified to maturity stages above stage II.

Results

Oogenesis

In the ovaries of European horse mackerel, oocyte development is divided into a primary growth phase

and a secondary growth phase as in most teleosts (Wallace and Selman, 1981; Mayer et al., 1988). The secondary growth phase is characterized by yolk deposition, nucleus migration to the animal pole, and hydration. In particular, oocytes in early vitellogenic stages (partially yolked), and advanced yolked oocytes that were included in the mature horse mackerel females had the following characteristics:

Partially yolked oocytes Yolk vesicle deposition following by the appearance of yolk granules and the formation of the zona radiata.

Advanced oocytes Increase of yolk granules resulting in compact dense yolk spherules, which filled the cytoplasm. The nucleus was eventually surrounded by the lipid droplets.

Reproductive cycle

Atresia stages and atretic states During the whole sampling period, 392 ovaries out of 1,152 females sampled were sectioned, and 85 were identified as immature, 143 as spawning, 87 as nonspawning, and 77 as postspawning (Table 1). Ninety-six ovaries were found having α-atresia in advanced yolked oocytes (Table 2).

We observed atresia throughout the spawning period in sequential stages—α(alpha), β(beta), and δ (delta), (Fig. 2, A–C). The α- and δ-stages of atresia showed similar characteristics to those described for northern anchovy (Hunter and Macewicz, 1985b). The γ (gamma) stage atresia was not observed; this may have been due to its short duration or to the fact that the follicle passes directly from the β to the δ stage without passing through the intervening γ stage (Hunter and Macewicz, 1985, a and b). In addition, the low incidence of δ-stage atresia observed in regressing ovaries of European horse mackerel indicates that some follicles might be completely resorbed during the β stage. In particular, the β-stage atretic follicle of European horse mackerel was characterized by the presence of many vacuoles, possible remnants of the lipid droplets that take longer than yolk to be absorbed (Macewicz and Hunter, 1993).

The spawning potential of females with atretic ovaries is generally thought to be low (Hunter and Macewicz, 1985b). To verify this expectation in the regressing ovaries of European horse mackerel, we estimated the percentages of females with the histological criteria of imminent spawning, past spawning, and nonspawning, which were classified into atretic states 1 and 2. Females in atretic state 1 showed evidence of past or imminent spawning (82.9%), whereas the percentage of spawning females in atretic state 2 was very low (7.7%) (Table 2). By the time that ovaries reached atretic state 2, more than half of the advanced yolked oocytes were not viable. In particular, about 80% of the ovaries in atretic state 2 had 90–100% atretic advanced yolked oocytes.

During this study, we identified two successive reproductive seasons, the first one from October 1989 to early July 1990, and the second one from December 1990 to May 1991. Onset of spawning was observed in December and January, respectively, and continued until July and May of the first and second seasons, respectively. In June 1990, no ovaries were sectioned because females were macroscopically classified as immature, whereas in July 1990 all but one (spawning) of the females were late postspawning (atretic state 3).

On the basis of histological classification of ovaries, 192 and 115 mature females were examined in the first and second reproductive seasons, respectively. The occurrence of α atresia was seen from the onset of spawning. During the first spawning season we observed that atretic state 1 was the most common atretic condition (Fig. 3A). Females in atretic

Table 2

Percentage of European horse mackerel, *T. trachurus*, females classified into two atretic states which occurred in each of four reproductive classes.

Atretic state	% totally yolked oocytes with α-atresia stage	Immenent spawning[1]	Past spawning[2]	Spawning past or imminent	Active nonspawning[3]	Total no. females
1	<50	15.3	67.6	82.9	17.1	73
2	≥50	0.0	7.7	7.7	92.3	23
					Total	96

[1] Migratory-nucleus-stage oocytes or hydrated oocytes present. Postovulatory follicles may be present.
[2] No migratory-nucleus-stage oocytes or hydrated oocytes present. Postovulatory follicles present.
[3] Yolked oocytes present and no histological characteristics as mentioned above.

states 2 and 3 appeared gradually in increasing numbers. The high percentage of atretic-state 2 females was evident near the end of the season, whereas at the end, females with yolked oocytes in the ovaries were not present, and atretic-state 3 females were predominant.

In the ovaries sectioned from September to November 1990, we observed only primary growth oocytes, and the onset of vitellogenesis was not detected until December 1990. During this second season, atretic patterns did not follow the trends observed in the first season (Fig. 3B). During March 1991 (mid-season), high numbers of postspawning females (atretic states 2 and 3) were noted, followed by an increase in the females classified in atretic state 0, which suggests a hiatus in spawning during a period considered to be the middle of the spawning season.

Spawning and postspawning females during the season In the first reproductive season, the sample of 28 December was the first to contain spawning females with evidence of past spawning (Table 1). Since the previous sample taken (20 November) had no spawning females but rather females with advanced yolked oocytes, 9 December (the middle of these dates) was taken as an approximate start of the spawning period. The fractions of spawning and postspawning females were plotted as a function of time elapsed since 9 December (Fig. 4).

A sharp increase occurred in spawning rate between January and February, indicating a change in the spawning frequency, and by the end of March all active females were spawning (Fig. 4). The rate at which females passed from the active to the inactive stage (postspawning rate) accelerated in April. Thus, the period from the end of March to the beginning of April was considered to be the peak of spawning in 1990 on the basis of histological samples.

During the spawning season, the sex ratio (females/total) from all fish sampled remained constant (mean=0.57, SD=0.035), indicating that no sex-based migration probably occurred in and out of the sampled area. The number of sections were insufficient to detect whether the incidence of atresia was age specific. However, it is known that all individuals of European horse mackerel do not have the same spawning season (Arruda, 1984), as is the case for northern anchovy (Hunter and Macewicz, 1985b). For this reason, we estimated the approximate spawning season for an average female by sub-

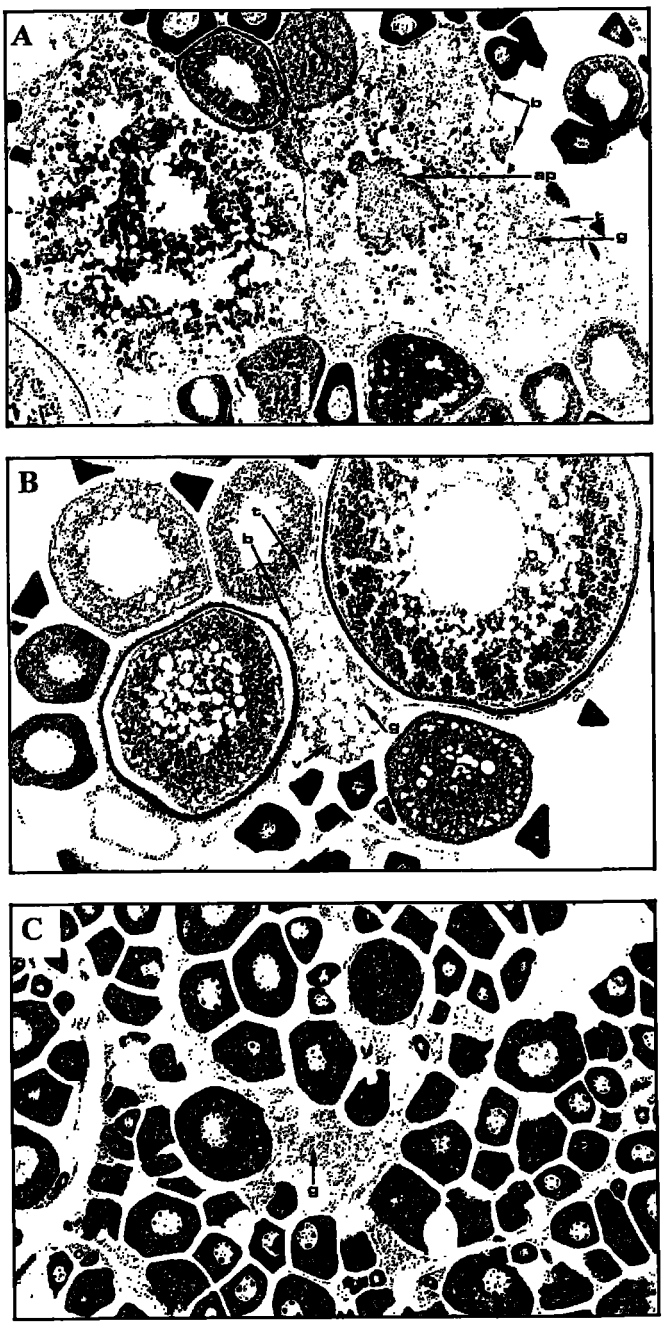

Figure 2

Atresia stages of European horse mackerel, *Trachurus trachurus*, oocytes. (**A**) α-stage atresia of two yolked oocytes. The zona radiata has been dissolved. The hypertrophied granulosa cells (g) have invaded the yolk. The thecal cell layer (t) with blood capillaries (b) is seen. The amorphous particle (ap) may be the remnant of the zona radiata or yolk. (**B**) β-stage atresia. The yolk spherules show degeneration. Granulosa cells (g) and many vacuoles (v) are present. The thecal cell layer (t) with blood capillaries (b) is seen. (**C**) δ-stage atresia. Few granulosa cells (g) in the ovarian tissue stroma. The thecal cell layer and the blood capillaries no longer encompass the follicle. Harris haematoxylin and eosin stains were used. Magnification: 137×.

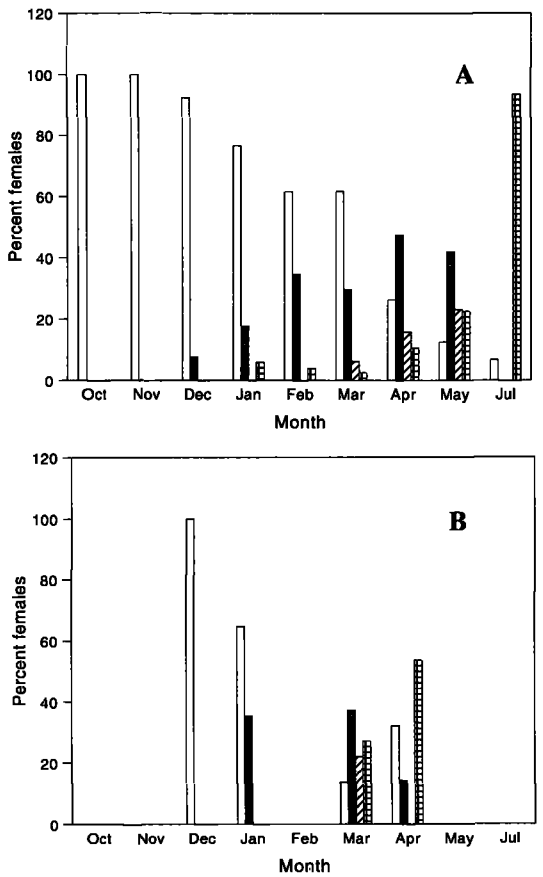

Figure 3

Percentage of mature European horse mackerel, *Trachurus trachurus*, females classified into atretic states (**A**) during the first reproductive season and (**B**) during the second reproductive season. No ovaries were sectioned in June (A). Five ovaries sectioned in May (B) were not classified into atretic states because of their low number. Open solid bar = atretic state 0; filled solid bar = atretic state 1; diagonally hatched bar = atretic state 2; cross-hatched bar = atretic state 3.

tracting the number of days to the 50% spawning point (67 days) from the number of days to the 50% postspawning point (161 days) which resulted in a spawning duration estimate of 94 days.

An increase in the mean number of potential and past-spawning stages per female occurred until early May, indicating a possible increase in spawning frequency (Fig. 5). By the end of May, when atretic states 2 and 3 were estimated to be very high, the mean number of these spawning stages decreased sharply. This shows that no other oocytes were recruited into vitellogenesis as the spawning period was ending.

Gonadosomatic and hepatosomatic index From the histological study we observed that no females of age less than 2 years spawned (Karlou-Riga[5]). Therefore, GSI and HSI were both calculated for females older than 1 year of age. The peak GSI value occurred in February 1989, when the histological data indicated that half of the mature females (52%) were spawning (Fig. 6). GSI decreased in the following months, whereas the peak HSI value was observed near the end of the first reproductive period (around May). During the summer and autumn of 1990, the two indices remained low, and an increase occurred in December 1990 denoting the onset of the second reproductive season (Fig. 6). During the second season, the peak GSI value was about one third of the respective value of the same index observed in the previous period (Fig. 6).

The correlation of the two indices was tested by using Spearman's rank correlation procedure (Zar, 1984). Disagreement was found during the sampling period (Oct. 1989–Nov. 1990: r_s=–0.2829, P<0.001, n=551; Dec. 1990–May 1991: r_s=–0.1955, P<0.001, n=429). The negative correlation between GSI and HSI indicates that GSI and HSI did not follow the same course, indicating most probably that ovarian growth proceeds at the expense of liver content as is the case for other teleost species (Wallace and Selman, 1981), including *Trachurus murphyi* (Kaiser, 1973).

Estimation of length at 50% mature

The sex ratio was examined by applying the paired-sample t-test in both reproductive periods, and no difference was found at 5% level of significance (t=1.92, P=0.127). Length-frequency distributions of females for the two periods were tested by applying the Kolmogorov-Smirnov two-sample procedure. No significant length differences were found between females that were macroscopically staged (P=0.96 [>0.05]) and those that were histologically staged (P=0.37 [>0.05]) for maturity status. Therefore, the data from the two periods were combined, and the ML_{50} values were estimated from the logistic curves separately for histological and macroscopical data (Fig. 7).

Fish with lengths close to ML_{50} were two to three years old (Karlou-Riga[5]). The macroscopically estimated ML_{50} (220 mm) was a little higher than the histologically estimated ML_{50} (211 mm), probably owing to the macroscopical misclassification of some mature females as immature. However, analysis of

[5] Karlou-Riga, C. 1995. Age and growth of *Trachurus trachurus* (L.) in the Saronikos Gulf (Greece). Unpubl. manuscr., Fisheries Laboratory, Ministry of Agriculture, 15 Karaoli and Dimitriou St., GR-18531 Piraeus, Greece.

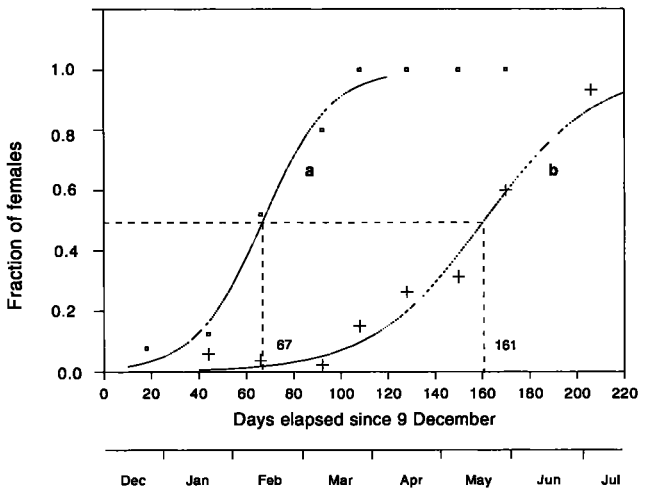

Figure 4

Fraction of European horse mackerel, *Trachurus trachurus*, spawning and postspawning females during the period from 9 December to 5 July (1989–90). (**a**) Females with active ovaries, which had one or more spawning stages (open squares); trend line is a logistic curve, where a = 4.699, b = 0. 070, r^2 = 0.98. (**b**) Females in atretic states 2 or 3, which have finished their spawning season (crosses); trend line is a logistic curve, where a = 6.757, b = 0.042, r^2 = 0.97. The approximate spawning season for the individual female (94 days) was estimated by subtracting the 50% spawning point (67 days) from the 50% postspawning point (161 days).

covariance of the $\log_e$-transformation of percent mature females on the length and maturity-staging method indicated that the difference between the two ML_{50} estimates was not significant (F=0.85, P=0.373).

Discussion

Reproductive cycle

In the present work, we found that histological atretic states were useful as an index of the population's reproductive capability for European horse mackerel. Atretic-state 1 females (<50% of advanced yolked oocytes in α-stage atresia) were apparently capable of spawning, whereas atretic-state 2 females (50% or more of advanced yolked oocytes in α-stage atresia) had a lower spawning probability. It seems most likely that once females are in atretic state 2 they do not spawn or spawn infrequently (Hunter and Macewicz, 1985b). Therefore, this state was the best absolute measure of ovary resorption. Atretic-state 3 females (showing no yolked oocytes but late atresia stages) were those in late postspawning condition. These females could not be distinguished from immature females by gross anatomical criteria. Consequently, this histological state was very useful in classifying mature females and estimating length at first maturity.

The high percentages of atretic oocytes observed in European horse mackerel throughout the spawning season are a normal occurrence in multispawners (Hunter and Macewicz, 1985b; Dickerson et al., 1992), an attribute which probably characterizes most species of *Trachurus* (Macewicz and Hunter, 1993). High numbers of atretic oocytes are also observed in Atlantic mackerel (*Scomber scombrus* L.) ovaries around peak spawning (Walsh et al.[6]). Therefore, atretic state 1 is expected to be the most common condition during the main spawning season.

During the first spawning season, we found that atretic state 2 increased near the end of the season, and that it was completely replaced by atretic state 3 at the end. Thus, it is useful to study both of these atretic states during the entire spawning season. However, it is also important to estimate atretic states near and after the end of the season. We were not able to assess the atretic state in June because of a lack of histological samples. However, because atretic state 3 lasts for one month or more in the ovary (Hunter and Macewicz, 1985, a and b), it is very likely that ovary resorption observed in high levels in late May continued through July, because all the mature females were in late postspawning condition by July. Low GSI values in June and July supported this conclusion. Thus, high levels of atretic state 2 actually forecasted the end of the European horse mackerel spawning season as has been noted for other fishes (Hunter and Macewicz, 1985b). Because GSI remained low during the summer and no atresia stages were observed in early September 1990, vitellogenesis probably did not occur in the time interval between July and September.

Females were inactive until December 1990, when the next reproductive season began. By the middle of this second season (March 1991), high levels of atretic states 2 and 3 were noted, and subsequently percentages of females in atretic state 0 (yolked but no atretic oocytes) increased, resulting in an unexpected pattern. It was not possible to explain either the "delay" of onset for this reproductive season or the mid-season increase in atretic rates. Variation

[6] Walsh, M., P. Hopkins, P. Witthames, M. Greer-Walker, and J. Watson. 1990. Estimation of total potential fecundity and atresia in the western mackerel stock, 1989. ICES Council Meeting H:31, 22 p.

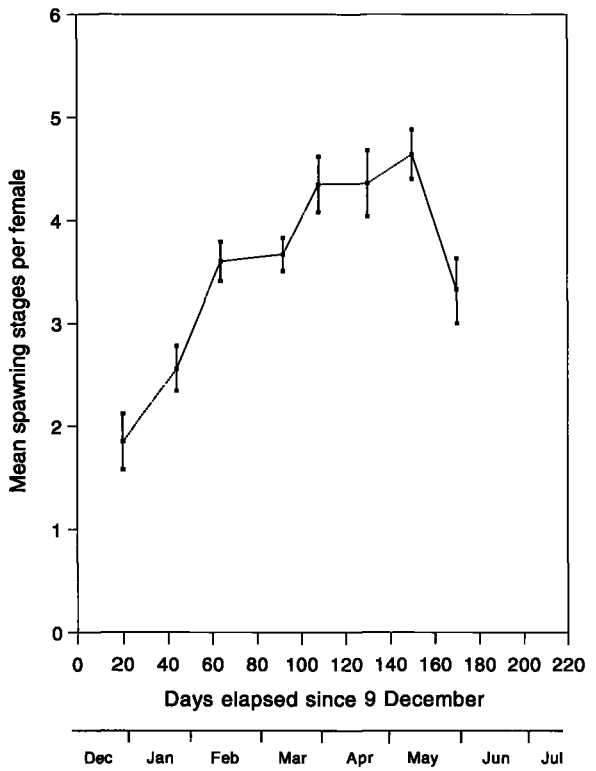

Figure 5

Mean number of potential and past-spawning stages per European horse mackerel, *Trachurus trachurus*, female during the period from 9 December to 5 July (1989–90); bars are two standard errors of the mean.

in temperature, one of the main factors influencing maturation (Billard et al., 1981), could not have affected these second season changes because temperature remained almost constant in the study area. Another factor known to stimulate ovary resorption is an imbalance in the sex ratio (Trippel and Harvey, 1990). However, in the present work this ratio did not differ between the two reproductive seasons and remained constant. Although a reactivation of regressing ovaries has been postulated as a possible event (Hunter and Macewicz, 1985b), it is not known whether postspawning European horse mackerel females can be reactivated during a spawning season. The high levels of atretic states 2 and 3 for European horse mackerel in the middle of the season may not necessarily indicate cessation of spawning but merely the end of a spawning cycle within the spawning season. This implies that European horse mackerel seems to be very flexible in adjusting its spawning time to different conditions and that its spawning cycle might be more variable than previously assumed. Such a flexibility may be very important for the survival of the species in highly oligotrophic waters, such as the Greek and northeast Mediterranean waters in general (Stergiou, 1993).

The index of spawning rate provided information about the spawning behavior of active European horse mackerel females during the first reproductive season. The increase of this rate, beginning very early in the season, indicated an increase in spawning frequency in the same period (Hunter et al., 1992). This increase was supported by an increase in the mean number of potential or past-spawning stages. The decrease in this number toward the end of the season likely indicated a decrease of spawning frequency, although all the remaining active females were spawning.

We noticed in using both histological and macroscopic data that the spawning season of European horse mackerel lasts about six months. This season ranges from 3 to 6 months for northern to southern areas of the eastern Atlantic, respectively (Arruda, 1984; Eaton, 1989; Eltink[7]). However, we believe the duration of the season, during which spawning was observed, differs from the spawning duration for the average female, which may be very representative of the population. Smaller northern anchovy females have a shorter spawning season because of high levels of atresia (Hunter and Macewicz, 1985b). The same may be true for European horse mackerel because all females did not start and finish spawning on the same day. The estimated spawning season for the average European horse mackerel female (94 days) is higher than that for the same species in the eastern Atlantic which is assumed to be 65 days (Eltink[2]).

The GSI, as an index of ovarian changes during the spawning season, is of lesser importance than histological data for multiple spawners. For instance, this index does not distinguish partly spent (active females with postovulatory follicles) and spent (inactive females with regressing ovaries) females. The peak GSI value may not indicate the peak spawning time but rather a later developing stage for most females (Arruda, 1984). However, high values of this index can be used to determine the period when hydrated oocytes can be identified (Hunter and Macewicz, 1985a). This is very useful for batch fecundity estimates, where hydrated oocytes need to be counted. GSI calculated over the entire year indicated the approximate reproductive period, and the low GSI values near the end of the season constituted a helpful guide to validate the end of the sea-

[7] Eltink, A. 1991. Horse mackerel egg production and spawning stock size in the North Sea in 1990. ICES Council Meeting H:27, 14 p. (Mimeo.)

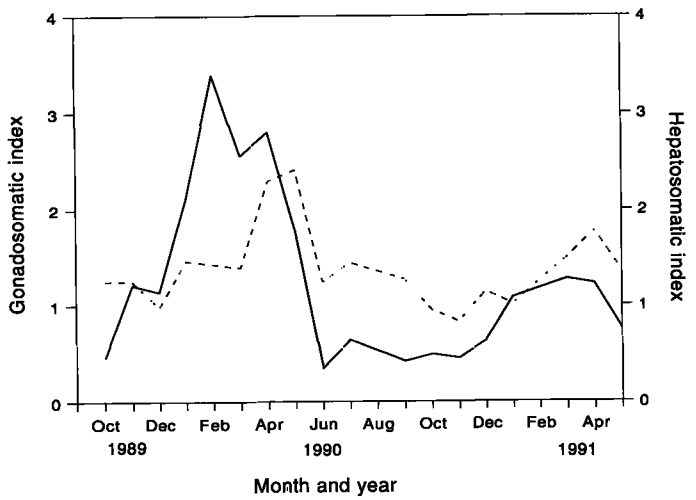

Figure 6

Gonadosomatic (mean GSI) and hepatosomatic (mean HSI) index of European horse mackerel, *Trachurus trachurus*, females per sampling month during the period from October 1989 to May 1991. Number of females examined = 980. Solid line = GSI; dashed line = HSI.

son as was indicated by high atretic states. During the second reproductive period, we noticed that GSI attained about one third of the value recorded in the previous period. The lower GSI values during the second period also support the high numbers of postspawning females that were observed histologically during mid-season, resulting in a possible drop of annual fecundity.

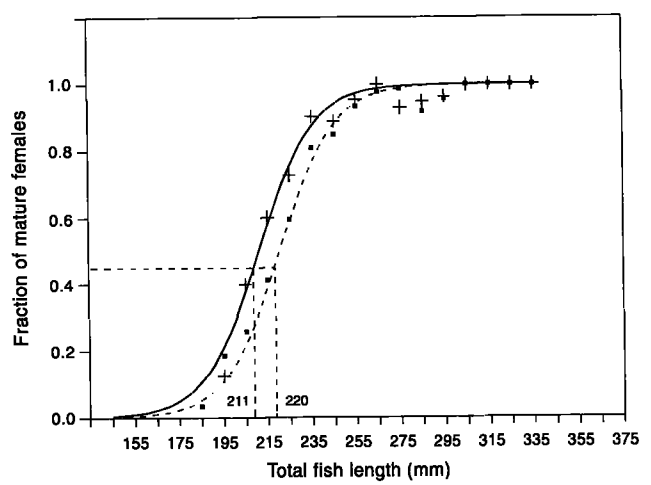

Figure 7

Fraction of European horse mackerel, *Trachurus trachurus*, females that were sexually mature on the basis of histological criteria (crosses and solid line) and macroscopic criteria (filled squares and dashed line) during two successive reproductive periods. The ML_{50}, based on 307 mature females, was estimated histologically to be 211 mm (logistic curve parameters: a=17.104, b=0.081, r^2=0.98); the ML_{50}, based on 595 mature females, was estimated macroscopically to be 220 mm (logistic curve parameters: a=17.863, b=0.081, r^2=0.99).

Sexual maturity

We found that the values of ML_{50} estimated histologically (211 mm) and macroscopically (220 mm) were very similar. This indicates that the separation between mature and immature females by gross examination of the gonads was relatively unbiased. However, a number of females with early developing or regressing ovaries were grossly misclassified as immature. These could be correctly identified only by histological examination, resulting in lower proportions of mature females with the macroscopic method. On the other hand, it is possible that ML_{50}, determined histologically, may be overestimated when measurements are made during the spawning season (Hunter et al., 1992). This did not happen in the present work because immature females were identified only at the beginning of the reproductive period, before spawning had started. Consequently, we believe the ML_{50} determined from histological sections was the least-biased estimate. Although the age at first maturity (i.e. 2 years) is in general agreement with Arruda's (1984) estimation, our ML_{50} values were not strictly comparable to those of Arruda, because the latter refers to standard length units and no conversion equation is given. However, our value was probably lower because Arruda considered only macroscopically "ripe" individuals as mature. A smaller number of stages used to define maturity was also the reason for a higher value of ML_{50} (254 mm) estimated by Kerstan (1985). Finally, the differences in sexual maturity referred to by various investigators should be compared carefully owing to possible different sampling times or, more importantly, to a strict use of anatomical criteria to identify the mature individuals resulting in a significant bias, especially for multiple spawners.

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Allometry of marine mortality of Pacific salmon

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Abstract.—Rearing experiments have shown that instantaneous growth rate, G (d^{-1}), of juvenile salmonids scales with body weight, W (g), as $G = aW^{-b}$, where b has an average value of 0.37. Research on nonsalmonid fishes has shown that instantaneous natural marine mortality rate, M (d^{-1}), also scales with body weight as $M = cW^{-x}$, where x has an average value of 0.37. Therefore, if $b - x \sim 0$, then $c < a$. These two hypotheses were tested for Pacific salmon with data on smolt-adult survival, s, smolt weight, W_0 (g), and adult weight, W (g), taken from the scientific literature. A nonlinear regression of survival on weight was developed, on the basis of allometric marine growth: $\log_e(s) = -(\alpha/\beta)(W^{\beta}-W_0^{\beta})$, where $\alpha = c/a$ and $\beta = b - x$. The regression model explained 33% of the variance in mean $\log_e(s)$ of sockeye salmon (*Oncorhynchus nerka*) with parameter values (±1SD) of $\alpha = 0.226 \pm 1.171$ and $\beta = 0.120 \pm 0.990$. The model explained 68% of the variance in the pooled mean $\log_e(s)$ of pink (*O. gorbuscha*), chum (*O. keta*), coho (*O. kisutch*), and sockeye salmon, as well as steelhead trout (*O. mykiss*), with parameter values (±1SD) of $\alpha = 0.528 \pm 0.490$ and $\beta = -0.053 \pm 0.221$. The near-zero estimates of β and the fractional estimates of α support the hypothesis that $x \sim 0.37$ and $c < a$. Therefore, the best estimate of M for Pacific salmon is $M = 0.528aW^{-0.37}$, or, since $a = G/W^{-0.37}$, $M = 0.528G$. These survival-size and mortality-size relationships may be used to make preliminary estimates of survival and mortality for wild populations of Pacific salmon.

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There are few accurate estimates of instantaneous natural marine mortality rate, M (d^{-1}), for the seven species of Pacific salmon (genus *Oncorhynchus*), despite the importance of this information for reconstructing stock histories (Pacific Salmon Commission, 1992) and for modeling the dynamics of salmon populations (Ricker, 1962, 1976; Walters et al., 1978). For example, Ricker's (1976) review of marine mortality of Pacific salmon identified only three estimates of monthly M for the last year of sea life, which had no known bias and small sampling errors. No new estimates of marine M of Pacific salmon have been added to the primary scientific literature in the last 15 years (Groot and Margolis, 1991), although many estimates of smolt–adult survival have been reported (Table 1).

The lack of new estimates of M is probably due to the difficulty of calculating it. Current methods of population enumeration provide, at most, an estimate of the number of smolts that go to sea and an estimate of the total number of adults that return 1–5 years later. They do not cover the 1–5 years of sea life during which marine mortality occurs. It is possible to calculate an average marine M for a brood year by dividing the natural logarithm of smolt–adult survival by the average duration of sea life. However, such estimates of average M cannot accurately predict the decrease in abundance of a salmon population for time periods shorter than a salmon's entire sea life, as is required by cohort analysis and by simulation models with time steps of days or weeks. This is because M of fishes is not constant over a life stage but decreases with increasing body size. Average marine M underestimates M of smolts and overestimates M of adults. The degree of bias is proportional to the duration of sea life and can be significant for salmon that spend more than one year at sea.

To model the marine dynamics of a salmon population, a model of the way in which M varies with body size is required. Following Ursin (1967), Peterson and Wroblewski (1984), Dickie et al. (1987), McGurk (1993), and others, I assume that M follows the allometric rule: $M = cW^{-x}$, where W = body weight (g), $c = M$ (d^{-1}) at a weight of 1 g, and x is a dimensionless exponent. In this paper, I provide the first empirically derived estimate of the weight exponent x for the marine life stages of five of the nine species of the genus *Oncorhynchus*: pink (*O. gorbuscha*), chum (*O. keta*), coho (*O. kisutch*), and sockeye (*O. nerka*) salmon, and steelhead trout (*O. mykiss*). The estimates are based on an analysis of the weight dependency of published estimates of smolt–adult survival for wild populations. I also provide a method for estimating the coefficient c for Pacific salmon from the instantaneous marine growth rate of salmon.

Before describing the methods used to estimate x and c, it is useful

Table 1

Mean $\log_e$-transformed smolt–adult survival, s, for wild populations of five species of Pacific salmon (genus *Oncorhynchus*). s is the total number of adult salmon from a single brood year that returned to their natal stream to spawn divided by the total number of smolts from that stream and brood year that went to sea 1–5 years earlier. The number of returning adults was the sum of all commercial and sport catch plus escapement. SD is the standard deviation of mean $\log_e(s)$, and "no." is the number of brood years used to calculate mean $\log_e(s)$. W_0 is mean smolt weight and W is mean adult weight at return. Data were taken from the scientific literature.

Nursery system	Lat. (°N)	W_0 (g)	W (g)	$\text{Log}_e(s)$ mean	SD	no.	Sources[1]
Pink (*O. gorbuscha*)							
Hooknose Creek, B.C.	52.1	0.25	2289	–3.139	0.938	7	1, 16, 23
Fraser River, B.C.	49.1	0.25	2597	–3.571	0.545	12	1, 18, 23
Lakelse River, B.C.	54.4	0.25	2208	–3.969	0.555	8	1, 11, 23
Jones Creek, B.C.	49.3	0.23	2644	–4.255	0.632	12	8, 23
Chum (*O. keta*)							
Inches Creek, B.C.	49.1	0.35	5073	–4.397	0.272	6	6, 23
Fraser River, B.C.	49.1	0.38	5217	–4.591	0.606	14	1, 2, 23
Big Qualicum River, B.C.	49.4	0.36	5015	–5.243	0.756	14	9, 23
Coho (*O. kisutch*)							
Vedder–Chilliwack River, B.C	49.1	11.00	3301	–1.424	0.088	4	7, 23, 24
Black Creek, B.C.	49.8	15.08	3160	–1.487	0.078	2	4, 23
Campbell River, B.C.	49.0	11.00	3301	–1.814		1	23, 25
Salwein Creek, B.C.	49.1	11.00	3301	–1.839		1	7, 23, 25
Carnation Creek, B.C.	48.9	8.44	3133	–1.860	0.385	17	13, 14
Salmon River, B.C.	49.1	8.90	3301	–1.895	0.185	3	23, 25
Carnation Creek, B.C.	48.9	4.91	3133	–2.093	0.514	17	13, 14
Salmon River, (Langley) B.C.	49.1	8.90	3301	–2.117	0.384	6	23, 26
Big Qualicum River, B.C.	49.4	11.18	3859	–2.273	0.335	15	9, 23
Oregon Production Area	44.0	11.15	4131	–2.487	0.408	26	5, 10
Upper Pitt River, B.C.	49.4	6.70	3301	–2.830	0.000	2	23, 24, 24
Birkenhead River, B.C.	50.4	11.00	3301	–3.194		1	23, 25
Steelhead (*O. mykiss*)							
Keogh River, B.C.	50.6	49.00	3794	–1.918	0.485	7	15, 28
Sockeye (*O. nerka*)							
Karluk Lake, AK	57.4	27.04	1679	–1.081	0.145	6	22
Big Lake, AK	61.5	19.46	1747	–1.179	0.449	4	19, 20
Karluk Lake, AK	57.4	31.71	1679	–1.211		1	22
Karluk Lake, AK	57.4	21.02	1679	–1.301	0.079	6	22
Egegik River, AK	58.2	15.10	2771	–1.380	0.353	5	29, 30
Hidden Lake, AK	60.5	44.48	2146	–1.473	1.156	17	19, 20
Leisure Lake, AK	59.5	5.81	2000	–1.491	0.598	8	19, 20
Hugh Smith Lake, AK	55.1	3.83	2934	–1.685	0.326	8	19, 20
Karluk Lake, AK	57.4	11.26	1679	–1.726		1	22
McDonald Lake, AK	56.0	3.13	3376	–1.775	0.345	8	19, 20
Tustumena Lake, AK	60.3	3.95	1700	–1.856	0.501	9	19, 20
Egegik River, AK	58.2	9.90	2771	–1.927	0.943	5	29, 30
Egegik River, AK	58.2	21.00	2771	–2.103	1.031	3	29, 30
Ugashik River, AK	57.5	17.90	2719	–2.307		1	29, 30
Crescent Lake, AK	60.4	2.96	2450	–2.345	1.465	2	19, 20
Kvichak River, AK	59.5	10.60	2498	–2.376	0.801	16	29, 30
Washington Lake, WA	47.3	18.50	2720	–2.466	0.478	11	3, 23, 27
Ugashik River, AK	57.5	11.90	2719	–2.477	0.940	4	29, 30
Chilko Lake, B.C.	51.4	4.62	2767	–2.502	0.596	34	12, 23
Hobiton Lake, B.C.	48.8	3.60	2152	–2.575	0.313	2	17, 23
Kvichak River, AK	59.5	5.90	2498	–2.615	1.131	16	29, 30
Wood River, AK	59.5	6.00	2550	–2.703	0.282	13	29, 30
Henderson Lake, B.C.	49.0	3.60	2152	–2.703	0.386	2	17, 23

Table 1 (continued)

Nursery system	Lat. (°N)	W_0 (g)	W (g)	$\text{Log}_e(s)$ mean	SD	no.	Sources
Great Central Lake, B.C.	49.4	3.57	2155	–2.783	0.205	3	17, 23
Babine Lake, B.C.	54.7	4.45	2784	–2.801	0.319	3	21, 23
Cultus Lake, B.C.	49.0	6.10	3074	–2.884	0.808	18	22, 23
Nuyakuk River, AK	60.0	6.60	2902	–2.917	1.662	4	29, 30
Bare Lake, AK	57.4	4.49	1847	–2.997	0.359	4	23
Ugashik River, AK	57.5	6.90	2719	–3.088	0.986	4	29, 30
Wood River, AK	59.5	8.60	2550	–3.163	0.949	14	29, 30
Babine Lake, B.C.	54.7	5.07	2715	–3.356	0.711	21	21, 23
Nuyakuk River, AK	60.0	4.60	2902	–3.474	1.374	4	29, 30

[1] Sources: 1 = Beachum and Murray (1990), 2 = Beachum and Starr (1982), 3 = Burgner (1991), 4 = Clark and Irvine (1989), 5 = Emlen et al. (1990), 6 = Federenko and Bailey (1980), 7 = Federenko and Cook (1982), 8 = Fraser and Federenko (1983), 9 = Fraser et al. (1983), 10 = Gunsolus (1978), 11 = Harding (1970), 12 = Henderson and Cass (1991), 13 = Holtby et al. (1990), 14 = Holtby and Healey (1986), 15 = Hooton et al. (1987), 16 = Hunter (1959), 17 = Hyatt and Stockner (1985), 18 = International Pacific Salmon Fisheries Commission (1986), 19 = Koenings et al. (1993), 20 = G. Kyle, Alaska Dep. Fish and Game, Soldatna, Alaska 99669, personal commun., 21 = Macdonald et al. (1987), 22 = Ricker (1962), 23 = Ricker (1981), 24 = Schubert and Federenko (1985), 25 = Schubert and Zallen (1990), 26 = Schubert et al. (1974), 27 = Thorne and Ames (1987), 28 = Ward and Slaney (1988), 29 = Woolington et al. (1991), 30 = Yuen et al. (1981).

to review briefly the history of research on the weight dependency of marine mortality in fishes in order to establish testable hypotheses about the probable values of x and c.

Previous research on allometry of *M*

It has been known for at least 40 years that smolt–adult survival of Pacific salmon is positively correlated with smolt size (Foerster, 1954; Ricker, 1962). Positive and significant correlations have been reported within single populations of coho salmon (Holtby et al., 1990) and steelhead trout (Ward and Slaney, 1988), and among populations of sockeye salmon (Ricker, 1962; Koenings et al., 1993). To date, the relationship between smolt–adult survival and adult size of Pacific salmon has not been examined, nor have the interrelationships between smolt–adult survival, smolt size, and adult size.

Mathews and Buckley (1976) were the first to model the functional relationship between M of Pacific salmon and body size. They assumed that marine M of hatchery-reared coho salmon released into Puget Sound, Washington, was proportional to W^{-1}. In his comprehensive review of marine M of salmon, Ricker (1976) judged their assumption to be intuitively reasonable but unproven. Furnell and Brett (1986, a and b) used the inverse-weight hypothesis to model the marine population dynamics of Babine Lake sockeye salmon, despite the lack of empirical support for the hypothesis (McGurk, 1986b).

In the nearly two decades since the inverse-weight hypothesis was presented, much literature has been published showing that the weight-exponent of mortality for fishes actually falls within the range of 0.25 to 0.40. Ursin (1967) was the first to measure the mortality-size relationship of fish; his review of published reports showed that natural mortality scaled with $W^{-0.33}$. Fenchel (1974) and Blueweiss et al. (1978) reported that the intrinsic rate of natural increase of animals, which is equal to M under equilibrium conditions, decreased with $M^{-0.25}$. Banse and Mosher (1980) showed that the weight exponent of the production-biomass ratio of animal populations, which is also equivalent to M under equilibrium conditions, was –0.37. Peterson and Wroblewski (1984) derived a size-dependent equation for the mortality rate of marine pelagic organisms, including invertebrates and fishes, from biomass spectrum theory and concluded that M scaled with $W^{-0.25}$. I reported a similar conclusion from a review of natural mortality of marine organisms that included invertebrates, fishes, and marine mammals (McGurk, 1986a) and later showed that M for larval and adult stages of both Atlantic herring (*Clupea harengus*) and Pacific herring (*C. pallasi*) scaled with dry weight to the power of –0.4 (McGurk, 1993).

These studies showed that data sets incorporating a wide variety of distantly related groups of animals tend to have weight exponents of M close to –0.25, whereas data sets restricted to a single species or a group of closely related species tend to have weight exponents close to –0.40. In an attempt to explain this observation, Dickie et al. (1987) proposed that there are two size-dependent processes: 1) over an entire ecosystem the slope of mortality versus

weight is about –0.18 and is due mainly to metabolic processes, but 2) within individual species the slope is about –0.37 and is related to ecological factors such as the relative sizes and distributions of predators and prey.

Therefore, the primary hypothesis to be tested in this study is that M scales as $W^{-0.37}$ for Pacific salmon.

Much less is known of the probable numerical value of the parameter c. However, an upper limit can be placed on c if some assumptions are made about the value of the weight exponent of growth rate in Pacific salmon. The instantaneous rate of growth of salmonid fishes, G (d^{-1}), decreases with body weight according to the allometric relationship $G = aW^{-b}$, where a is the instantaneous growth rate (d^{-1}) at a weight of 1 g, and b is a dimensionless exponent (Brett and Shelbourne, 1975; Elliott, 1975; Jobling, 1983). The biomass of a brood year of salmon is usually assumed to increase continuously with age, at least until the brood year is old enough to be fished. Therefore, if $b \sim x$, then c must have an absolute value that is lower than a. Otherwise, the biomass of a brood year would not increase with age, and may even decrease with age, thereby extinguishing the brood year before it was able to reproduce. To assess the validity of the assumption that $b \sim x$, I briefly reviewed the history of growth experiments with salmonid fishes.

Previous research on allometry of *G*

Estimates of b have been published for seven species of salmonid fishes: five species of Pacific salmon (pink, coho, and sockeye salmon, as well as chinook salmon [*O. tshawytscha*] and steelhead trout), brook trout [*Salvelinus fontinalis*], and brown trout (*Salmo trutta*). Reported values of b have ranged from 0.20 to 0.50 with a mean of 0.37 (SD=0.08, n=19) (Iwama and Tautz, 1981). With one exception, all values were estimated from juvenile salmonids weighing 0.3 to 350 g that were reared in hatcheries or laboratory aquaria. The exception was Parker and Larkin (1959) who reported that b ranged from 0.20 to 0.33 for sexually mature steelhead captured from the Chilliwack River, B.C., and from 0.37 to 0.44 for chinook salmon captured in their final year of sea life off southeast Alaska.

Brett and Shelbourne (1975) were the first to identify a universal value of b; they concluded that the average value for salmonids was 0.41 (SD=0.06, n=10). Elliott (1975) reported exponents ranging from 0.28 to 0.33 for juvenile brown trout, which led Brett (1979) to suggest that the range of exponents for salmonids may be wider than that reported by Brett and Shelbourne (1975). Iwama and Tautz (1981) argued that the best value of b for the purpose of modeling growth of hatchery-reared salmonids was closer to 0.33 than 0.41 because the line of $W^{1/3}$ versus time was linear with temperature over the temperature range commonly found in fish hatcheries and because $W^{1/3}$ is easily converted to length. Jobling (1983) reported that b for Atlantic cod (*Gadus morhua*) and seven other nonsalmonid fishes weighing 0.9 to 150 g ranged from 0.33 to 0.63 with a mean of 0.41 (SD=0.06, n=52) and argued that a universal slope of 0.4 was applicable to all species of fish. Wangila and Dick (1988) found that the average value of b for two strains of rainbow trout, the freshwater form of steelhead trout, was 0.31 but that slopes varied significantly among strains and rearing temperatures, suggesting that a universal value of b must be employed with caution.

In summary, the best estimate of b for salmonids is the grand mean of all exponents or 0.37 (Iwama and Tautz, 1981). The value of b for sockeye salmon, the species of salmon on which the most experimental work has been conducted, ranges from 0.39 to 0.49 with a mean of 0.41 (SD=0.05, n=4). This shows that b is indeed close to the most probable value of x, which in turn supports the hypothesis that c is a constant fraction of a, i.e. $c = \alpha a$.

Therefore, the second hypothesis to be tested by this study is that α has a value greater than zero but less than one.

Allometry of survival

To test the hypotheses that $x = 0.37$ and $c = \alpha a$, a mathematical model that relates smolt–adult survival to smolt weight and adult weight is required. Such a model can be created by using size as an index of age in the simple allometric model of natural mortality. The first step in developing the model is the adoption of a growth model that can be easily integrated over time so that age and size can be interchanged.

Over periods of days, growth in weight of salmon can be accurately modeled with the well-known exponential model:

$$dW/dt = GW. \quad (1)$$

However, over longer periods of time, G decreases with increasing weight. Substituting $G = aW^{-b}$ into Equation 1 leads to

$$dW/dt = aW^{1-b}, \quad (2)$$

which can be integrated over time to give the growth model:

$$W = (W_0^b + abt)^{1/b}, \quad (3)$$

where W_0 = initial weight (g). Equation 3 was first introduced by Parker and Larkin (1959) to describe marine growth of chinook salmon and steelhead trout. Elliott (1975) and Iwama and Tautz (1981) used the model to describe successfully the freshwater growth of several species of salmonids. Apart from being based on an allometric growth argument, this model has the important advantage of easier integration over time in comparison with other three-parameter growth models that have been applied to fish.

Mortality of Pacific salmon can also be modeled as a power function of body weight:

$$dN/dt = -MN = -cW^{-x}N, \quad (4)$$

where N is the population number and c has units of d^{-1} (Ursin, 1967; Peterson and Wroblewski, 1984; McGurk, 1993). Substituting Equation 3 into Equation 4 and integrating over the duration of sea life gives an expression for smolt–adult survival, s, in terms of body weight:

$$\log_e(s) = \log_e(N/N_0) = -\left(c/(a(b-x))\right)\left(W^{b-x} - W_0^{b-x}\right), \quad (5)$$

where N = the total number of adults that return to their natal stream (the sum of catches in all commercial and recreational fisheries plus the number of fish that escaped the fisheries and were counted on the spawning grounds); N_0 = the number of smolts; W = adult weight (g); and W_0 = smolt weight (g). Aggregating parameters in Equation 5 gives a simple expression that is suitable for nonlinear regression:

$$\log_e(s) = -(\alpha/\beta)(W^\beta - W_0^\beta), \quad (6)$$

where $\alpha = c/a$ and $\beta = b - x$. Both α and β are dimensionless numbers.

In this paper, Equation 6 was used to regress $\log_e(s)$ on W and W_0 and thereby estimate values of α and β. I tested two hypotheses about the values of α and β: 1) β is a small number that is not significantly different from zero because $b \sim x \sim 0.37$, so $\beta = b - x = 0$; and 2) α has a value significantly lower than 1.0 but greater than zero because $\alpha = c/a$ and $c < a$.

In fitting Equation 6 to the available smolt–adult survival data, it was necessary to pool survival and size information from five species of Pacific salmon because, with the exception of sockeye salmon, the range of mean survivals and mean sizes within a single species was too narrow to estimate reliable values of α and β for particular species. Therefore, I assumed that there are average values of c and x for *Oncorhynchus* species which have practical utility over different time and space scales (species, population, and brood year) and that overlaid on this average allometry is species-specific, population-specific, and brood-year specific variability which cannot as yet be estimated given the information available in the primary literature.

Materials and methods

Sources of data

Survival I searched the primary scientific literature for well-documented records of smolt–adult survival for wild populations of *Oncorhynchus*. Records derived entirely from secondary sources were not included because of difficulties in obtaining information on body sizes. A few records reported in primary sources were also excluded for the same reason. Populations of pink, chum, and coho salmon that were composed predominately of hatchery production were excluded because of controversy over whether hatchery fish have the same smolt–adult survival as wild fish of the same body size. The exceptions to this rule were estimates of smolt–adult survival calculated from populations of sockeye enhanced by stocking of young fry into nursery lakes (e.g. Leisure Lake, Alaska: Koenings and Burkett, 1987; Koenings et al., 1993). These fish spent a minimum of one year after release in a natural nursery system before migrating to sea.

Smolt–adult survivals were collected only for brood years, defined as the production of adult fish of all ages from a single year's spawning in a single nursery system. To account for multiple ages of return, the number of returning adults of the ith brood year, N_i, was summed over all ages as

$$N_i = \sum^{t} (C_{it} + E_{it}), \quad (7)$$

where C_{it} = the catch of the ith brood year at an age of return of t years; and E_{it} = the escapement of the ith brood year at an age of return of t years. To account for multiple ages of smolting, the number of smolts was summed over all smolt ages. For all populations of pink and chum salmon, there was only one smolt age because the newly emergent fry immediately went to sea. The same situation applied to some coho and sockeye populations that were predominantly of a single smolt age. For example, 95% of Chilko Lake sockeye smolts migrate to sea at an age of 1+ yr (Henderson and Cass, 1991). The exception

to the rule of combining smolt ages were those populations of coho and sockeye salmon for which the number of returning adults could be assigned an age at smolting based on scale patterns. In those cases, each age class of smolts was treated as a separate "brood year" and separate smolt–adult survivals calculated for each smolt age class.

Smolt–adult survival is log normally distributed (Peterman, 1981), so the best estimate of the central tendency of smolt–adult survival for a system is the geometric mean survival or the arithmetic mean of the $\log_e$-transformed survivals for each brood year for a particular system. Only $\log_e(s)$ was used to estimate the parameters of Equation 6 because only in a few cases was each brood year's survival accompanied by a mean smolt weight or a mean adult weight, or both. In almost all cases, all that was available from the literature was a mean smolt weight and a mean adult weight for each system. The exceptions were those systems for which mean smolt weights and mean smolt–adult survivals were available for each of several age classes of smolts (i.e. sockeye salmon from rivers entering Bristol Bay, Alaska; Yuen et al., 1981; Woolington et al., 1991).

Weight In the absence of direct reports, mean smolt weights of pink and chum salmon were assumed to be the midpoints of the ranges of emergent fry weights reported by Beachum and Murray (1990) for eggs incubated at a constant 8°C (0.25 g for pink and 0.35 g for chum). For studies that did not report mean smolt weight for coho and sockeye salmon, and for which there were no accompanying reports that included smolt weights, mean smolt weight was estimated from mean smolt length by using weight-length equations reported by Chapman (1965) and Koenings and Burkett (1987).

Mean adult weight of coho salmon from Carnation Creek was calculated from mean length of returning adults by using the weight-length relationship reported by Holtby and Healey (1986). Mean adult weight of steelhead trout from the Keogh River was calculated from mean length of returning spawners with the weight-length regression reported by Hooton et al. (1987). Mean adult weights for other systems were taken from records of commercial fisheries because there was no published information on their mean size at re-entry to freshwater (Gunsolus, 1978; Ricker, 1981; Yuen et al., 1981; Kyle[1]). I converted mean lengths (L, mm) of Bristol Bay sockeye to mean weights (W, g) using a functional regression of $\log_e(W)$ on $\log_e(L)$ calculated from mean weights and lengths for separate age groups of Bristol Bay sockeye for the years 1963–77: $W = 1.713 \times 10^{-5}L^{3.00}$ (n=61, r^2=0.94, P<0.001). Mean adult weight for each nursery system was the mean weight for the ocean statistical area adjacent to the stream for which smolt–adult survivals were available. This procedure assumes that the majority of the catch from a population is taken by marine salmon fisheries near the mouth of the population's natal stream.

In most systems in British Columbia, mean adult weight was calculated from the years for which smolt–adult survivals were reported. This is important because mean weight of pink, chum, coho, and sockeye salmon in British Columbia has decreased over the last 30 years (Ricker, 1981). However, this was not possible for all systems, particularly those with smolt–adult survivals reported after 1981. In those cases, mean adult weight was taken from the latest catch data available. Thus, the accuracy and reliability of mean adult weights is variable, being relatively high for most systems in British Columbia but lower for most systems in Alaska. The exceptions are the sockeye rivers of Bristol Bay where a 20-yr time series of adult sockeye weights was reported by Yuen et al. (1981).

Mean adult weight for nursery systems with more than one age group of smolts was assumed to be the same for all smolt ages. This assumption was necessary because adult weights were rarely reported for separate smolt ages.

Fitting the model

Equation 6 was fitted with nonlinear regression (NLR) by using the Levenberg-Marquardt algorithm contained in the NLR procedure of the computer program SPSS (SPSS Inc., 1993). The mean $\log_e(s)$ for each system was first regressed on mean W and W_0 for sockeye salmon and then for all species combined. Mean $\log_e(s)$ was weighted by sample size under the assumption that the accuracy of mean $\log_e(s)$ is directly proportional to the number of brood years used to calculate it. The coefficients of determination (r^2) of the regression models were adjusted for the number of degrees of freedom in the model. Standard errors of regression parameters were based on asymptotic or large-sample approximations. It was not possible to test the statistical significance of a nonlinear regression using the usual F-test applied to linear regressions, because the residual mean square of a nonlinear regression is not an unbiased estimate of the error variance (SPSS Inc., 1993). The significance level, P, for linear correlations was set at 5%, i.e. P = 0.05.

[1] Kyle, G. 1994. Alaska Dep. of Fish and Game, 34828 Kaliforsky Beach Road, Soldatna, AK 99669-3150. Personal commun.

Estimation of x and c from β and α

An estimate of x was obtained by subtracting an estimate of β from the weight exponent of growth rate, b, i.e. $x = b - \beta$. Estimates of β were obtained by fitting regression Equation 6 to survival and weight data. The appropriate value of b was obtained from a review of the scientific literature on salmonid growth experiments (see introductory section). Estimates of c could not be obtained directly. Instead, c was expressed as a fraction of the initial growth rate, i.e. $c = \alpha a$. Estimates of α were obtained from regression Equation 6.

Results

I found 20 studies that reported 52 mean smolt–adult survivals for five species of Pacific salmon (Table 1). The means were calculated from 432 brood years released from 38 nursery systems ranging over more than 15° of latitude from the Oregon coast (44.0°N) to southcentral Alaska (61.5°N). Over 60% of the mean survivals were reported for sockeye salmon.

Sockeye salmon

The regression of $\log_e(s)$ on W and W_0 for sockeye salmon explained 33% of the variance in mean $\log_e(s)$, with parameter values (±1SD) of $\alpha = 0.226 \pm 1.171$ and $\beta = 0.120 \pm 0.990$ (Fig. 1). The estimate of α indicated that c had a value that was only 22.6% of the value of a. The estimate of β indicated that x has a value of 0.29, if b for sockeye salmon is assumed to be is closer to 0.41 than to 0.37 (Brett and Shelbourne, 1975).

There were no significant correlations between residual mean $\log_e(s)$ and W_0, W, latitude of the nursery system, or the predominant smolt age, indicating that body weight was the single most important variable affecting smolt–adult survival. The sensitivity of α and β to possible underestimation or overestimation of adult sockeye weight was examined by fitting Equation 6 after altering W by –25 to +25% at 5% intervals: α decreased by 8% for a 25% decrease in W and increased by 6% for a 25% increase in W, indicating that α was relatively insensitive to bias in estimation of W (Table 2); β increased 26% for a 25% decrease in W and decreased 17% for a 25% increase in W, indicating that β was about three times more sensitive to bias in estimation of W than was α. The adult weights of sockeye salmon shown in Table 1 are more likely to be underestimates of the true weight at return than overestimates because they were calculated from mean weights of commercial catches rather than mean weights of spawners in their natal stream. The last few months of growth may not be included in adult weights from commercial catches. Because underestimation of W tends to inflate β, the true value of β for sockeye salmon is lower than 0.120 and, therefore, the true value of x for sockeye salmon is greater than 0.29.

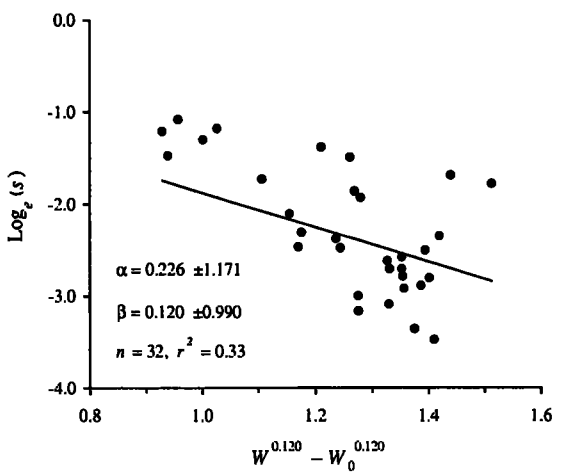

Figure 1

Nonlinear regression (Eq. 6 in the text) of mean $\log_e$-transformed smolt–adult survival, s, on smolt weight, W_0 (g), and adult weight at return, W (g), for sockeye salmon (*Oncorhynchus nerka*). Values (±1 SD) of the regression parameters α and β are shown. α is the ratio of the coefficient of instantaneous natural mortality rate, c, to the coefficient of instantaneous growth rate, a. β is the difference between the weight exponent of growth rate, b, and the weight exponent of natural mortality rate, x. Data from Table 1.

Combined species

A regression of mean $\log_e(s)$ on W and W_0 for the five species of salmon combined explained 68% of the variance in mean $\log_e(s)$ with parameter values (±1SD) of $\alpha = 0.528 \pm 0.490$ and $\beta = -0.053 \pm 0.221$ (Fig. 2). The estimate of α indicated that c had a value that was 52.8% of the average value of a. The estimate of β indicated that x had a value of 0.38 to 0.42 for an average b of 0.33 or 0.37, respectively. The doubling of the r^2 statistic over that measured for the sockeye regression was accompanied by a substantial decrease in the variance of α and β. The coefficient of variance of α, CV_α (=$SD_\alpha \cdot 100/\alpha$), decreased from 518% for the sockeye regression to 93% for the combined regression. CV_β decreased from 825% for the sockeye regression to 417% for the combined regression.

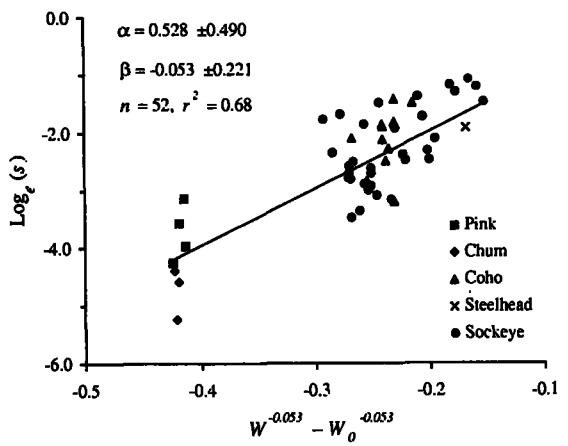

Figure 2

Nonlinear regression (Eq. 6 in the text) of mean $\log_e$-transformed smolt–adult survival, s, on smolt weight, W_0 (g), and adult weight at return, W (g), for five species of Pacific salmon: pink (*O. gorbuscha*), chum (*O. keta*), coho (*O. kisutch*), steelhead (*O. mykiss*), and sockeye (*O. nerka*). Values (±1 SD) of the regression parameters α and β are shown. α is the ratio of the coefficient of instantaneous natural mortality rate, c, to the coefficient of instantaneous growth rate, a. β is the difference between the weight exponent of growth rate, b, and the weight exponent of natural mortality rate, x. Data from Table 1.

There were no significant correlations between residual mean $\log_e(s)$ and W_0, W and latitude of nursery system. Residual mean $\log_e(s)$ did not vary significantly among species (ANOVA: $F_{4,47}$=1.995, P=0.111), indicating that body weight was the most important variable affecting mean smolt–adult survival. A sensitivity analysis showed that α changed by 1% or less for a ±25% change in W, indicating that its value was essentially independent of bias in estimation of W (Table 2). β increased by 21% for a 25% decrease in W and decreased by 15% for a 25% increase in W. However, the maximum change in the absolute numerical value of β caused by ±25% changes in W was only 0.008, indicating that the near-zero value of β was essentially independent of bias in estimation of W.

Discussion

Parameters α and β

The estimates of α and β derived in this study are consistent with the original hypotheses. The small, near-zero value of β estimated for sockeye salmon alone and for five species of *Oncorhynchus* combined supports the hypothesis that the weight exponents of growth and mortality for *Oncorhynchus* species are virtually identical. There is no consensus on the exact value of the weight exponent of growth rate of Pacific salmon. However, the average of all reported values of salmonid b is 0.37 (Iwama and Tautz, 1981), which is identical to the weight-exponent of natural mortality for single species that was proposed by Dickie et al. (1987). Thus, the cumulative evidence supports the hypothesis that, on average, marine M of Pacific salmon scales with $W^{-0.37}$. Although the average value of x is close to 0.37, it may also vary among populations and species, and among year classes within populations and species. For example, this study found that x varied from a low of 0.29 for sockeye salmon to a high of 0.42 for the data from five species.

The second important feature of the regression parameters is that α is significantly lower than 1.0 which supports the hypothesis that initial mortality rate, c, is a fraction of initial growth rate a. The combined regression indicates that c has a value equal to 52.8% of the value of a at any body weight. Therefore, the best estimate of M for all species of Pacific salmon combined can be predicted as: $M = 0.528aW^{-0.37}$. Estimates of M can be obtained if one has an independent estimate of the parameter a, perhaps through scale analysis. Alternatively, if one assumes that $a = G/W^{-0.37}$, then $M = 0.528G$. In other words, average marine M for a short time period can be estimated if one has an independent estimate of average G over the same short period.

Third, the absence of significant differences in residual mean $\log_e(s)$ among species suggests that a single survival-weight relationship may be applicable to all five species of *Oncorhynchus*. This finding supports the basic assumption of this paper—that species within the genus *Oncorhynchus* share similar allometries of growth and mortality but differ in smolt and adult body sizes. However, it is clearly inappropriate to assume that the survival-weight and mortality-weight relationships developed in this study can be applied without qualification to every salmon population or to every brood year within each population. Accurate brood-year-specific prediction of salmonid survival will depend on information collected from that brood year.

Sources of error

This paper presents preliminary numerical estimates of α and β for Pacific salmon. Improved estimates will undoubtedly be calculated in the future as more information on smolt–adult survival and smolt and adult weights become available in the primary literature.

Table 2

Analysis of the sensitivity of the regression parameters α and β of text Equation 6 to changes in the mean adult body weights, W, of Pacific salmon (genus *Oncorhynchus*) shown in Table 1. Mean weights were changed by –25% to +25% at 5% increments and α and β were recalculated at each increment. The 95% confidence limits (CL) of α and β are also shown. Analyses were performed for sockeye salmon alone and for five species of salmon combined: pink (*O. gorbuscha*), chum (*O. keta*), coho (*O. kisutch*), steelhead (*O. mykiss*), and sockeye (*O. nerka*).

Percent change in W	α–95%CL	α	α+95%CL	β–95%CL	β	β+95%CL
Sockeye (*O. nerka*)						
–25	–0.190	0.207	0.605	–0.222	0.151	0.523
–20	–0.192	0.211	0.614	–0.225	0.144	0.513
–15	–0.193	0.215	0.624	–0.228	0.137	0.503
–10	–0.194	0.219	0.632	–0.231	0.131	0.494
–5	–0.195	0.222	0.640	–0.234	0.126	0.485
0	–0.197	0.226	0.648	–0.236	0.120	0.477
5	–0.197	0.229	0.655	–0.239	0.116	0.470
10	–0.198	0.232	0.662	–0.241	0.111	0.463
15	–0.199	0.235	0.669	–0.243	0.107	0.456
20	–0.200	0.238	0.675	–0.244	0.103	0.450
25	–0.200	0.240	0.681	–0.246	0.099	0.444
Pacific salmon combined						
–25	0.386	0.522	0.659	–0.105	–0.042	0.021
–20	0.387	0.524	0.661	–0.107	–0.045	0.018
–15	0.388	0.525	0.662	–0.109	–0.047	0.015
–10	0.389	0.526	0.663	–0.111	–0.049	0.013
–5	0.390	0.527	0.664	–0.113	–0.051	0.010
0	0.391	0.528	0.665	–0.115	–0.053	0.008
5	0.392	0.529	0.666	–0.116	–0.055	0.006
10	0.392	0.530	0.667	–0.118	–0.057	0.004
15	0.393	0.530	0.668	–0.119	–0.058	0.002
20	0.394	0.531	0.669	–0.120	–0.060	0.001
25	0.394	0.532	0.669	–0.122	–0.061	–0.001

The most important source of error in this analysis was associated with estimating mean body weights of smolts and adults. The methods of estimating mean adult weights were less than optimal mainly because of a lack of information on this subject in the primary literature. Part of the problem in obtaining adult weights is that salmon fisheries are rarely located at the ocean terminus of the salmon's spawning migration. Rather, fishing pressure on a single stock is often distributed over thousands of square kilometers and over several separate management jurisdictions. For those studies that did not report mean adult weight, it was necessary to assume that all fisheries were terminal in order to estimate adult weight from catch records. The assumption was undoubtedly violated for many stocks that are subjected to fishing mortality for a considerable portion of their last year of sea life. For those populations, mean weight at sea will tend to underestimate weight at re-entry.

A second source of error was the inability to adjust mean adult weight for the presence of jacks, those male salmon that mature at an early age and small size. The effect of a significant number of jacks in a population is to underestimate adult weight at return, thereby increasing the bias introduced by assuming that adult weight can be estimated from commercial catches. However, sensitivity analyses showed that adult weight would have to be consistently over- or under-estimated by more than 25% before these two sources of error would seriously affect the conclusions of this study.

A third source of error was the use of weights predicted from length rather than observed weights, because weight-length relationships may vary among populations and among brood years within populations. However, Koenings and Burkett (1987) reported that known weight-length relationships for sockeye smolts in Alaska were virtually identical. Further, this source of error would not bias the analysis in a specific direction.

The lack of smolt and adult weights derived from the same brood years resulted in the within-population variation in survival being confounded with

among-population variation in survival. This does not invalidate the model as long as one assumes that within a single species or group of closely related species, the weight exponents of growth and mortality are stable parameters with similar ranges and little variation.

The second most important source of error was the choice of an appropriate value of b for the growth model. Most estimates of b were available from experiments with young salmonids grown in enclosures at constant temperatures and fed to satiation or ad libitum. These are not conditions commonly faced by wild salmonids, and thus making use of these estimates in estimating marine mortality for wild salmonids is suspect. There is clearly a need for more research on the weight-, ration- and temperature-dependence of growth of large, sea-going salmonids derived from wild stocks and grown in marine enclosures.

Effect of latitude on smolt–adult survival

Koenings et al. (1993) demonstrated that smolt–adult survival of sockeye salmon increased with latitude of nursery systems as well as with smolt length, a finding that was not confirmed by this study for sockeye salmon or for any other species of *Oncorhynchus*. There are at least two possible reasons for the lack of a latitude effect in this study. First, within-system variation in smolt–adult survival was ignored because adult weights were not available for each brood year for each system. In contrast, Koenings et al. (1993) were able to compare smolt–adult survivals and smolt lengths for individual brood years within each system. Second, this study regressed smolt–adult survival on both adult weight and smolt weight rather than on smolt weight alone. This allowed variation in survival to be adjusted for variation in adult size between nursery systems as well as for variation in smolt size. The latitude effect observed by Koenings et al. (1993) may have resulted from restricting analysis of survival-weight relations to smolt size.

Applications of allometry of mortality for Pacific salmon

The equations reported in this study may be useful for making preliminary estimates of survival and mortality for wild populations of *Oncorhynchus* species for which information is limited. For example, the results of this study imply that smolt–adult survival of wild chinook salmon should be similar to other species of salmon with similar smolt and adult weights. There are at present no published estimates of wild chinook smolt–adult survival in the primary literature. The allometry of M reported in this study may also be useful for modeling survival and mortality of Pacific salmon in spatially explicit simulation models (i.e. Walters et al., 1978). Not only may it provide more realistic daily mortality rates than could be calculated from fry-smolt and smolt–adult survivals, but by relating mortality with body size it links survival to trophic dynamics and to density-dependent growth.

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Michael Bradford provided a preliminary list of references on survival of Pacific salmon. Gary Kyle provided adult sockeye weights for most of the Alaskan nursery systems cited by Koenings et al. (1993). Critical reviews of early drafts of this paper were done by Michael Bradford, Stephen Mathews, and several anonymous referees.

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Accuracy of age estimates for larval *Sebastes jordani*

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Abstract.—We examine some issues concerning the accuracy of larval age estimates for *Sebastes jordani*. To localize a starting point for daily increment counts, gestating and planktonic larvae were examined to determine whether an extrusion check forms at parturition. We also assessed 1) the resolution limitations of optical microscopy in ageing larvae, 2) the precision of age estimates, and 3) the effect of specimen age on the reliability of ages.

Preextrusion increments are commonly observed in gestating and planktonic larvae, but a distinctive extrusion check forms in the otolith at parturition. This feature occurs predictably at a radius of 15–19 μm and provides an unambiguous starting point for increment counts. Observations of larval otoliths with a scanning electron microscope revealed that the minimum size of postextrusion increments is ~0.6 μm, which is large enough to be resolved with a high-quality optical system. Cross-checking of ages among three readers showed 84% agreement to within ±1 d and no systematic differences among readers. The clarity of otolith microstructure resulted in high confidence scores for age estimates; however, very young larvae (0–3 d) were the most difficult to age. An exponential growth model fitted to 2,203 aged larvae indicated that during the first month of life, growth in length proceeds at the rate of 2.75%·d^{-1}.

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Fishery Bulletin 94:89–97 (1996).

Ichthyoplankton surveys are used routinely to estimate spawning stock biomass (Gunderson, 1993; Hunter et al., 1993). Fundamentally, this type of calculation requires a determination of total daily egg production (P_0 [eggs·d^{-1}]), which is estimated by regressing egg abundance on egg age. Typically, egg ages are obtained indirectly by 1) description of egg-stage ontogeny, 2) laboratory studies of the temperature dependency of egg developmental rates, 3) measurement of thermal conditions in the environment at the time of sampling, and 4) back calculation of egg age. Not surprisingly, serious complications can occur with this approach, especially when spawning occurs in deep water (e.g. Lo et al., 1993; Picquelle and Megrey, 1993).

Members of the rockfish genus *Sebastes* (family Scorpaenidae) are viviparous, bearing advanced yolk-sac larvae at the time of parturition (Wourms, 1991; Bowers, 1992). Previous work has shown that *Sebastes* larvae can be aged directly by enumeration of daily otolith increments (Penney and Evans, 1985; Laidig et al., 1991). Thus, rockfishes exhibit a life history adaptation, i.e. viviparity, which potentially lends itself to accurate estimation of daily larval production rates (P_0 [larvae·d^{-1}]).

The purpose of this study is to examine the accuracy of larval *Sebastes* age estimates obtained through the study of otolith microstructure (Stevenson and Campana, 1992). To be considered accurate, a sample statistic must be close to the true underlying "population" value it estimates. Inaccuracy is due to the combined effects of estimator bias and imprecision. Although direct ageing of rockfish larvae circumvents many of the problems associated with staging eggs (see above), accurate larval age estimates, characterized by low bias and high precision, are still prerequisite to an accurate larval production estimate of spawning stock biomass. Because larval mortality rates in the marine environment are high, commonly exceeding 0.15·d^{-1} (Pepin, 1991; Houde, 1994), systematic larval ageing errors as small as one day can significantly bias estimates of spawning biomass.

Sebastes jordani is an abundant but lightly utilized rockfish that occurs along the central California coast (Lenarz, 1980). Importantly, it can be readily identified at all early life history stages (Moser et al., 1977). In addition, a detailed growth model for the first six months of life has been previously described (Laidig et al., 1991). Those authors validated a 1:1 correspondence between changes in counts of daily growth increments and age for a developing cohort of pelagic juvenile *S. jordani* (age 3–5 mo).

In this study we examine more closely the accuracy of *S. jordani* age estimates derived from the first month of life. In particular, we address the following questions: 1) Are daily increments large enough to be resolved with an optical microscope (Neilson, 1992)? 2) Does the *Sebastes* "extrusion check" (Penney and Evans, 1985; Laidig et al., 1991) actually form at parturition? 3) How variable are age estimates obtained from different readers? 4) How variable are individual larvae in their expression of otolith microstructure? and 5) Does larval age influence the reliability of age estimates?

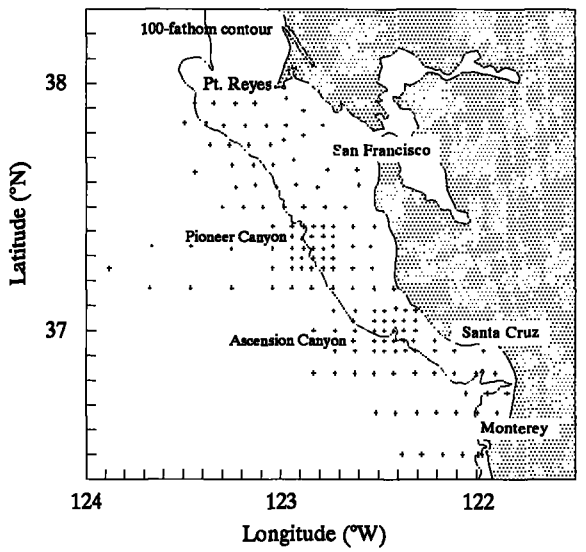

Figure 1

Map of the study region showing the locations of bongo-net stations.

Materials and methods

The primary set of ichthyoplankton samples used in this study was obtained during a cruise aboard the NOAA RV *David Starr Jordan* conducted from 8–15 February 1991. During that six-and-a-half-day period, 150 bongo-net stations were occupied in the region bounded by lat. 36°30'N and 38°00'N, and offshore by a maximum distance of 130 km (Fig. 1). This region is known to harbor large spawning aggregations of *S. jordani* during the months of January and February, especially in the vicinities of Pioneer and Ascension Canyons (Lenarz, 1980; MacGregor, 1986; Chess et al., 1988).

Field and laboratory processing of the samples closely followed prescribed CalCOFI guidelines (i.e. Kramer et al., 1972; Smith and Richardson, 1977). However, because *Sebastes* larvae generally occur in the upper mixed layer (Ahlstrom, 1959; Kenchington, 1991; senior author's unpubl. data), the maximum amount of wire deployed was 200 m, resulting in a maximum depth fished of 140 m. After retrieving and washing down the 505-μm mesh nets, the samples were preserved in 80% ethanol (EtOH), which was changed 24 hours later. In the laboratory the alcohol was changed again, the samples were sorted, and *S. jordani* larvae were identified and enumerated. Sorted larvae from each of the 150 ethanol-preserved bongo nets were randomly subsampled and their otolith microstructure was examined. Notochord length (NL) was measured from each larva in the subsample and the otoliths were extracted and affixed to glass slides with clear fingernail polish.

Individual ages were determined by the methods outlined in Laidig et al. (1991). In brief, otoliths were viewed whole under oil emersion with a compound microscope that was equipped with a video camera and monitor (e.g. McGowan et al., 1987), producing a working magnification of 1,250×. Counts of daily increments were initiated at a distinct check mark that occurred consistently at a radius of ~15–19 μm. The mark clearly encircled the otolith core and also a more recent zone of faint incremental growth. Penney and Evans (1985) and Laidig et al. (1991) both observed this feature and inferred that the check was formed at the time of larval extrusion (i.e. parturition). Otoliths with this mark and no additional increments were therefore given a nominal age of zero. Increments were counted from the mark to the most distal point along the longest growth axis. A digitizer was used to measure the radius (μm) of the otolith at the extrusion check (R_0) and the inner edge of the dark, protein rich D zone of each subsequent daily increment (R_1, R_2, R_3, ..., etc.). During postprocessing the width of each increment (W_i) was then calculated by subtraction (i.e. $W_i = R_i - R_{i-1}$). A series of computer programs automated this procedure (Laidig and Pearson, 1992).

A confidence code ranging from 1–5 was assigned by the reader at the time each larva was aged. The

codes were as follows: 1 = otolith was not readable; 2 = low confidence in age estimate, changing the focal plane may have resulted in a different increment count; 3 = moderate level of confidence, preextrusion increments sometimes evident, extrusion check sometimes at an unusually large or small otolith radius; 4 = high confidence in age estimate; and 5 = otolith exhibits remarkable clarity, no ambiguity concerning increment interpretation. To compare age estimates obtained from different readers and to quantify measurement error, every tenth specimen in a tow subsample was aged independently by two people.

Preextrusion larvae from gestating females were examined to characterize otolith growth prior to parturition. Samples for this study came from another cruise of the RV *David Starr Jordan* (17–27 February 1993). Mature gestating female *S. jordani* were collected by bottom trawl (26-m headrope, 15-cm mesh, 1.25-cm codend), their ovaries were removed, and embryos and prolarvae preserved in 95% ethanol. Prolarvae (i.e. hatched embryos) were staged in the laboratory on the basis of a modified version of Yamada and Kusakari's (1991) system and on the basis of information on the temporal course of development, inferred from laboratory experiments on *Sebastes flavidus* (Eldridge[1]). Specifically, the following prolarval stages were assigned: 1 = parturition in 5–6 d; 2 = parturition in 4–5 d; 3 = parturition in 3–4 d; 4 = parturition in 2–3 d; 5 = parturition in 1–2 d; and 6 = parturition in 0–1 d. Parturition was considered imminent in stage-6 prolarvae that had depleted yolk reserves but had a well-developed oil globule. After staging and measuring the prolarvae, the otoliths were removed, affixed to glass slides, and the otolith radius measured (μm). No more than five prolarvae were examined from any single gestating female.

Otoliths of gestating and planktonic larvae (n=60) were examined with a scanning electron microscope (SEM). To prepare otoliths for viewing, whole larval specimens were dehydrated in successive rinses of 95 and 100% ethanol (24 hours in each) and immersed in Spurr's embedding medium. Notochord length (NL) was measured with the aid of a binocular microscope and calibrated ocular micrometer scale. Each fish was covered with the medium and oriented on its side in a silicone rubber embedding mold (Haake et al., 1982). Curing required 24 hours at 70°C. The otoliths from these larvae were hand ground with 9-μm aluminum oxide microfinishing film and mechanical lapping wheels to produce a midsagittal section from one of the two sagittae. The grinding progress was monitored by frequent inspection of the sample with both transmitted and incident illumination in a metallographic microscope. Final polishing was achieved with 3- and 1-μm diamond pastes. After the final polish, the mounts were rinsed with distilled water and air dried. Immersion and gentle agitation in a 5% solution of ethylenediaminetetraacetic acid (EDTA) (pH adjusted to 7 with potassium hydroxide [KOH]) etched the otoliths for observation under a SEM. Required etching times of 10–40 seconds were determined by periodic rinses and inspection with a light microscope. Owing to shifting of the otoliths in the otic capsules or to twisting or distortion of the larvae, approximately one third of the samples resulted in a somewhat oblique to transverse section through the sagitta. Measurements of radii or increment widths were not significantly affected by this occurrence because otoliths have almost perfect radial symmetry during the earliest postextrusion stages. The etched preparations were then vacuum sputter-coated with gold palladium before viewing with a back-scattered electron detector (BEI) in the SEM. At least two micrographs were taken for each sample, usually at 2,000–3,500× and 10,000×. The photographic images were digitized and measurements were made with the aid of an image analysis software package (Optimus Corp.). A custom program was used for semi-automated measurements of maximum otolith radius (from the center of the otolith primordium) and maximum radius to the presumptive extrusion check. The first 7–10 postextrusion increments were then marked and measured.

Results

The distribution of *S. jordani* larvae in the survey region was quite variable, with catch rates ranging from 0 to 10,670 larvae·10 m^{-2} of sea surface. Like many ichthyoplankton surveys, the distribution of catch rates was strongly skewed. For example, the five largest tows accounted for 3.33% of the effort, yet produced 65.4% of the catch. The overall mean catch rate of larvae was 328 larvae·10 m^{-2} (n=150, $\hat{\sigma}$=1,285, CV=392%).

A total of 2,203 larvae was subsampled from the total catch and aged by optical microscopy. Larvae ranged in age from 0–34 d (median=4 d). Among the aged larvae, the average radius of the otolith measured to the extrusion check (R_0) was 16.88 μm ($\hat{\sigma}$=1.41 μm), with 90% of all values lying in the range 14.5–19.1 μm (Fig. 2).

[1] Eldridge, M. 1994. Tiburon Laboratory, Southwest Fisheries Science Center, NOAA, 3150 Paradise Drive, Tiburon, CA 94920. Unpubl. data.

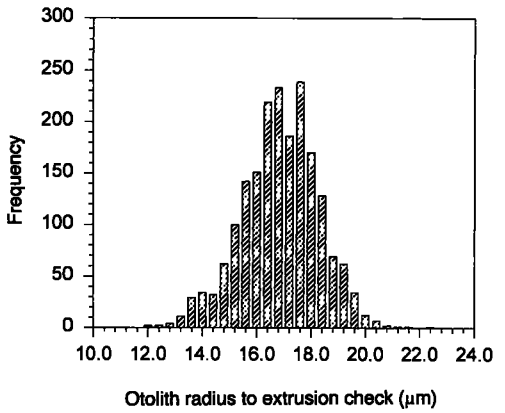

Figure 2

Frequency distribution of the otolith radius, measured to the extrusion check, among aged planktonic larvae, *Sebastes jordani*.

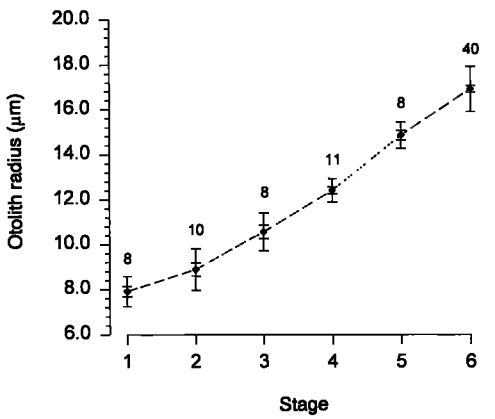

Figure 3

Growth in otolith size with development in gestating prolarvae, *Sebastes jordani*. Means are bracketed by ±1 standard error and ±1 standard deviation (samples sizes above).

A sample of 85 gestating prolarvae were staged from mature female specimens and the total radius of the otolith measured. Results show that prolarval otoliths grow in size as embryonic development proceeds (Fig. 3), and that by attainment of stage 6 the average total otolith radius was 16.91 μm ($\hat{\sigma}$=1.01 μm). A pooled variance t-test (Snedecor and Cochran, 1967), comparing the mean otolith radius at the extrusion check (R_0) of planktonic larvae with the mean total otolith radius of stage 6 gestating prolarvae, was not significant (t=–0.136; df=2,241; P>0.50). This test was powerful, with a difference in the means as small as 0.43 μm being significant at α = 0.05. Moreover, an extrusion check was not observed in any otoliths from gestating larvae. These results indicate that the check mark forms at parturition.

Observations of gestating and planktonic *S. jordani* otoliths with the SEM revealed a well-defined microstructure (Fig. 4). The central area comprised a primordial region which often displayed a cluster of etchant-resistant, crystal-like particles (Fig. 4, B and C). Surrounding the particles was a more deeply etched zone presumed to be predominated by matrix material. Distal to this was a calcified region which generally displayed up to three weakly expressed concentric zones. Incremental growth was considered to be very ambiguous here; the core area included this calcified region around the primordium and was defined by a distinct deeply etched zone (Fig. 4, B, C, and D). Distal to the core boundary, regular incremental growth was observable in most of the preparations. Increments in this preextrusion growth phase were typically 0.3–0.6 μm wide but were of low topographical and compositional contrast in the BEI images (Fig. 4, B and C). There were moderately consistent patterns of broader light and dark areas within the region of preextrusion otolith deposition.

The defining boundary for the preextrusion otolith is a deeply etched zone which corresponds to the extrusion check noted in light microscope observations (Fig. 4, A, C, and D). Distal to this landmark, incremental growth consisted of a regular depositional pattern with distinct zonation and gradually increasing spacing (Fig. 4, C–F). There was individual variation in the spacing pattern of the first 5–10 increments. Some larvae had closely packed increments (Fig. 4F), whereas at the other extreme, some larvae exhibited obviously faster otolith growth immediately after extrusion (Fig. 4E).

A comparison of increment widths derived from optical microscopy with those derived from SEM observations shows that otolith microstructure was adequately resolved with the optical system (Fig. 5). Importantly, the SEM did not detect the existence of increments too small to resolve with optical microscopy. Increment widths typically increase in size during the earliest stages of larval growth (e.g. Campana et al., 1987) and this increase was observed in *S. jordani*. The width of the first postparturition increment was approximately 0.6–1.0 μm, which can be resolved by optical methods. Subsequent increments, at least up to day five, slowly increased in size.

A growth model for the first month of life was derived from the age and length data. Length was first log-transformed because NL variance was propor-

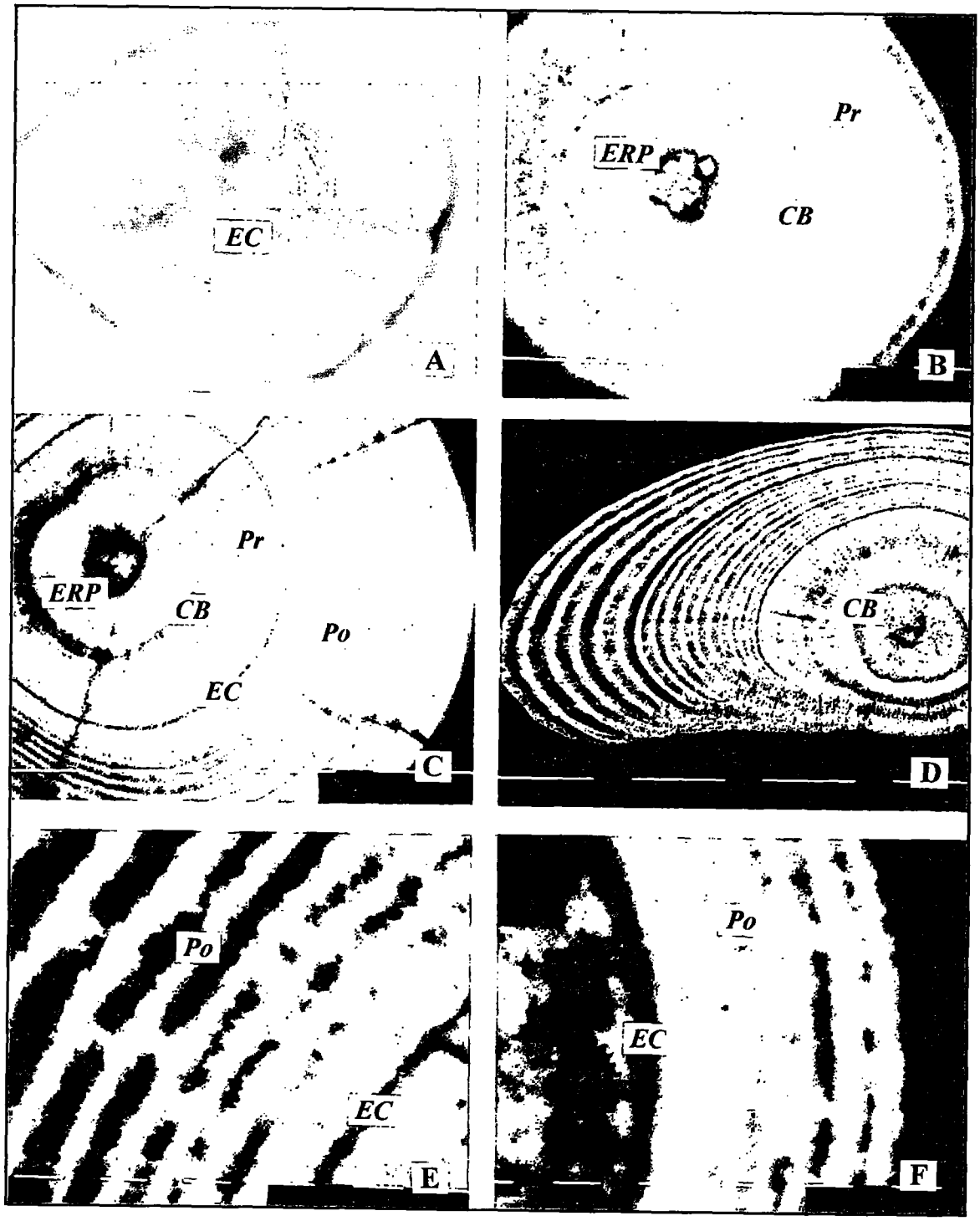

Figure 4

Micrographs of larval shortbelly rockfish, *Sebastes jordani*, otoliths: *EC* = extrusion check; *ERP* = etchant-resistant particles in primordium; *CB* = core boundary; *Pr* = preextrusion incremental growth; *Po* = postextrusion increments. (**A**) optical micrograph (400×) of a wholemount sagitta from a 8.5-mm planktonic larva showing increment microstructure; (**B**) SEM micrograph from a stage–6 gestating prolarva (scale bar = 10 μm); (**C**) sagittal section SEM micrograph from a 7.3-mm planktonic larva (scale bar = 10 μm); (**D**) transverse section SEM from an 8.2-mm planktonic larva (scale bar = 10 μm); (**E**) wide post-extrusion increments (scale bar = 1 μm); (**F**) narrow postextrusion increments (scale bar=1 μm).

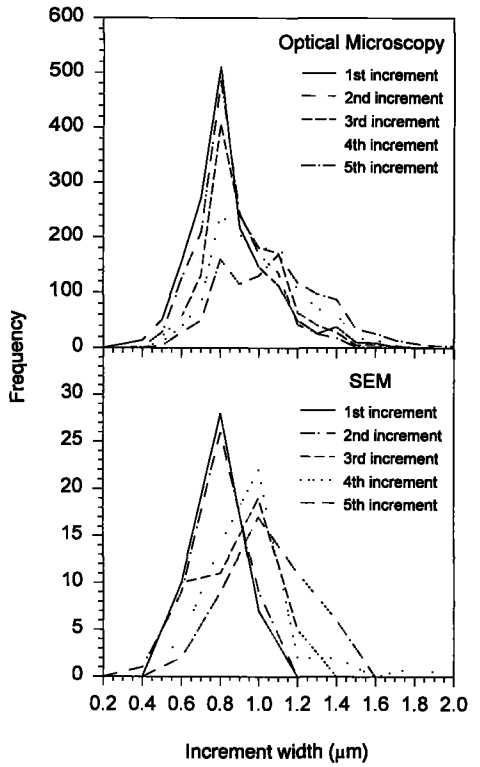

Figure 5

Frequency distributions of the widths of the first five daily increments ($W_1 - W_5$) measured with optical microscopy and SEM.

tional to the mean. A linear ($Y=a + (bx)$) least-squares regression of $\log_e$(NL) on age yielded estimates of b = 0.0272 (s_b=0.000250) and a = 1.640 (s_a=0.00231) with an r^2 value of 0.849 and $\hat{\sigma}^2_{mse}$ = 0.00598. A back transformation of predicted length at age, with bias correction (Miller, 1984), is presented in Figure 6. Also shown in the figure are the original untransformed data and the predicted length-at-age relationship reported by Laidig et al. (1991).

When different readers examined the same otoliths there was good agreement among age estimates (Fig. 7). For example, among the combined total of 87 cross-validations, the three age readers agreed to the day 41% of the time. Moreover, they were within ±1 d 84% of the time and ±2 d 93% of the time. In addition, all paired t-tests for systematic age differences among the readers were not significant (Fig. 7). The statistical power of these tests was such that mean differences in age in the range 0.38–0.88 d were detectable at the α = 0.05 level of significance.

Good agreement among age estimates was also reflected in a high level of certainty in the data. Confidence codes for 67% of all age readings indicated high confidence or better (codes ≥4), 97% were at least moderate confidence (codes ≥3), and only one sample was discarded as unreadable (code=1). Moreover, among the three age readers, the distributions of codes were alike, indicating similar perceptions with respect to the overall clarity of otolith microstructure. There were some differences, however, in the confidence codes of very recently spawned fish and those of older larvae. Fish 1–3 d old were deemed the most difficult to age, whereas ages assigned to older fish (≥7 d) were viewed most confidently.

Discussion

We have shown that a check mark forms in the otoliths of *S. jordani* larvae at parturition. This extrusion check can be identified by its optical characteristics and by its location in the otolith (≈17 μm radius). Penney and Evans (1985) first described an extrusion check in *Sebastes* on the basis of observations of larval redfish in the northwest Atlantic Ocean. These authors described it as "a heavy ring composed of a wide, translucent band followed by a prominent, high-contrast dark band." The check was absent in gestating larvae but was consistently observed in planktonic larvae. Our results are in agreement with theirs and confirm the findings of Laidig

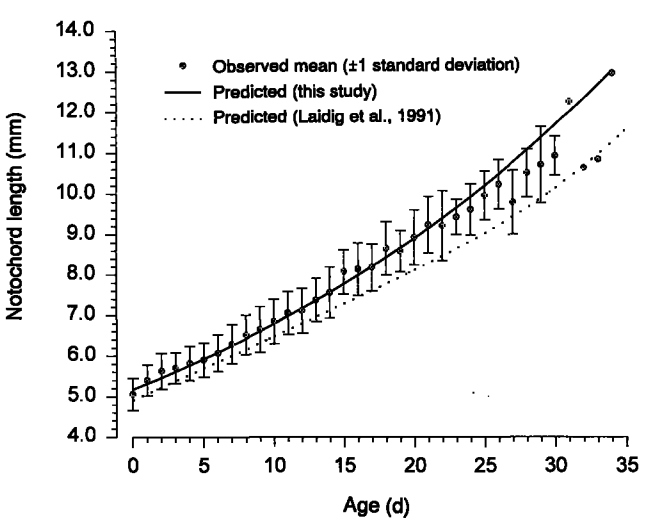

Figure 6

Observed and predicted growth of ethanol-preserved larval shortbelly rockfish, *Sebastes jordani* (means are bracketed by ±1 standard deviation).

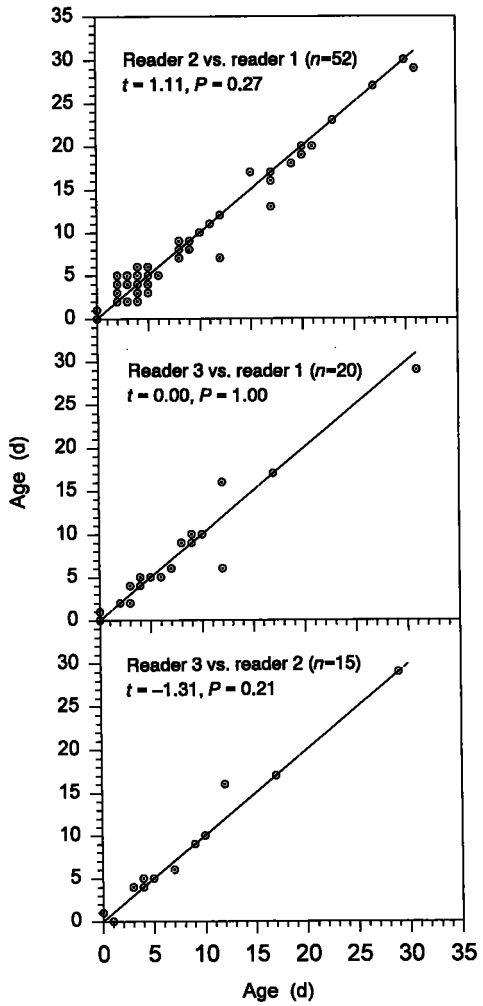

Figure 7

Comparison of age readings of larval *Sebastes jordani* among three different age readers. Diagonal lines represent lines of equality (some points superimposed).

et al. (1991), who first described an extrusion check in the otoliths of *S. jordani*. A distinct "birth mark" has also been observed to form in the otoliths of the viviparous surfperch *Micrometrus minimus* at the time of parturition (Schultz, 1990).

In certain situations otolith size at hatch is known to depend on temperature (e.g. Campana, 1989) and in our study area temperature varies substantially among years (Ralston, 1995; Ralston and Howard, 1995). Because the planktonic larvae we used were collected in 1991, whereas the gestating larvae were collected in 1993, it is important to consider the effect this might have on otolith size at extrusion and the conclusions we have drawn. Results presented in Laidig and Ralston (1995) bear specifically on this issue; i.e. they found no interannual differences in otolith radius at the extrusion check for six species of *Sebastes* (including *S. jordani*) that were sampled over a six-year period (1984–89). However, interannual differences in the width of the first postextrusion increment were observed.

There are, moreover, interspecific differences in extrusion check radius, and these can aid in identifying rockfish species (Laidig and Ralston, 1995). In this regard, *S. jordani* has a particularly large preextrusion radius and can be distinguished 68% of the time on this basis alone. We speculate that the *Sebastes* extrusion check may owe its origin to an osmotic or ionic shock that occurs to the larvae when they first contact seawater and that temporarily alters calcium metabolism.

It is noteworthy that many otoliths exhibited incremental growth during gestation (see also Schultz, 1990). We observed these preextrusion increments in both gestating and planktonic larvae. Although the expression of these structures was quite variable, their existence highlights the importance of accurately locating the extrusion check. We speculate that the physiological basis of preextrusion increments in these larvae is linked to the transmittal of the diel maternal calcium cycle into the ovarian embryonic environment (Mugiya et al., 1981).

The existence of a clear, well-defined mark that is formed at parturition satisfies an important requirement for accurate larval age estimates. An unambiguous starting point for counting increments is a necessary, but not sufficient, condition for obtaining reliable data. Increment counts must also be precise. For *S. jordani* this requirement was met, given the high percent agreement among age readers (93% within ±2 d) and the lack of systematic reader differences in ageing. High precision was also reflected in the relatively high confidence that readers assigned to their work, stemming from the consistent clarity of increment microstructure in the otoliths. Fish 1–3 d old were the most difficult to interpret. This was probably due 1) to optical interference from light diffraction around the otolith margin, 2) to the fact that daily increments present at those ages were the narrowest in width, and 3) to the fact that fewer increments hampered visual recognition of a growth pattern.

A serious potential source of bias in ageing larval fish is the limited resolution of optical microscopes (Neilson, 1992). Studies have shown that optical systems are sometimes incapable of resolving fine increment microstructure (Campana et al., 1987; Jones and Brothers, 1987; Morales-Nin and Ralston, 1990; Secor and Dean, 1992). However, our results for *S. jordani* show that measurements of increment width

obtained with a high-quality optical microscope system produced results similar to an SEM.

From these findings we can conclude that optical increment counts are unbiased with respect to SEM. It need not follow, however, that age estimates are unbiased. If the physiological shock that produces the extrusion check is severe enough, it is possible that increment deposition could be completely arrested for a period of time (Campana and Neilson, 1985). Increment microstructure might then be accurately resolved, but an exact 1:1 correspondence between increments and days may be briefly violated (Geffen, 1992; Neilson, 1992). We have no means of dismissing this possibility from the data we have gathered, although all our results indicate that age estimates of larval *S. jordani* are quite accurate.

Growth of *S. jordani* larvae over the first month of life was well described by a simple exponential model. The predicted length of larvae at parturition (l_0) is 5.17 mm NL, which is quite similar to results presented in Laidig et al. (1991), who reported $l_0 = 4.9$ mm NL. Growth in length then proceeds at about 2.75%·d^{-1}, although there is some indication that growth rate begins to slow sometime around 25 d, which is consistent with the growth stanza model of Laidig et al. (1991). Our observed and predicted lengths at age are ~5–15% higher than the data presented in that study. This discrepancy is possibly due to interannual differences in larval growth, because their samples were collected in 1989 and ours were from 1991. Woodbury and Ralston (1991) reported comparable interannual differences in the growth of five species of pelagic juvenile rockfish, including *S. jordani*.

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Spawning time, frequency, and batch fecundity of yellowfin tuna, *Thunnus albacares*, near Clipperton Atoll in the eastern Pacific Ocean

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Abstract.—Spawning of yellowfin tuna, *Thunnus albacares*, around Clipperton Atoll, in the eastern Pacific Ocean, occurred between 2230 and 0330 h on the basis of the presence of migratory-nucleus and hydrated-stage oocytes and new postovulatory follicles in ovaries of females sampled at different times of the day. Histological criteria were developed to estimate the ages of the postovulatory follicles and used to estimate spawning frequency. Histological examinations of testicular tissues provided criteria on the structural characteristics of the sperm duct useful for estimation of spawning frequency. The mean interval between spawnings was 1.14 days for females and 1.22 days for males. The average batch fecundity was 1.57 million oocytes, or 68 oocytes per gram of body weight. The average daily cost of spawning, excluding behavioral activities, is estimated to be 0.97% and 0.28% of the body weight per day for females and males, respectively.

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Knowledge of the reproductive biology of yellowfin tuna, *Thunnus albacares*, is essential for a comprehensive understanding of the population dynamics of this species. Previous investigations on the reproductive biology of yellowfin tuna have addressed the topics of spawning distribution, sex ratios, length at maturity, and fecundity (Wild, 1994). However, fundamental information on maturation and spawning has not previously been elucidated for either male or female yellowfin tuna.

Knowledge of the appearance and longevity of postovulatory follicles in ovaries after spawning is necessary for estimating spawning frequency. The frequency of ovaries containing postovulatory follicles has been used to estimate spawning frequency in some scombroid fishes, including skipjack tuna, *Katsuwonus pelamis* (Hunter et al., 1986); yellowfin tuna (McPherson, 1991); bigeye tuna, *Thunnus obesus* (Nikaido et al., 1991); and chub mackerel, *Scomber japonicus* (Dickerson et al., 1992). However, the age and longevity of postovulatory follicles have been determined only for skipjack tuna and chub mackerel held in captivity (Hunter et al., 1986; Dickerson et al., 1992). The use of histological methods generally provides more precise criteria than do gonosomatic indices or oocyte diameter measurements for assessing reproductive status of individuals (Hunter and Macewicz, 1985; West, 1990).

Although structural changes over seasonal cycles have been described from histological examinations of teleost testes (Grier, 1981) and used to estimate length at maturity and define spawning seasons, there have been no investigations of diel testicular changes in relation to rhythmic spawning activity. Information on testicular histology in tunas is scarce because most researchers have been satisfied with gross morphological or gonosomatic indices to measure the reproductive activity of males. Although histological examinations of the testes from albacore tuna, *Thunnus alalunga* (Ratty et al., 1990), and bigeye tuna, *Thunnus obesus* (Nikaido et al., 1991), have provided descriptions of some aspects of spermatogenesis and characteristics of sexual maturity in male tunas, there have been no descriptions of histological characteristics of tuna testes which can be used to determine when a male has spawned and which would thus be useful for estimating the spawning frequency and reproductive effort of males.

Yellowfin tuna, like many subtropical and tropical pelagic fishes, continuously produce batches of hydrated oocytes (Hunter et al., 1985). Their annual fecundity is indeterminate and exceeds the standing stock of oocytes within the ovaries at any given time. Annual

fecundity can be estimated from batch fecundity (the number of oocytes released per spawning) and spawning frequency. However, only at the final stages of oocyte maturation, beginning with the migratory-nucleus phase and followed by hydration, is there a distinct hiatus in the distribution of oocytes from which the batch fecundity can be determined. Previous batch fecundity estimates for yellowfin tuna in the eastern Pacific (Joseph, 1963) were based upon counts of yolked oocytes or upon more advanced stages from ovarian tissue samples that had been placed in Gilson's fluid. This methodology, however, creates a potential bias in batch fecundity estimates because Gilson's fluid causes significant shrinkage of oocytes and compaction of the oocyte size distribution, which then complicates partitioning of the most advanced group of oocytes from the adjacent group of smaller oocytes.

The objectives of this study are 1) to determine the time of day that yellowfin spawn and to develop histological criteria for estimating spawning frequency; 2) to estimate batch fecundity from migratory-nucleus or hydrated-stage oocytes in order to provide an estimate of total fecundity; and 3) to estimate energetic investment in spawning.

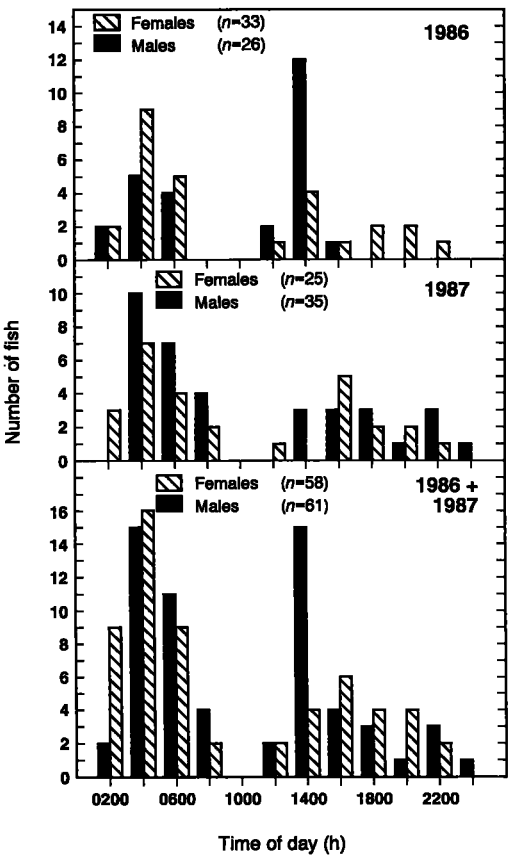

Figure 1

Number of yellowfin tuna, *Thunnus albacares*, sampled for reproductive data during May of 1986 and 1987 from around Clipperton Atoll in the eastern Pacific Ocean by times of day.

Materials and methods

Sampling and processing

Yellowfin tuna were caught by rod and reel aboard the MV *Royal Polaris*, a San Diego-based long-range sportfishing boat, around Clipperton Atoll in the eastern Pacific Ocean (lat. 10°118'N, long. 109°13'W) during the first two weeks of May during both 1986 and 1987 throughout the diel period (Fig. 1). Clipperton Atoll is located in an area in which large catches of yellowfin tuna are taken by purse seiners (Bayliff, 1991). Sea-surface temperatures during these periods were 83° to 84°F (28° to 29°C).

Specimens close to or greater than 900 mm fork length (FL) were measured to the nearest millimeter and their gonads removed immediately after capture (Fig. 2). The decision to sample only yellowfin greater than about 900 mm FL was based on earlier research by Orange (1961), who found that about 70% of fish greater than 900 mm FL were reproductively active. A 2-cm cross section from the central region of the ovaries or testes of each specimen was fixed in 10% neutral-buffered formalin (Hunter, 1985). The ovaries or testes from each specimen, minus the section, were frozen at sea, thawed in the laboratory, blotted dry, and weighed to the nearest centigram on a Mettler electronic balance. A portion of each sample of preserved gonadal tissue was embedded in Paraplast, sectioned at approximately 6 μm, and stained with Harris hematoxylin followed by eosin counterstain. The slides were viewed by light microscopy with a Nikon optiphot microscope fitted with a microflex HFX-II photographic attachment and Kodak T-max 100 film.

Histological classification

The classification of yellowfin tuna ovaries was based on a modification of the system of Hunter and Macewicz (1985). For each ovary the most-developed oocytes were classified as follows: 1 = unyolked, 2 = partially yolked, 3 = fully yolked, 4 = migratory-nucleus stage, and 5 = hydrated. Identification of ovarian atresia (resorption of oocytes) was restricted to advanced yolked oocytes (stage 3). Ovaries were classified into one of three categories of alpha (α)

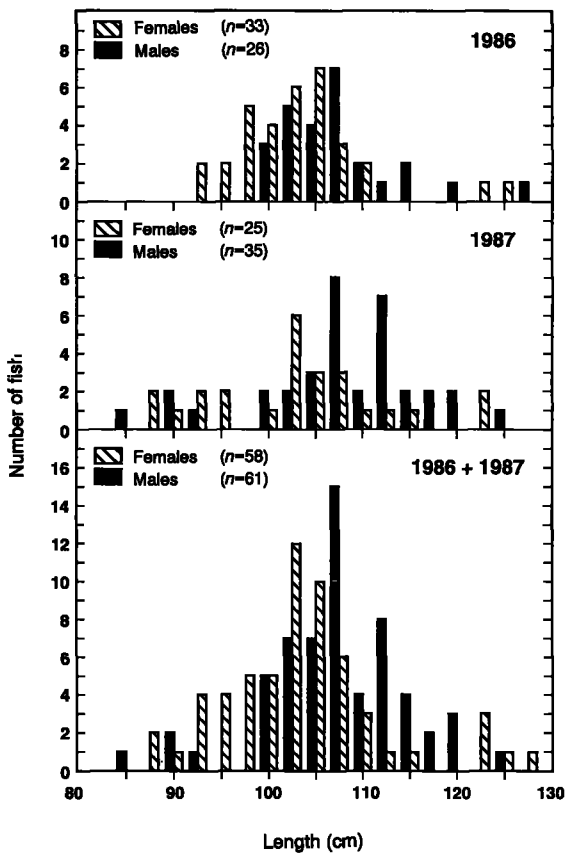

Figure 2

Length frequencies of yellowfin tuna, *Thunnus albacares*, sampled for reproductive data during May of 1986 and 1987 from around Clipperton Atoll in the eastern Pacific Ocean.

atresia (none, <50%, and >50%), i.e. atretic classes 1, 2, and 3, based on visual estimates of the proportion of atretic oocytes and presence or absence of beta (β) atresia, atretic class 4.

Postovulatory follicles were staged according to their appearance and were assigned ages on the basis of the time of capture relative to the estimated time of spawning. The degeneration and resorption of yellowfin tuna postovulatory follicles were described and classified into a series of distinct stages, each with an assigned time after spawning, in 6-hour intervals. An estimate of the spawning time and frequency for females was obtained from the evaluation of this series of yellowfin tuna ovarian tissues.

The classification of yellowfin tuna testes was based on the size of the duct, the thickness of the myoid tissue (Grier et al., 1989) surrounding the duct, the amount of spermatozoa within the duct, the degree to which the duct was convoluted, whether the tissue adjacent to the duct appeared to be heavily nucleated, and the staining characteristic of the tissue adjacent to the duct.

Slides were scored by stage number and specimen identification was not revealed. The original variables were subjected to discriminant analysis operating on the covariance matrix by using BMDP statistical software (Dixon et al., 1990). This procedure separates individuals into two or more groups based on characteristics of variables by which the groups differ (Johnson and Wichern, 1982). The two groups evaluated with this technique were those individuals sampled between 0001 and 1200 h (group 1) and those sampled from 1201 to 2400 h (group 2). These two time intervals were chosen on the basis of the approximate modal time of spawning for females. An estimate of the spawning frequency for males was obtained from the evaluation of this series of yellowfin tuna testicular tissues.

Oocyte size distributions and estimation of batch fecundity

Oocytes from a 1-g tissue sample were measured to the nearest 0.03 mm at 30× magnification with an ocular micrometer in a dissecting microscope. For each fish, mean diameter (random axis) was determined from 20 oocytes present in the most advanced mode of oocytes.

Following the procedures of Hunter et al. (1985), batch fecundity (number of oocytes released per spawning) was estimated for 12 females. For each female, counts of migratory-nucleus or hydrated oocytes in three subsamples of about 0.05 g each were weighed to the nearest 0.1 mg. Migratory-nucleus and hydrated oocytes can be easily distinguished from other oocytes by their larger size and appearance. Those with migratory nuclei are less opaque than yolked oocytes, whereas hydrated oocytes are translucent. No new postovulatory follicles were present in the ovaries used for estimation of batch fecundity.

Each of the three subsamples yielded an estimate of batch fecundity for each female, calculated from the product of the number of migratory-nucleus or hydrated oocytes per unit weight of the subsample and the total weight of the ovaries. The mean of these three estimates provided the spawning batch fecundity estimate for each fish. The weight of each fish used to estimate batch fecundity was estimated from the length-weight relationship of Chatwin (1959) in order to calculate relative fecundity (oocytes per gram of body weight). To describe the relationship between batch fecundity and FL for this set of data, a linear regression between the natural logarithms of the

batch fecundity estimates and natural logarithms of FL for each fish was calculated. The result of the regression analysis is given in the antilog form as a power curve. Analysis of covariance was applied to the log-transformed batch fecundity and length data from this study and the data of Joseph (1963) (whose data were truncated so that the length ranges of the two data sets coincided) to compare the two sets of data.

In order to estimate the cost of spawning a single batch of eggs, 12 preserved oocytes (10% neutral-buffered formalin) in the migratory-nucleus stage from each of two fish, were individually measured, rinsed in distilled water, placed on a nucleopore filter for about 10 seconds, and then weighed to the nearest 0.001 mg. The average weight of an oocyte in the migratory-nucleus stage multiplied by the mean relative fecundity provided an estimate of the cost of spawning a single batch of eggs in percentage of body weight (Hunter et al., 1986).

The costs of a single spawning for both females and males were also estimated by subtracting the percentage of calculated body weight of the gonads just after spawning from the percentage of body weight of the gonads just before spawning occurred.

Results

Classification of ovaries and spawning incidence

The estimate of spawning time and rates of resorption of postovulatory follicles for yellowfin tuna was based on the classification of ovaries taken from 58 fish sampled at different times of the day (Table 1). All females had reached sexual maturity. Sexually mature females were those whose ovaries contained advanced yolked oocytes (oocyte classes 3, 4, or 5) in the most advanced modal group, or had partially yolked oocytes (oocyte class 2) along with α or β atresia, or both (atretic classes 1, 2, 3, or 4). Of the 58 females sampled, 52 were classified as reproductively active. Reproductively active females are those whose ovaries contain advanced yolked oocytes and may or may not contain postovulatory follicles and those in whom α atresia is either absent or less than 50% (atretic states 0 or 1).

Analyses of the ovaries sampled in 1986 and 1987 indicated that yellowfin tuna spawning occurred between approximately 2230 and 0330 h. This estimate was based on the following observations: 1) ovaries sampled during the afternoon (1300–1800 h) had migratory-nucleus stage oocytes in the most advanced mode and those sampled between 1800 and 2000 h had hydrated oocytes; 2) ovaries collected between 2230 and 0330 h had new postovulatory follicles (Tables 1 and 2). The earliest spawning appears to have occurred around 2230 h, as evident in an 1145-mm FL female; this fish had new postovulatory follicles with no evidence of cellular degeneration and had large numbers of ovulated eggs within the lumina of both ovaries.

The mean diameter of the most developed group of oocytes within ovaries, plotted by time of day (Fig. 3), provided further evidence of the spawning time for yellowfin tuna. From 0001 to 1200 h, the mean oocyte diameter increased from about 0.55 mm to 0.64 mm. From 1201 to 2000 h, the oocytes began the migratory-nucleus stage, during which the mean diameter increased to about 0.80 mm by 1601 to 2000 h. This advanced batch of oocytes became hydrated, was then ovulated, and was spawned sometime after 2000 h. The mean diameter of the remaining most-developed modal group of oocytes was about 0.50 mm.

Postovulatory follicles with no signs of degeneration were classified as 0 to 6 hours old (Fig. 4, A and B). These postovulatory follicles had an involuted shape with numerous folds and a relatively open follicular cavity. The granulosa cell layer lining the lumen (epithelium) showed regularly aligned cuboidal cells with prominent basal nuclei. The thecal connective tissue layer was distinct, in only minimal contact with the granulosa, and appeared to be of about the same thickness as the latter.

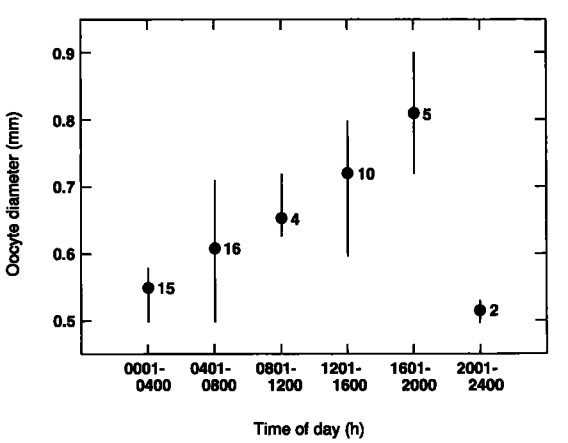

Figure 3

Mean diameters (mm) of the most advanced group of oocytes of yellowfin tuna, *Thunnus albacares*, by time of day. Means are represented by solid circles, ranges by vertical lines, and the numbers of females are noted.

Table 1

Reproductive status of female yellowfin tuna, *Thunnus albacares* (n = 58).

Year and day of month	Time of day (h)	Length (mm)	Oocyte class[1]	Postovulatory follicle class[2]	Atretic state[3]
1986					
5	0531	975	3	2	0
5	0534	1,025	3	2	1
5	0547	980	3	2	1
5	0550	982	3	2	0
5	0553	1,060	3	2	0
6	0220	985	3	1	0
6	0230	1,060	3	1	0
6	0230	949	2	0	4
6	0230	995	3	1	0
6	0240	915	3	1	1
6	0537	1,070	3	2	1
7	0235	1,057	3	0	2
7	0310	966	3	1	0
7	1310	997	3	3	0
7	1320	1,034	4	3	0
7	1335	1,044	4	3	0
7	1340	1,088	4	3	1
7	1700	1,240	4	4	0
7	1700	1,220	4	4	0
8	0300	990	3	1	0
8	0310	1,034	3	1	0
9	0410	1,066	3	2	0
9	0410	942	3	2	0
9	0415	1,045	3	2	1
9	0420	1,075	3	2	1
9	0420	1,015	3	0	1
9	1507	1,052	4	3	0
10	1121	1,048	2	0	4
12	0330	935	2	0	4
12	0330	1,022	3	2	1
12	0438	1,093	3	2	1
12	0505	1,005	3	0	2
12	0530	1,018	2	0	4

Postovulatory follicles estimated to be 6 to 12 hours old showed distinct signs of cellular degeneration (Fig. 4, C and D). They were smaller and less convoluted, and there were some irregular cells and pycnotic nuclei in the granulosa and thecal layers. The granulosa no longer showed a well-organized alignment of cell walls or nuclei and was in obvious contact with the theca. At this stage the thecal layer appeared thicker.

Postovulatory follicles estimated to be 12 to 18 hours old showed advanced cellular degeneration (Fig. 4, E and F). They were considerably smaller and lacked the distinctly convoluted appearance of previous stages, but still had follicular cavities. A thicker thecal layer surrounded the much thinner granulosa cell layer, and the two were in close contact. The granulosa layer was still distinguishable, although it now consisted of a few irregular cells with pycnotic nuclei.

Postovulatory follicles estimated to be 18 to 24 hours old showed signs of the final stages of degeneration (Fig. 4, G and H). The follicle was smaller still, not convoluted but elongate, and had a follicular cavity. The granulosa layer consisted of few cells, was very thin, and not clearly separable from the thicker thecal layer. Prominent, sharply staining pycnotic nuclei were apparent in the degenerating thecal layer.

Several observations indicated that postovulatory follicles are histologically detectable for no more than 24 hours after spawning. Postovulatory follicles of only a single degenerative stage were found in ovaries sampled throughout the day, and the stage of degeneration was consistent among ovaries sampled

Table 1 (continued)

Year and day of month	Time of day (h)	Length (mm)	Oocyte class[1]	Postovulatory follicle class[2]	Atretic state[3]
1987					
3	0310	1,030	3	2	0
3	0315	1,025	3	1	1
3	0445	1,034	3	2	0
3	0510	953	3	2	0
3	0520	1,035	3	2	1
3	1850	925	5	4	0
3	2300	1,115	3	1	1
4	0330	1,046	2	0	4
4	1510	880	4	3	1
4	1515	945	4	3	1
4	1515	900	3	0	4
4	1525	1,090	4	3	1
4	1525	1,056	4	3	0
5	0330	1,008	3	2	0
5	0330	1,029	3	1	0
5	0330	1,080	3	1	0
5	0345	1,042	3	0	2
5	1900	1,023	5	4	0
6	0810	1,073	3	2	0
6	0810	1,220	3	2	1
6	0912	1,054	3	2	0
6	1125	1,062	3	0	2
6	1729	880	4	4	0
6	2230	1,145	3	1	0
7	0610	921	2	0	4

[1] Most advanced oocytes are 1 = unyolked; 2 = partially yolked; 3 = fully yolked; 4 = migratory nucleus stage; 5 = hydrated stage.
[2] Postovulatory follicles are 0 = absent; 1 = age 0–6 h; 2 = age 6–12 h; 3 = age 12–18 h; 4 = age 18–24 h.
[3] Atretic classes are 0 = absent; 1 = <50% α; 2 = >50% α; 3 = β; 4 = $\alpha + \beta$.

at similar times over several different days and during the two different years. Postovulatory follicles estimated to be 12 to 24 hours old occurred in ovaries which also contain migratory-nucleus or hydrated oocytes (Table 1).

The incidence of both postovulatory follicles and late-stage oocytes indicated daily spawning in yellowfin tuna (Fig. 5). Five of the six fish collected between 1300 and 1700 h in 1986 and all seven fish collected between 1500 and 1900 h in 1987 that had oocytes in the migratory-nucleus or hydrated stages also had postovulatory follicles present (Table 1). Assuming that the postovulatory follicles are not detectable for longer than 24 hours, this observation indicates that these fish had spawned the previous night and would spawn again the next night. For the combined samples of 1986 and 1987, the fraction of mature females with postovulatory follicles was 0.79, equivalent to a mean spawning interval of about 1.27 d. If only females that were classified as reproductively active are considered, the fraction of fish spawning (those with postovulatory follicles) was 0.88, a mean interval of 1.14 d. The mean spawning intervals for each of the years were similar, 1.27 d in 1986 and 1.25 d in 1987.

Table 2

Spawning state of female yellowfin tuna, *Thunnus albacares*, by time of day.

	Advanced oocytes		Postovulatory follicles		
Time (h)	Migratory nucleus	Hydrated	New[1]	Old[2]	Total
0001–0400	0	0	10	3	18
0401–0800	0	0	0	14	18
0801–1200	0	0	0	3	5
1201–1600	7	0	0	9	10
1601–2000	3	2	0	5	5
2001–2400	0	0	2	0	2
Total					58

[1] No histological evidence of cellular degeneration.
[2] Histological evidence of cellular degeneration.

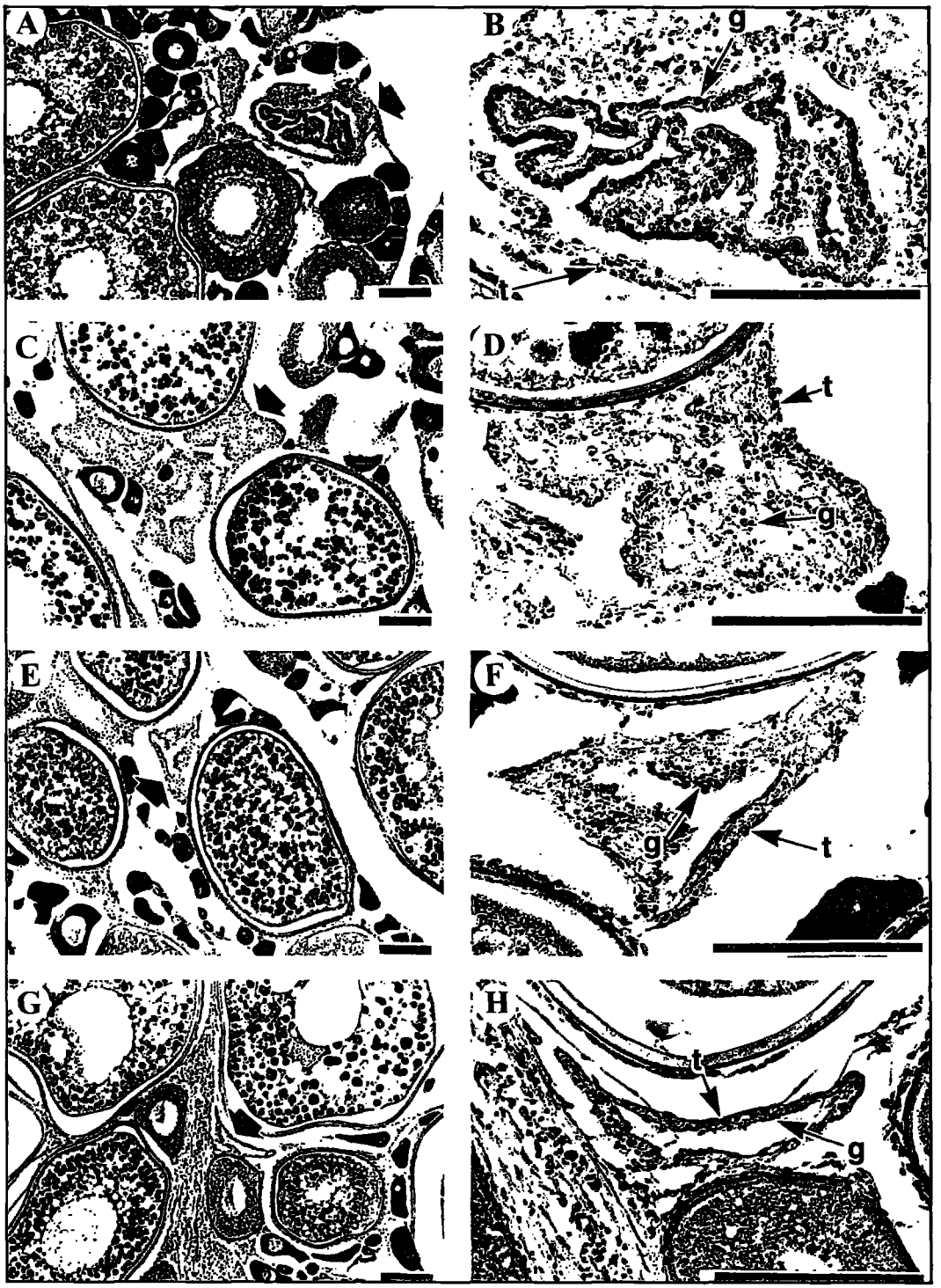

Figure 4

Degeneration of postovulatory follicles of yellowfin tuna, *Thunnus albacares*, at various times after spawning. Arrows in left panels indicate the postovulatory follicles shown under higher magnifications in right panels. (**A** and **B**) 0–6 h after spawning (no signs of degeneration); (**C** and **D**) 6–12 h after spawning (distinct signs of degeneration); (**E** and **F**) 12–18 h after spawning (advanced stages of degeneration); (**G** and **H**) 18–24 h after spawning (final stages of degeneration). Bar = 0.1 mm; g = granulosa epithelial cell layer; t = thecal cell layer.

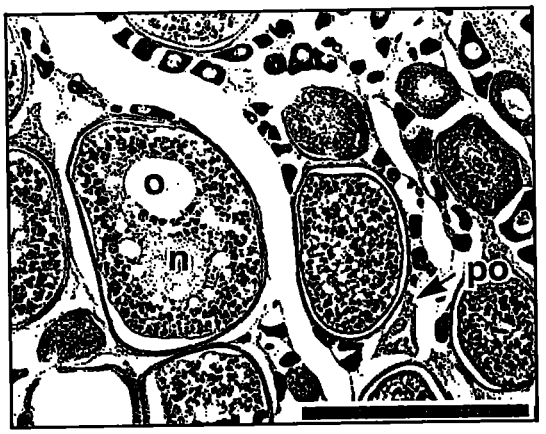

Figure 5

Migratory-nucleus-stage oocyte and a postovulatory follicle in advanced stage of degeneration in yellowfin tuna, *Thunnus albacares*. Bar = 0.5 mm; n = nucleus; o = oil droplet; po = postovulatory follicle.

Classification of testes and spawning incidence

The yellowfin tuna testis is bilobed and each lobe consists of interstitial and germinal compartments. The germinal compartments are situated within lobules that radiate perpendicularly from the central longitudinal sperm duct (vas deferens) or efferent duct and terminate at the periphery of the lobe, the tunica albuginea. Primary spermatogonia are distributed along the lobule lengths, and this typical lobular-type testis is classified as an unrestricted spermatogonial testis type (Grier, 1981, 1993). The lobules of reproductively active yellowfin tuna are filled with sperm that are released after completion of spermiogenesis into the lobular lumen, which is continuous with the vas deferens (Nagahama, 1983). The vasa deferentia are straight tubes with thick, muscular walls, which merge caudally and exit through the genital orifice. The lumen of the vas deferens is lined along its length with cuboidal to columnar epithelium and varies in general appearance from smooth to convoluted.

Structural characteristics of the vas deferens, subjected to discriminant analyses, indicated significant differences ($F_{0.05(3,57)}$=19.96, P<0.001) among yellowfin tuna sampled between 0001 and 1200 h (group 1) and those sampled between 1201 and 2400 h (group 2) for the pooled 1986 and 1987 data (Table 3). The results are similar for the years examined separately. Although the second group, on the basis of spawning time of 2230 to 0330 h, may contain males that had spawned within 12 h, there were no males sampled during that time interval in 1986 and only four in 1987. The characteristics that best distinguish between fish of the two groups are the amount of sperm in the duct, shape of the duct, and staining characteristics of the vas deferens epithelium (Table 3). The fish from group 2 are characterized by a relatively sperm-filled vas deferens, an open duct that is smooth along its border, and no conspicuous dark staining of the vas deferens epithelium (Fig. 6). The spaces apparent in Figure 6 (C–F) between the wall of the duct and the sperm clumped in the center of the duct are most likely artifacts of the preparation method caused by embedding the tissue sample in paraffin

Table 3

Summary of stepwise discriminant analyses between yellowfin tuna, *Thunnus albacares*, groups 1 (0001–1200 h) and 2 (1201–2400 h) for the pooled 1986 and 1987 data, using the six sperm duct characteristics.

Step number	Variable entered	Number of variables	Approximate F-statistic	Degrees of freedom
1	Fullness	1	41.57	59
2	Shape	2	26.32	58
3	Stain	3	19.96	57

Classification matrix

			Number of fish	
Group	n	Percent correct	Group 1	Group 2
1	33	81.8	27	6
2	28	82.1	5	23
Total	61	82.0	32	29

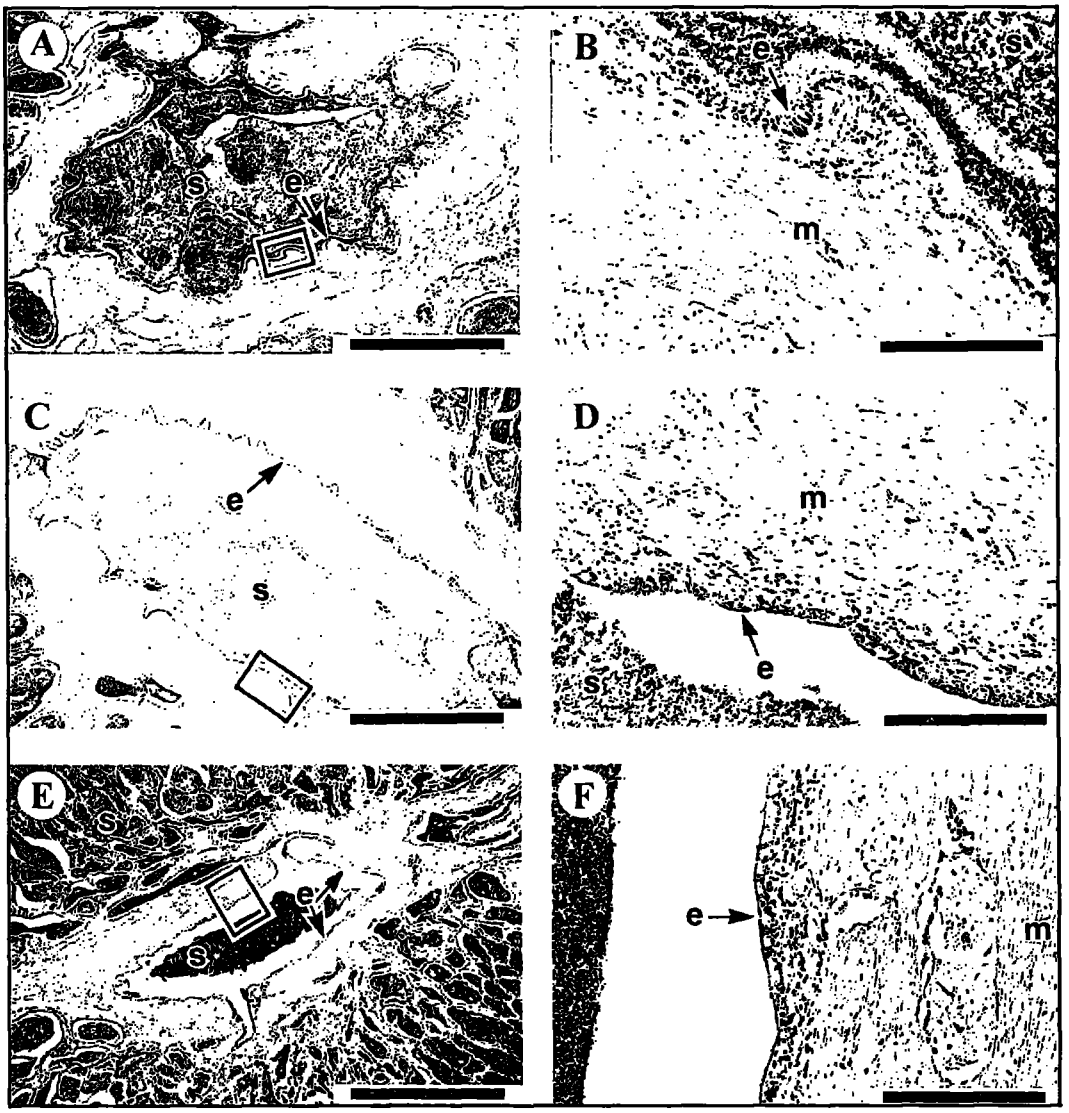

Figure 6

Vas deferens filled with sperm from three yellowfin tuna, *Thunnus albacares* (**A** and **B**; **C** and **D**; **E** and **F**) sampled during 1201–2400 h. The rectangles in left panels indicate the regions shown under higher magnifications in right panels. Bar = 1 mm in A, C, and E; 0.1 mm in B, D, and F. e = epithelium; m = myoid tissue; s = sperm.

(Quintero-Hunter et al., 1991). The fish from group 1 are characterized by a vas deferens relatively devoid of sperm, an extremely convoluted duct, and a darkly stained vas deferens epithelium (Fig. 7).

The percent-correct classification for the pooled 1986 and 1987 data was a total of 82.0%, with 81.8% for group 1 and 82.1% for group 2 (Table 3). The histogram of the canonical variable (Fig. 8) from this analysis for the two groups shows the two distributions. The six fish sampled during the 0001 to 1200 h period that were not classified into group 1 showed no characteristics of spawning within 12 hours and were thus misclassified into group 2. Of the five fish misclassified into group 1, three fish were sampled during the spawning period, two at 2245 and one at 2300 h, and showed characteristics of the other individuals in group 1 that had spawned within 12 hours. Another fish sampled at 1300 h showed characteristics more similar to those of group 1, and the other fish showed intermediate characteristics between the two groups but were more similar to those of group 1.

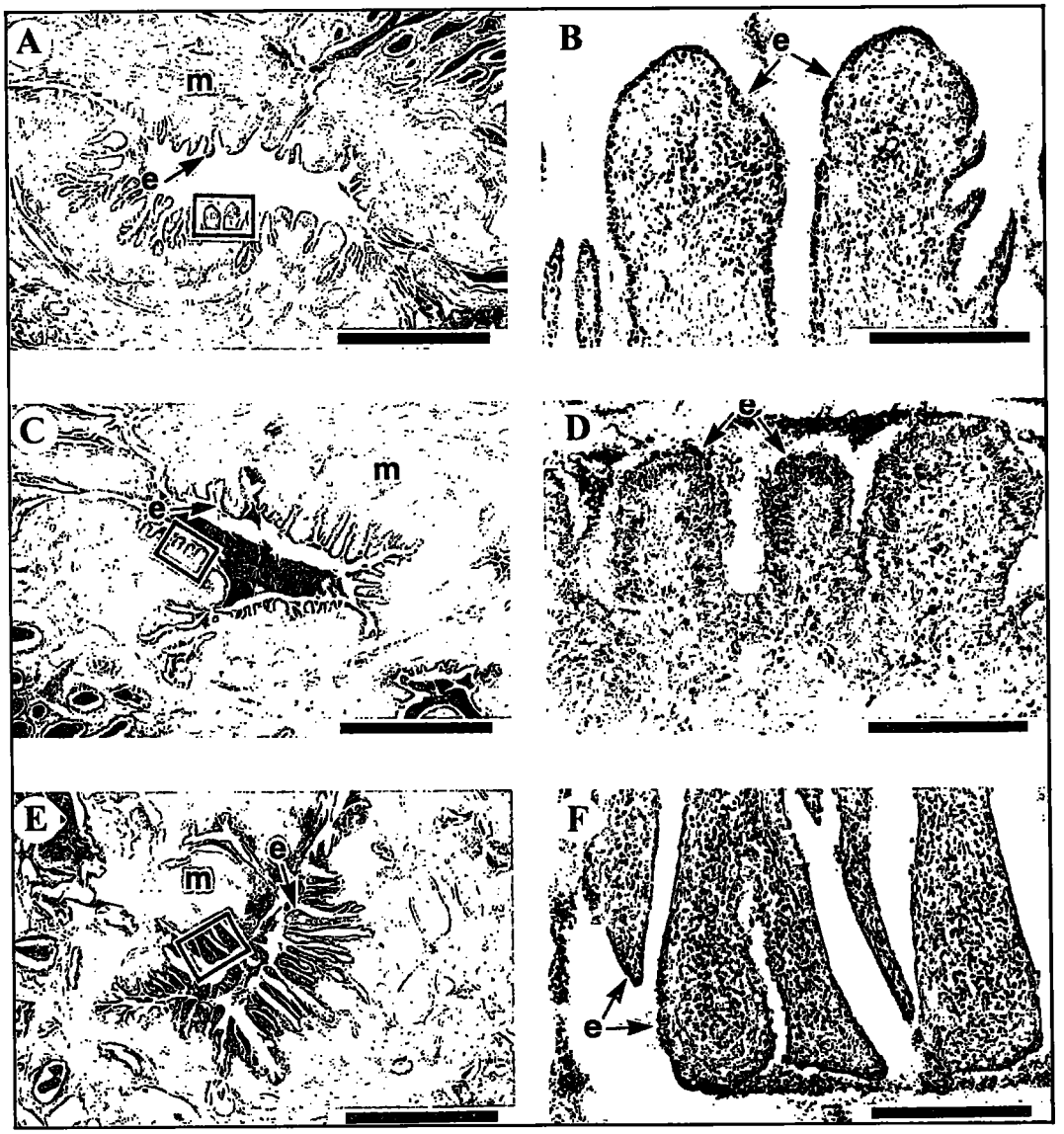

Figure 7

Vas deferens relatively devoid of sperm from three yellowfin tuna, *Thunnus albacares* (**A** and **B**; **C** and **D**; **E** and **F**), sampled during 0001–1200 h. The rectangles in left panels indicate the regions shown under higher magnifications in right panels. Bar = 1 mm in A, C, and E; 0.1 mm in B, D, and F. e = epithelium; m = myoid tissue; s = sperm.

These data indicate that evidence of recent spawning in males is detectable for only about 12 hours after the spawning event. Apparently the lobules, which are full of sperm in mature fish, refill the main sperm duct during this time, and the other characteristics, such as the convoluted shape of the duct and the conspicuous dark staining of the vas deferens epithelium return to the state observed in prespawning individuals. Assuming that spawning males are detectable between 0001 and 1200 h, an estimate of the daily spawning frequency of males during the six days of sampling in 1986 and the four days in 1987 at Clipperton Atoll can be derived. Ten of the 12 fish in 1986 and 17 of the 21 fish in 1987 that were sampled between 0001 and 1200 h were classified as having spawned in the past 12 hours. Thus about 83.3% and 81.0% of the males had spawned within the past 24 hours in 1986 and 1987, respectively. This indicates that the mean interval between spawnings was about 1.20 days in 1986 and

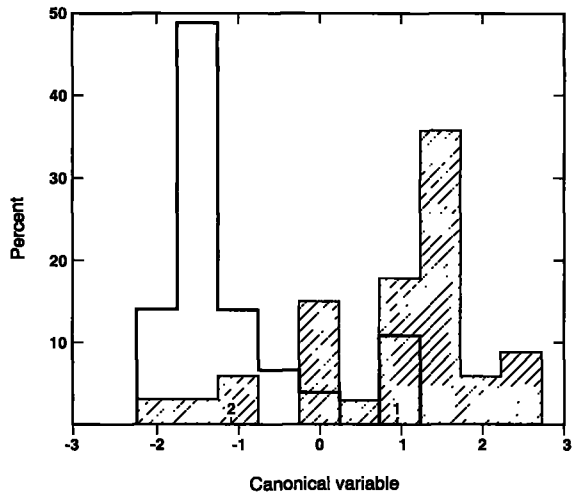

Figure 8

Histogram of the canonical variable from discriminant analysis of the data for the two groups and six characteristics of the vas deferens. The shaded portion represents group 1 (sampled between 0001 and 1200 h) and the white area outlined in bold represents group 2 (sampled between 1201 and 2400 h). The group centroids are also plotted.

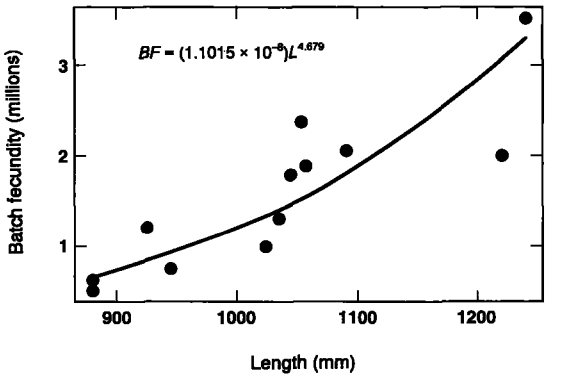

Figure 9

Batch fecundity as a function of length for yellowfin tuna, *Thunnus albacares*, collected around Clipperton Atoll in the eastern Pacific Ocean during May of 1986 and 1987. BF = the batch fecundity in number of oocytes and L = the length in millimeters in the predictive regression equation.

1.24 days in 1987 (1.22 days for the pooled data). In other words, spawning occurred nearly every day for males, as was the case for females.

Batch fecundity

The estimated mean relative fecundity and standard deviation for 12 fish was 68.0 ±20.7 oocytes per gram of body weight (Table 4). The relationship between batch fecundity and length (Fig. 9) can be described by the following equation:

$$BF = (1.1015 \times 10^{-8})L^{4.679}, \qquad [r^2 = 0.76]$$

where BF = batch fecundity in number of oocytes; and

L = length in millimeters.

The predicted batch fecundities and 95% prediction intervals from this equation for yellowfin tuna of 1,000 mm and 1,200 mm FL are 1,199,841 (991,129; 1,452,359) and 2,815,639 (2,025,445; 3,913,724), respectively.

Cost of spawning

Yellowfin tuna oocytes in the most advanced group enter the migratory-nucleus phase about 6 to 8 h before spawning and begin to hydrate about 4 to 6 h before spawning (Fig. 3; Table 1). The hydration process results in a rapid increase in size of the oocytes and in wet weight of the ovary but there is no increase in dry weight (LeClus, 1979). The mean size of oocytes in the migratory-nucleus stage just before the hydration process begins is 0.75 to 0.80 mm (Fig. 3; Table 1). The mean wet weight of a yellowfin tuna oocyte in the migratory-nucleus stage was estimated to be 0.157 mg. This estimate was based on two females of 945 and 1056 mm FL whose oocyte diameters were $\bar{x}$ = 0.78 mm [SD=0.01 mm] and $\bar{x}$ = 0.79 mm [SD=0.01 mm] and whose oocyte weights were $\bar{x}$ = 0.156 mg [SD=0.015 mg] and $\bar{x}$ = 0.158 mg [SD=0.011 mg], respectively. The mean relative fecundity of yellowfin tuna, from this study, is 68.0 oocytes per gram of body weight. The cost of a single spawning (excluding behavioral activities) is thus about 1.1% of body weight. If a female spawns every 1.14 d, the average daily cost of spawning a batch of eggs is 0.97% of the body weight per day.

The costs of a single spawning (excluding behavioral activities) for both females and males were also estimated by subtracting the percentage of calculated body weight of the gonads just after spawning (0001–0400 h) from the percentage of body weight of the gonads just before spawning occurs (1600–2000 h). For females, the average weight of the ovaries with oocytes in the migratory-nucleus stage (preceding spawning) was 2.12% of body weight, and just after spawning was 0.78%, which yields an estimate for the cost of spawning of 1.34% of body weight. For the males, the average weight of the testes preceding spawning was 1.43%, and just after spawning

Table 4

Batch fecundities of 12 female yellowfin tuna, *Thunnus albacares*, with the most advanced group of oocytes in the migratory nucleus or hydrated stage.

Length (mm)	Estimated body weight (kg)	Ovary weight (g)	Batch fecundity	
			Number of oocytes	Oocytes per gram of body weight
880	13.7949	183.85	495,984	36.0
880	13.7949	207.50	620,679	45.0
925	16.0256	368.32	1,194,253	74.5
945	17.0950	246.71	738,153	43.2
1023	21.7215	462.31	984,394	45.3
1034	22.4346	562.91	1,296,181	57.8
1044	23.0963	667.20	1,776,735	76.9
1052	23.6349	793.42	2,356,848	99.7
1056	23.9103	766.20	1,876,038	78.5
1090	26.3084	927.76	2,047,401	77.8
1220	36.9719	986.41	1,984,357	53.7
1240	38.8329	1,485.34	3,496,706	90.0

was 1.09%, which yields an estimate for the cost of spawning of 0.34% of body weight. Based on the estimated mean interval between spawnings of 1.14 days for females and 1.22 days for males, estimates of the average daily costs of spawning are 1.18% and 0.28% of the body weight per day for females and males, respectively.

Discussion

Spawning time

The estimated time of spawning for yellowfin tuna at Clipperton Atoll was between 2230 and 0330 h. This is similar to the spawning time of 2100 to 2400 h by a group of 3- and 6-year-old yellowfin tuna reported by Masuma et al. (1993). The spawning of yellowfin tuna at night was reported earlier by Harada et al. (1980) on the basis of running-ripe and fully hydrated oocytes. Based on oocyte developmental stages and new postovulatory follicles, the assumption was made that yellowfin tuna spawn after 2200 h in the Coral Sea (McPherson, 1991) and bigeye tuna from about 1900 to 2400 h off Java and southwest of Hawaii (Nikaido et al., 1991). Captive skipjack tuna typically spawn at 2400 h, which appears to be close to the time of natural spawning on the basis of histological examinations of skipjack ovaries (Hunter et al., 1986). Although there are some reported observations of courting behavior in scombrids during daylight hours (Iverson et al., 1970), they are primarily anecdotal and appear to be exceptions to the normal behavior of night spawning. Nocturnal spawning also appears to be a common pattern among clupeoids (Blaxter and Hunter, 1982), coral reef species that have pelagic larvae (Helfman, 1986), and other groups of fishes (Ferraro, 1980). Spawning at night may be an adaptation to minimize predation by planktivores or damage by ultraviolet light, or both.

Spawning frequency

The 1986 and 1987 yellowfin tuna samples from Clipperton Atoll indicated that the average interval between spawnings was 1.27 d. Based on the frequency of ovaries containing postovulatory follicles of known age, the average interval between spawnings was 1.18 d for skipjack tuna from the South Pacific (Hunter et al., 1986), 1.54 d for yellowfin tuna in the Coral Sea (McPherson, 1991), and 1.11 d for bigeye tuna off Java and southwest of Hawaii (Nikaido et al., 1991). Spawning occurred during 127 of 155 days for a group of 3- and 6-year-old yellowfin held in a sea pen, but the spawning frequency of individuals was not determined (Masuma et al., 1993). This implies that reproductively active yellowfin tuna, as well as skipjack and bigeye tunas, in tropical waters, spawn almost daily. This high frequency of spawning implies that in a reproductively active female there is continuous maturation of oocytes, which are recruited from the reservoir of primary oocytes. Deviations from the apparently normal daily spawning pattern could be related to recent feeding success (Wootton, 1990) or physiologi-

cal stress, as shown for captive skipjack tuna (Hunter et al., 1986).

The yellowfin tuna postovulatory follicle is similar to that described for most other marine fishes. The rate of postovulatory follicle degeneration in yellowfin tuna, however, is more rapid than that for fish inhabiting cooler waters. The degeneration process of the postovulatory follicle, along with the oocyte developmental rate, is apparently correlated with temperature. Clarke (1987) showed that the Hawaiian anchovy (*Encrasicholina purpurea*) spawns at intervals of about 2 d, as compared with about 7 d for northern anchovy (*Engraulis mordax*) (Hunter and Goldberg, 1980) and about 6 d for the Peruvian anchovy (*Engraulis ringens*) (Alheit et al., 1984), both cooler-water species. The postovulatory follicle can be detected in the northern anchovy for just under 48 hours (Hunter and Goldberg, 1980), whereas for yellowfin and Hawaiian anchovy that period is no more than 24 hours.

This paper provides a method for direct estimation of the frequency of spawning of males by histological examination of testicular tissues. Structural characteristics of the vas deferens, specifically the amount of sperm present, the shape of the duct, and the staining of the epithelium are useful for detecting whether a male yellowfin tuna has recently spawned. Specific cellular characteristics have not been utilized in the separation of the testis into prespawning and postspawning groups. Although positive identification of cell types along with nuclear and cytoplasmic features may be of additional value in detection of reproductive activity, this would have required an ultrastructural investigation of cell types, which was beyond the scope of the present investigation. The main limitation to the technique is that spawning cannot be detected more than 12 h after it occurs. Because yellowfin tuna are normally captured during daylight hours in the purse-seine fishery in the eastern Pacific, spawning-frequency estimates from males could be determined only for fish caught during the relatively short time between about 0600 and 1200 h. Spawning-frequency estimates for yellowfin tuna from throughout the eastern Pacific are thus better estimated from the presence of postovulatory follicles that are detectable in ovaries from fish captured throughout the entire day, with the assumption that the males spawn at similar times.

Batch fecundity

There is only a short period from the late afternoon until about 2200 h (previous to spawning) when ovaries with migratory-nucleus or hydrated oocytes are found in yellowfin tuna. McPherson (1991) reported hydrated oocytes from yellowfin tuna collected between 1200 h and 2000 h in Australian waters, and Hunter et al. (1986) reported the presence of migratory-nucleus oocytes from skipjack tuna collected at 1955 h in the South Pacific. The use of migratory-nucleus or hydrated oocytes for batch-fecundity determinations is crucial because only oocytes in these stages can be distinguished from the less-developed subsequent batch of oocytes.

The estimate of mean relative fecundity for yellowfin tuna obtained from this study (68.0 oocytes per gram of body weight) is considerably less than that of Joseph (1963) (106 oocytes per gram of body weight). Analysis of covariance applied to the log-transformed batch fecundity and length data from the present study and the truncated data set from Joseph (1963) indicated a significant difference in the test for equality of slopes ($F_{0.05(1,65)}$=10.74, P<0.005). Furthermore, the adjusted mean batch fecundity of 1,461,465 oocytes for the data from the present study is less than the adjusted mean batch fecundity of 2,454,049 oocytes from the data set of Joseph (1963). The differences in these estimates are probably due to the methods used, rather than to spatial or temporal variation. The biases associated with the method used by Joseph created an overestimate of the number of oocytes in the spawning batch. The batch fecundities for numerous species of fish have been shown to vary geographically and temporally. This may be a function of inter- and intra-population variation influenced by both genetic and environmental components (Wootton, 1979).

Cost of spawning

The best estimates of the average daily cost of spawning in yellowfin tuna are 0.97% and 0.28% of the body weight per day in females and males, respectively. Although the two methods employed for estimating the costs of spawning for females are both appropriate and produce close estimates, the method based on oocyte weight and relative fecundity is more precise.

An estimate of total daily energy costs for reproductively active yellowfin tuna can be obtained from a bioenergetics approach. Olson and Boggs (1986) estimated a mean daily ration of 5.2% body weight from a bioenergetics model incorporating energy expenditures for swimming, standard metabolism, growth, excretion, egestion, and food assimilation. The estimated mean energy expenditure for growth was about 0.41% of body weight per day. If the estimated daily costs of spawning for females and males of 0.97% and 0.28% of the body weight per day are added to the overall bioenergetics estimate, daily

ration estimates of about 6.2% and 5.5% of body weight for females and males, respectively, is obtained for total energy expenditures.

There are two implicit assumptions in these calculations of reproductive costs: 1) the energy content of oocytes and milt is equivalent on a weight basis and 2) dry-weight–wet-weight relationships are similar for somatic and gonadal tissues. Furthermore, these estimates should be considered conservative because there are other physiological and behavioral costs associated with spawning that are not included in these calculations.

For skipjack tuna, Hunter et al. (1986), estimated the cost of a single spawning to be about 2% of the body weight. Based on an estimated spawning frequency of 1.18 days, the daily cost of spawning a single batch of eggs would be 1.7% of body weight per day. However, reproductive costs were probably overestimated because a value of 100 eggs per gram of body weight (Matsumoto et al., 1984) was used. This relative fecundity estimate was not based upon counts of hydrated oocytes. In addition, the calculation included the weight of a spawned egg, rather than the weight of a late-migratory–nucleus-stage oocyte immediately before hydration. An estimate of the cost of a single spawning in black skipjack tuna (Schaefer, 1987) was reported to be 1.77% of the body weight. Based on an estimated spawning frequency of 2.1 to 5.7 days, the daily cost of spawning a single batch of eggs would be 0.31 to 0.84% of body weight per day. These estimates may also be biased because of the inherent problems in an estimation of spawning frequency by the occurrence of fish with hydrated ovaries versus by the postovulatory follicle method (Hunter and Macewicz, 1985).

Estimates of the average daily cost of spawning for female and male yellowfin tuna from the present study appear to be reasonable in terms of energy allocation. The annual investment of energy in reproduction as a proportion of total energy is estimated to be about 16% for females and 5% for males. These values are within the range of those reported for other fishes (Wootton, 1990). Given that yellowfin tuna probably spawn year round in the tropical regions of the eastern Pacific Ocean (Orange, 1961) and that the mean interval between spawnings is around 1.2 days, a female (90 to 100 cm FL) would spawn the equivalent of about 3.5 times its body weight per year, whereas a male (90 to 100 cm FL) would spawn about the equivalent of its body weight per year. For a female, this is almost 2.5 times the energy allocated for somatic growth, whereas for a male it is only about 0.75 times (Olson and Boggs, 1986).

These preliminary results provide the necessary histological criteria for further assessment of the spawning dynamics of yellowfin tuna. Previous batch-fecundity estimates for yellowfin tuna and other scombrids not based on counts of migratory-nucleus or hydrated oocytes are probably overestimates. A more comprehensive investigation of the reproductive biology of yellowfin in the eastern Pacific (Bayliff, 1991) will provide size-specific estimates of batch fecundity and spawning frequency.

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Comparison of submersible-survey and hydroacoustic-survey estimates of fish density on a rocky bank

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Abstract.—Submersible belt-transect surveys along a rocky bottom were combined with acoustic surveys of the water column to estimate depth distribution and density of fishes at Stonewall Bank, Oregon, in the northeastern Pacific Ocean from September through October 1991. The objectives of the study were to determine the proportion of fish in the water column that were not detected by submersible survey techniques and to compare estimates of fish density near the bottom from submersible surveys with density estimates from hydroacoustic surveys. More than 75% of the fishes recorded on acoustic surveys resided in the bottom third of the water column. Rockfishes (family Scorpaenidae) were the predominate fish taxa observed in the study area. Estimates of fish density from submersible surveys were more than six times greater than estimates of fish density near the bottom from hydroacoustic surveys. Submersible and acoustic surveys provided different, but complementary, information regarding the use of rocky banks by fish. Submersible surveys provided estimates of fish density near the bottom and provided valuable ground-truth for acoustic equipment. Hydroacoustic surveys provided estimates of fish density in the portions of the water column not observed on submersible transects and provided additional information on the vertical and horizontal distribution of fishes. The combined use of submersible and acoustic sampling techniques provided a better understanding of how fish use rocky banks than did either technique alone.

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Large aggregations of fishes are associated with rocky banks along the Pacific coast of North America. Many of these banks are located along the edge of the continental shelf and provide important habitat for commercially and recreationally valuable species (Carlson and Straty, 1981; Nagtegaal, 1983; Pearcy et al., 1989). Fishes harvested from the rocky banks are often associated with bottom habitats, especially fishes in the family Scorpaenidae (rockfishes and their relatives).

Assessment of the distribution and relative abundance of these bottom dwelling fishes is difficult because of the limitations of existing field-sampling techniques. Bottom trawls have been used to assess fishery resources over the continental shelf and along the edge of some offshore rocky banks since the 1970's (Gunderson and Sample, 1980; Leaman and Nagtegaal, 1982; Dark et al., 1983; Weinberg et al., 1984), but rugged topography has precluded the use of trawls for assessing fishes on the tops of the banks. Trawls are also a poor tool for sampling rocky areas (Carlson and Straty, 1981; Butler et al., 1991). A few researchers have successfully sampled rocky areas using

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gill nets but have detected large biases in species and size composition of the catches (Matthews and Richards, 1991).

Acoustic surveys have proven useful in estimating distribution and abundance of many species of fishes in mid-water (e.g. see Karp, 1990), but the techniques require some method of validation (Johannesson and Mitson, 1983). Recently, there has been an interest in developing acoustic methods to survey fishes in rocky areas (Leaman et al., 1990; Richards et al., 1991; Kieser et al., 1993; Phillips, 1994). Assessing fish near the bottom, however, is difficult with acoustic techniques (Mitson, 1983), particularly over rocky habitats. Most echo integrators have difficulty distinguishing between targets near the bottom and bottom echoes in high-relief terrain (Burczynski, 1979). The acoustic shadowing that occurs in high-relief terrain also presents difficulties for echo integrator signal processors. Fishes in the acoustic lee of a rock are often not echo integrated.

In the late 1980's, several investigators began using submersibles to assess fishes inhabiting rocky banks in the northeastern Pacific Ocean (Richards, 1986; Pearcy et al., 1989; Stein et al., 1992; Krieger, 1993; O'Connell and Carlile, 1993; Murie et al., 1994). With the exception of Krieger (1993), these studies were designed to provide information only on fishes closely associated with the bottom. These submersible surveys were successful in assessing fishes associated with bottom habitats but missed an unknown number of fishes swimming above the bottom. For example, Pearcy et al. (1989) noted large schools of fish in the water column that were near the bottom but not counted by the submersible observers.

In this study, we combined submersible and hydroacoustic techniques to estimate more accurately the distribution and relative abundance of fishes on a rocky bank off Oregon. Our objectives were to determine the proportion of fishes in the water column that were not detected with submersibles and to compare estimates of fish density near the bottom from submersible surveys with density estimates generated for the same region from hydroacoustic surveys.

Methods

From 24 September to 3 October 1991, we surveyed fish assemblages on Stonewall Bank, a large (200 km^2), relatively flat, rocky bank located about 22 km southwest of Newport, Oregon (Fig. 1). Stonewall Bank ranges in depth from 41 m to over 75 m and comprises a gently sloping rock bottom with dissected ridges of siltstone and mudstone. We used the research submersible *Delta* to survey fixed stations on the top and side of Stonewall Bank. At three stations, both submersible and acoustic surveys were conducted (Fig. 1).

Submersible surveys

We completed three submersible transects at each of three survey stations. In addition to the nine transect dives, we completed three bounce dives to evaluate large schools in the water column that were detected acoustically. On the bounce dives, the submersible was launched and directed into schools in the middle of the water column. Observers estimated species and size composition of schooling fishes.

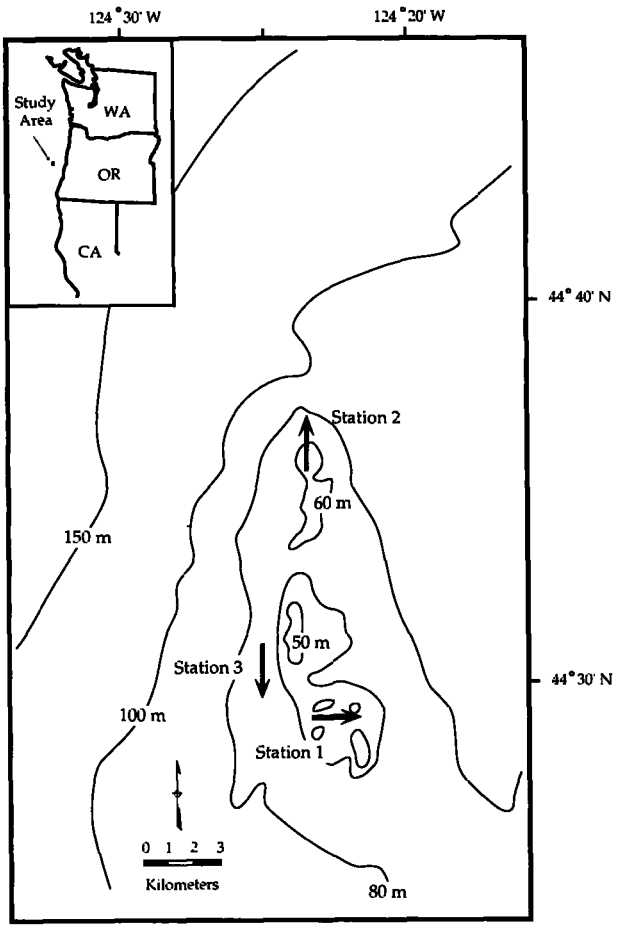

Figure 1

Location of Stonewall Bank off Newport, Oregon, where acoustic and submersible surveys were conducted from September through October, 1991. Arrows indicate the length and direction of transects.

Submersible belt transects followed techniques used in SCUBA surveys (Brock, 1954; Brock, 1982; Ebeling, 1982; Sale and Sharp, 1983; Davis and Anderson, 1989) and in our previous submersible surveys (Pearcy et al., 1989; Stein et al. 1992; Hixon et al.[1]). Each transect consisted of two 30-minute segments, separated by a 10-minute rest period. The submersible started from a preselected location and traveled on a preselected course. Course headings were chosen to keep transects at a uniform depth.

During the transect, the pilot attempted to maintain a constant speed of 3 km·hr^{-1} and a constant altitude of 2 m above the bottom. Actual speed and altitude varied because of the difficulties of piloting the submersible over rough terrain. However, in no case did the submersible observer count fish that were more than 4 m off the bottom. To plot the actual submersible path, the support ship RV *Pirateer* was periodically positioned directly over the submersible by using a Trackpoint II system, and latitude and longitude were recorded with a global positioning system (GPS) receiver.

Submersible observation techniques followed those of Pearcy et al. (1989) and Stein et al. (1992) and are more fully described by Hixon and Tissot.[2] Observers looked forward and downward through a viewing port in the bow of the DSV *Delta* to identify fishes. In addition to identifying fish to species when possible, the observer counted and estimated the sizes of all fish observed to the nearest decimeter. We estimated fish density by dividing the number of fish counted by the area visually surveyed. The area visually surveyed was calculated by multiplying the length of the transect by the width of the average field of view (2.3 m) along the transect.

Acoustic surveys

A total of 14 hours of echo integration and dual-beam target strength data were collected before, during, and after submersible surveys. Acoustic data collected during submersible transects were not usable because of interference from the submersible. Acoustic equipment used in this study included a 120-kHz dual-beam ceramic transducer with nominal beam widths of 10 and 22 degrees deployed in a towed body, a BioSonics Model 101 echosounder with dual 20 log R and 40 log R time-varied-gain receiver board, a Sony digital tape recorder and interface, and a microcomputer used as a signal processor. The microcomputer integrated signals in real time and stored integration values in five-second intervals. Latitude and longitude data obtained from the ship's GPS were automatically written into echo integration files. Dual-beam target strength data were taped concurrently for processing later.

In situ dual-beam methods provide measurements of target strength in the natural environment (Ehrenberg and Lytle, 1977) but can be problematic in surveys of schooling fishes because they require resolution of individual organisms. An alternative method of estimating target strength is to use the mathematical relationship empirically derived by Love (1971, 1977) to relate fish length and intensity of echoes from the dorsal surface of a fish. The relationship, expressed in terms of acoustic frequency, is

$$TS = 19.1 \log (L) - 0.9 \log (f) - 62.0,$$

where TS = target strength in decibels (dB); L = fish length (cm); and f = frequency (kHz).

To avoid the problems associated with dual-beam methods caused by schooling fishes, we chose to use the mean length of fish observed (Love's equation) to scale echo integrator output. Although Love's equation provided the primary method for scaling echo integrator output, we also generated target strength estimates using dual-beam data. We compared target strength estimates obtained from Love's equation (Love, 1971) with those generated by dual-beam acoustic methods by converting the dual-beam estimates of target strength from logarithmic units (decibels) to linear units, using the equation $TS = 10 \log (\sigma)$, where TS = target strength and σ = backscattering cross section, a linear measure of the reflective nature of a target.

Ship speed on transects ranged from 0.5 to 3 m·sec^{-1}; thus integration sequences covered about 3–15 m of linear bottom. In the vertical dimension, we summed echoes in 2-m depth bins from the surface to the bottom. Acoustic surveys provided both areal (fish·m^{-2} over water column sampled) and volumetric (fish·m^{-3}) estimates of fish density.

To compare the submersible and acoustic surveys, we divided the acoustic data into two strata. In one stratum, we summarized the echo integration data collected from the surface to 4 m above the bottom. These data represent fish that were above the area that the submersible surveyed ("above sub" stratum).

[1] Hixon, M. A., B. N. Tissot, and W. G. Pearcy. 1991. Fish assemblages of rocky banks of the Pacific Northwest [Heceta, Coquille, and Daisy Bank]. A final report by the Department of Zoology and College of Oceanography of Oregon State University for the U.S. Department of the Interior, Minerals Management Service Pacific OCS Office, Camarillo, CA.

[2] Hixon, M. A., and B. N. Tissot. 1992. Fish assemblages of rocky banks of the Pacific Northwest [Stonewall Bank]. A final report supplement by the Department of Zoology of Oregon State University for the U.S. Department of the Interior, Minerals Management Service Pacific OCS Office, Camarillo, CA.

As a second stratum, we summarized the acoustic information collected from 4 m above the bottom down to the bottom. These data represent acoustic information collected for the same area that was surveyed by the submersible ("below sub" stratum).

Navigation

The support ship crew navigated using GPS instrumentation with an expected positional accuracy within 100 m (Hurn, 1989). At two stations, submersible observers and pilots saw the same object on subsequent dives. In each case, the object was within a few meters of the intended path of the submersible. Although these observations provided evidence that the navigational precision of the support vessel was better than 100 m, we did not expect the submersible to duplicate the path of a previous dive. Similarly, GPS variation, and wind and sea conditions prevented the support ship from duplicating an acoustic transect. Thus, the acoustic and submersible transects did not cover identical segments of the bottom. Instead, each survey provided three estimates of fish density in a rectangle that was approximately 300 m wide by 2,500 m long (Fig. 2).

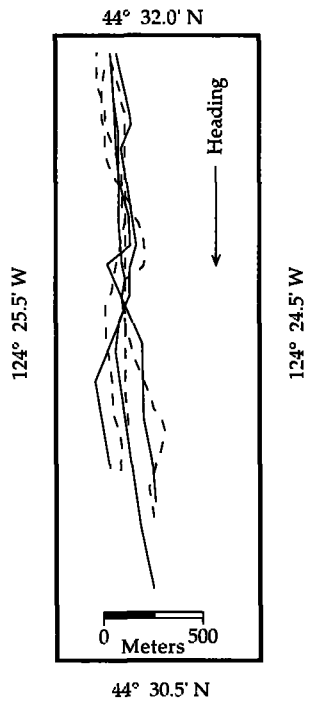

Figure 2

Example of multiple submersible and acoustic transects that occurred at station 3 from September through October 1991, off Newport, Oregon. At this station, submersible and acoustic transects sampled an area 100 m wide by 2,500 m long. Dashed lines indicate acoustic transects. Solid lines represent submersible transects.

Results

Fish species observed

On submersible transects, observers counted a total of 1,928 fish from 28 taxa. Rockfish species accounted for 15 of the taxa observed and 89% of all fishes counted (Table 1). Mean length of fishes observed on submersible transects ranged from 19.3 to 21.0 cm (Table 2). On bounce dives into large schools in the water column, submersible observers saw mixtures of three species: blue (*Sebastes mystinus*), yellowtail (*S. flavidus*), and widow (*S. entomelas*) rockfish. Schools in the middle of the water column all contained large (> 30 cm) adult rockfishes.

Rockfishes observed from the submersible fell into three strata with respect to location in the water column: there were fishes touching the bottom, fishes swimming a short distance (1 m) off the bottom, and fishes schooling well off the bottom. Species such as rosethorn rockfish, *S. helvomaculatus*, were more frequently observed on the bottom or in crevices; species such as redstripe rockfish, *S. proriger*, were more frequently observed swimming singly or in small groups about 1 m off the bottom; and species such as blue and yellowtail rockfish were more commonly observed in small or large schools that extended upward from 1 m off the bottom to past the limit of visibility. Juvenile rockfish of unknown species occasionally occurred in very large schools 1 m or more above the bottom.

Fish density

Estimates of areal density generated by submersible surveys ranged from 76.2 fish·ha^{-1} to 1,101.7 fish·ha^{-1}. Estimates obtained from acoustic surveys of the entire water column ranged from 3.4 fish·ha^{-1} to 5,716.6 fish·ha^{-1} (Table 3). We observed no significant difference in mean fish density between acoustic surveys conducted before and after submersible transects (Wilcoxon paired sample test, n=8, z= –0.14, P=0.89). Mean densities estimated from submersible and acoustic surveys exhibited a significant positive correlation (Kendall Rank Correlation, n =9, τ=0.72, z=2.71, P=0.007).

Table 1

Number of fishes in the ten most abundant taxa observed on submersible dives at Stonewall Bank, Oregon, from September through October 1991.

Scientific name	Common name	Station 1	Station 2	Station 3	Total	Percent	Cumulative percent
Sebastes spp. (juv.)	Rockfish juveniles	103	617	214	934	48.4	48.4
Sebastes mystinus	Blue rockfish	31	0	159	190	9.9	58.3
Sebastes flavidus	Yellowtail rockfish	26	97	64	187	9.7	68.0
Sebastes proriger	Redstripe rockfish	15	56	81	152	7.9	75.9
Sebastes helvomaculatus	Rosethorn rockfish	7	60	59	126	6.5	82.4
Hexagrammos decagrammus	Kelp greenling	15	17	27	59	3.1	85.5
Sebastes pinniger	Canary rockfish	40	2	16	58	3.0	88.5
Sebastes ruberrimus	Yelloweye rockfish	3	21	15	39	2.0	90.5
Rathbunella spp.	Ronquil spp.	1	9	19	29	1.5	92.0
Sebastes entomelas	Widow rockfish	0	0	27	27	1.4	93.4

Table 2

Mean length (cm) of fishes observed from the submersible (sub), target strength (TS in dB) calculated from mean length of observed fishes, and target strengths acoustically measured at Stonewall Bank, Oregon, from September through October 1991.

Station	No. fish observed (sub)	Mean length (cm)	Mean TS[1] (dB)	No. dual-beam targets	Dual-beam TS (dB)	Mean length[2] (cm)
1	280	19.3	–39.4	40	–39.1	19.9
2	902	18.3[3]	–39.8[4]	1224	–36.7	26.6
3	747	21.0	–38.6	1794	–38.7	20.8

[1] Estimated by using Love's equation (Love, 1971).
[2] Calculated by inserting dual-beam TS into Love's equation (Love, 1971).
[3] Mean length of fish estimated from the submersible at station 2 is 11.8 cm if juvenile rockfish from dive 2604 are included in the analysis.
[4] TS equals –43.4 dB if juvenile rockfish from dive 2604 are included in the analysis.

Fish densities estimated acoustically in the "above sub" stratum were on average 15.6 times higher than those in the "below sub" stratum (Table 3). However, submersible surveys indicated that fish density near the bottom was greater than that indicated by acoustic measurements. For the stratum near the bottom, submersible estimates of areal fish density were significantly greater than acoustic estimates of fish density (Wilcoxon paired sample test, n=9, z=–2.67, P=0.008). Fish density estimated from submersible operations was higher in each case than corresponding acoustic estimates (Fig. 3); fish density estimated from submersible transects averaged 6.7 times higher than acoustic density estimates (Table 3).

Fish distribution

At all three stations on Stonewall Bank, more than 75% of the fishes insonified on acoustic surveys were located in the lower third of the water column (Fig. 4). There was no significant difference in depth distribution of fishes between stations (Kruskal Wallis test, df=2, h=0.089, P=0.96). Station 1 was located on the top of Stonewall Bank. The bottom at station 1 was relatively flat bedrock in primarily 50–55 m of water; it contained low relief and few fish. Submersible and acoustic surveys at station 1 exhibited the lowest estimate of fish density generated from the cruise (Table 3). Schools were sparsely distributed (Fig. 5), averaged 11.1 m (SE=1.6) wide, and had a mean vertical thickness of 2.6 m (SE=0.1). Of the fish observed acoustically, 78% were located in the bottom third of the water column (Fig. 4).

Station 2 was located near the north edge of Stonewall Bank, primarily in 60–70 m of water. The bottom at station 2 contained smooth ridges of rock, with occasional scarps 2–3 m high. Submersible observers at station 2 saw few fish, except for occasional

Table 3

Estimates of fish density obtained from acoustic and submersible (sub) surveys of Stonewall Bank, Oregon, from September through October 1991.

	Submersible transects			Acoustic transects	
Station	Max. depth (m)	Density (fish/ha)	Total (fish/ha)	Above sub (fish/ha)	Below sub (fish/ha)
	56	134.0	264.6	227.3	37.3
1	55	76.2	3.4	2.4	1.0
	56	344.3	96.2	55.0	41.2
	69	118.3	32.2	28.7	3.5
2	76	353.9	26.5	15.6	10.9
	73	1101.7	5716.6	5573.5	143.1
	65	418.6	312.9	278.7	34.2
3	59	525.5	1142.1	967.5	174.6
	65	454.1	644.4	563.3	81.1
	Mean	391.9	915.4	856.9	58.5
	Mean[1]	303.1	315.3	267.3	48.0

[1] Mean density without dive 2604 (see text for details).

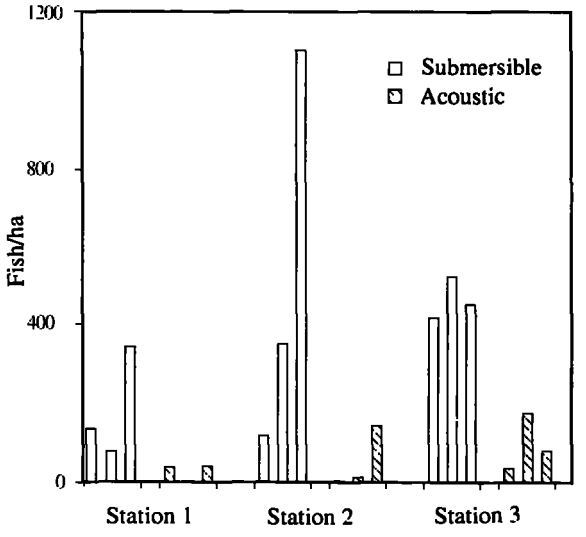

Figure 3

Comparison of submersible estimates of fish density near the bottom with acoustic estimates of fish density from 4 m above the bottom to the bottom for surveys conducted from September through October 1991, off Newport, Oregon.

very large schools of juvenile rockfish. The large schools of juvenile rockfish observed at station 2 created an anomalously high density estimate derived from one submersible transect (Table 3). Similarly, acoustic surveys showed few fish, except for occasional large schools that were situated near the bottom (Fig. 5). Schools were on average 32.2 m (SE=1.8) wide, and had an average vertical thickness of 3.8 m (SE=0.2). Of the fish observed acoustically, 93% were located in the bottom third of the water column (Fig. 4).

Station 3 was located near the west edge of Stonewall Bank in primarily 50–60 m of water. The bottom at station 3 contained more vertical relief than other stations. It comprised numerous rock ridges with 3–4 m high scarps. Submersible observers saw small schools of unidentified juvenile rockfish, and large schools of blue rockfish, yellowtail rockfish, canary rockfish (*Sebastes pinniger*), and widow rockfish. Acoustic transects also recorded more fish at station 3 than at other stations. Schools were on average 34.5 m (SE=1.1) wide, and had an average thickness of 4.1 m (SE=0.2) (Fig. 5). Of the fish observed acoustically, 79% were located in the bottom third of the water column (Fig. 4).

Target strength estimates

Target strength estimated from Love's equation ranged from –38.6 to –43.4 decibels (dB) (Table 2). Target strength estimated from dual-beam analysis ranged from –36.7 to –39.1 dB. Back-scattering cross section estimated from dual-beam analysis were 1.1 and 1.0 times, respectively, that estimated from Love's equation at stations 1 and 3 (Table 4). At station 2, dual-beam methods provided a back-scattering cross section that was 4.8 times higher than the back-scattering cross section estimated from Love's equation.

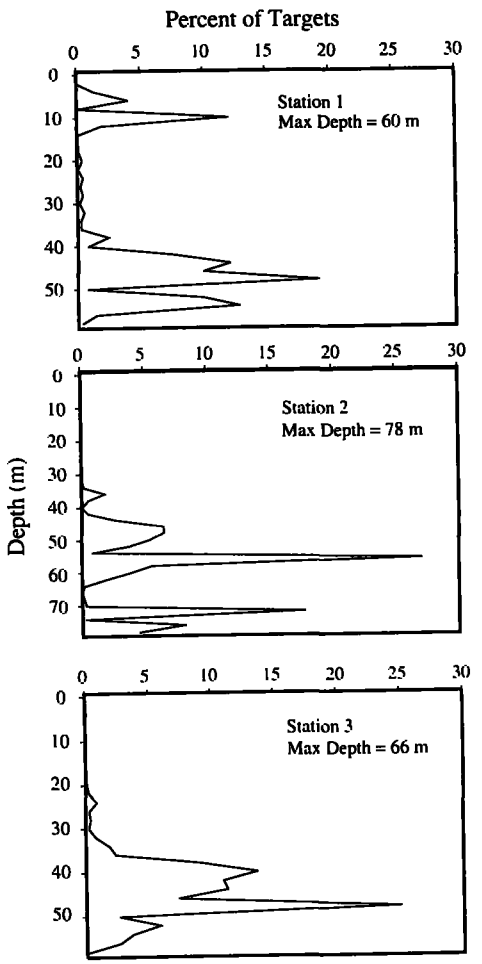

Figure 4

Vertical distribution of fishes insonified at stations 1–3 during acoustic surveys conducted from September through October 1991, off Newport, Oregon.

Table 4

Comparison of backscattering cross section (σ) from dual-beam estimates (DB σ) and from Love's equation (Sub σ). Target strength (TS) was converted to backscattering cross section (σ) by using the equation $TS = 10 \text{ Log } \sigma$.

Station	DB σ	Sub σ	DB σ/Sub σ
1	0.000123	0.000116	1.06 (0.65)[1]
2	0.000214	0.000045	4.76 (2.04)[1]
3	0.000135	0.000138	0.98 (0.56)[1]

[1] Ratio of DB σ/Sub σ using mean lengths of nonschooling fishes only (see text for details).

Discussion

Comparison of submersible and acoustic surveys

On the basis of our previous submersible surveys of rocky banks off Oregon and anecdotal information from sport and commercial fishers, we expected to observe demersal rockfishes from the submersible and to insonify large schools of rockfishes in the water column well above the rocky substrate of Stonewall Bank. Data collected from submersible transects and bounce dives did indicate that rockfishes were the predominate fish taxa inhabiting Stonewall Bank at the time of the surveys. However, most schools appeared to be associated with bottom features and were not isolated in the middle of the water column. Most large schools of fishes extended from the bottom upward for as much as 20 m into the water column, and submersible observers were able to view the lower portions of these schools.

The extension of rockfish schools from the bottom upwards into the water column has been reported from other submersible surveys. Krieger (1993) visually surveyed an area from 0 to 10 m above the bottom and noted that Pacific ocean perch, *Sebastes alutus,* ranged from 0 to 7 m above the bottom. He observed that small groups of rockfishes were close to the bottom, whereas larger groups were higher off the bottom. Krieger observed no rockfish schools higher in the water column than 7 m above the bottom. Researchers in Alaska (O'Connell and Carlile, 1993), British Columbia (Murie et al., 1994), Oregon (Pearcy et al., 1989; Stein et al., 1992), and California (Yoklavich et al., 1995) also observed schools of semipelagic rockfishes above high-relief bottom features.

"Plumes" of rockfish rising above pinnacles are readily apparent on echograms from our acoustic surveys (Fig. 5). Wilkins (1986) described this characteristic shape for widow rockfish schools as tall, narrow columns rising over an irregular bottom. Richards et al. (1991) developed techniques to estimate species composition of rockfishes in the plume from the patterns of acoustic signals. They suggested that computer processing of acoustic signals could lead to a remotely operated technique for species identification of schooling rockfishes. Acoustic identification of rockfish species would improve acoustic surveys and seems possible, given the characteristic acoustic shape of rockfish schools. However, single species aggregations were atypical in our study. Species discrimination based on acoustic pattern recognition would have been difficult, although we were able acoustically to identify aggregations of mixed

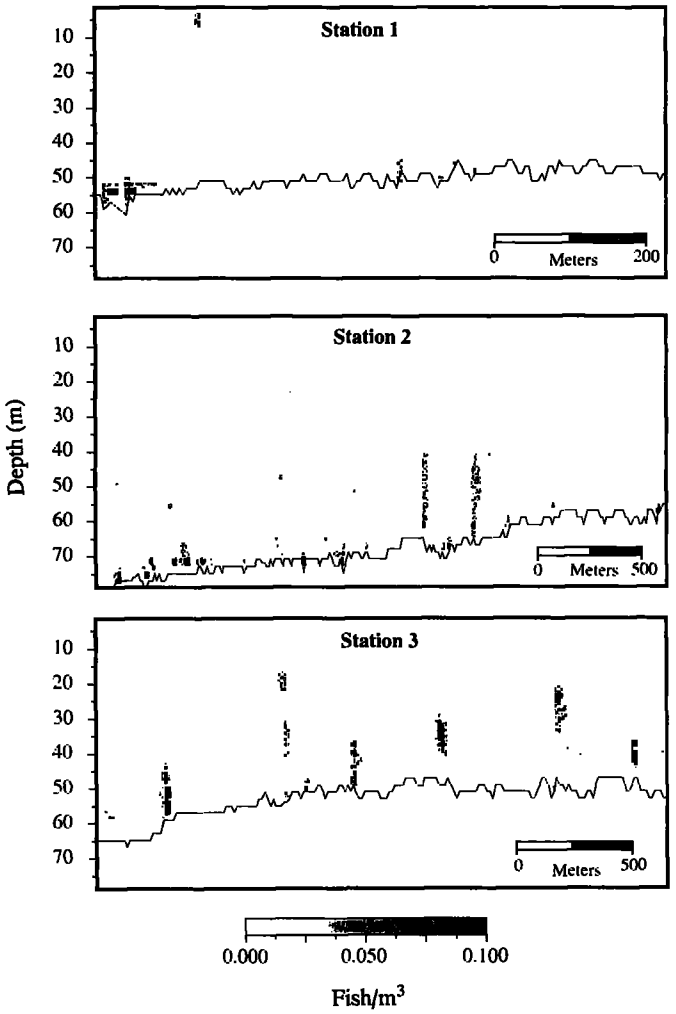

Figure 5

Examples of the density and distribution of fish schools recorded by sonar at stations 1–3 during acoustic surveys conducted from September through October 1991, off Newport, Oregon. Bottom depth is depicted by the solid line and fish densities are indicated by shaded areas.

species of rockfishes. Submersible observations contributed greatly to the acoustic surveys because species composition of large schools could be characterized once they had been located acoustically.

Acoustic surveys enabled us to quantify the vertical distribution of fishes and to determine the proportion of fishes not detected by the submersible surveys. Although several researchers have noticed an avoidance of survey vessels by mid-water fishes (e.g. Olsen et al., 1983; Misund, 1990; Ona and Godø, 1990), we observed no difference between acoustic surveys conducted before and after submersible transects. The affinity that most rockfishes have for bottom features may make them less likely to actively avoid a vessel passing overhead. At all stations, fishes recorded by acoustic equipment were located primarily in the lower third of the water column, often above rock scarps or pinnacles. This pattern occurred in all acoustic transects and is similar to observations of fish density increasing with depth for both shallow and deep water rockfishes (Hallacher and Roberts, 1985; Leaman et al., 1990; Love et al., 1991; Richards et al., 1991; Sullivan, 1991).

The acoustic estimate of mean areal density in the "above sub" stratum was 2.3 times greater than the mean submersible estimate of fish density. Submersible surveys, therefore, accounted for almost one-third of the fishes inhabiting Stonewall Bank during the time of the study. However, the mean density estimates of both submersible and acoustic surveys were each greatly affected by one transect. Submersible and "above sub" acoustic estimates of fish density were more similar when two transects that skewed the mean were removed from analysis (Table 3). On dive 2604 at station 2, the submersible observer recorded several large schools of juvenile rockfishes. Similarly, large, patchy schools were detected on the accompanying acoustic transect. We assumed that the high fish densities associated with these transects were due to the presence of schools of juvenile rockfishes. After removing these data from the analysis, density estimates from the submersible transects were 14% higher than those generated acoustically for the "above sub" stratum, suggesting that the relative abundance of adult rockfishes was approximately equal above and below the level of the submersible.

The estimates of fish density generated from submersible transects were more than six times those from acoustic surveys for the same depth stratum. This difference reflects the inherent limitations of acoustic sampling in rocky, high-relief locations and demonstrates the influence of sampling method on survey results. Pearcy et al. (1989) and Stein et al. (1992) observed rockfish species over a variety of benthic habitats ranging from smooth mud to high-relief rock and also reported schools of rockfishes in the water column. Given the variety of habitats in which rockfishes are located, it appears that several sampling tools are needed to assess their relative abundance.

Trawls have historically been used to assess fish abundance over smooth bottoms. Weinberg (1994),

however, documented high variability in trawl survey estimates of rockfish abundance and implied that trawl surveys may not adequately estimate rockfish abundance. Krieger (1993) compared trawl and submersible estimates of rockfish abundance on flat bottoms and came to the same conclusion. He suggested that on flat terrain, trawl surveys overestimate rockfish abundance because bridles and otter doors herd rockfish into a trawl and bias density estimates. Adams et al. (1995) found remotely operated vehicle (ROV) surveys to be better than trawl surveys for benthic species on flat bottoms. They reported that ROV estimates of fish density were higher and had lower coefficients of variation than did trawl estimates. For rockfishes swimming off the bottom, however, the reverse was true. Trawls yielded better estimates of rockfish density and densities of other species with patchy distributions and off-bottom behavior. Despite the improvement in estimates, Adams et al. (1995) suggested that neither ROV nor trawl methods adequately assessed off-bottom rockfishes. Both Krieger (1993) and Adams et al. (1995) acknowledged that trawls are poor tools for assessing rockfishes on high-relief terrain. Kulbicki and Wantiez (1990) compared trawl surveys with diver observations and determined that trawl surveys and direct observations each have biases that are dependent upon habitat usage by different fishes. In their study, species size, shape, coloration, and swimming habits greatly influenced the ratio of diver to trawl density estimate. Thus, a combination of survey methodologies is probably needed to estimate adequately the abundance of many fish species. A similar conclusion was reached by Uzmann et al. (1977) in comparing submersible, camera sled, and otter trawl techniques.

Acoustic target strength analysis

The target strength of a fish is dependent upon a variety of factors, including the size of the fish, its orientation to the acoustic signal, and its swimbladder characteristics (Ehrenberg and Lytle, 1977). Of particular importance is the orientation of the fish to the acoustic signal. Small changes in the tilt angle of a fish caused by differences in fish behavior can cause large changes in target strength. Traynor and Williamson (1983), for example, estimated a 3-dB difference in target strength of fishes due to day-night differences in behavior. Dual-beam echo processing methods can resolve many of the problems associated with differences in fish orientation (Traynor and Williamson, 1983) but require the resolution of individual targets. Dual-beam methods cannot estimate target strength in the case of overlapping echoes, such as those produced by schooling fish.

We chose to use the mean length of fish observed (Love's equation) instead of dual-beam methods to scale echo integrator output for two reasons. First, the number of individual, nonoverlapping targets needed for dual-beam analysis was relatively small in several of the acoustic transects (Table 2). Second, Traynor et al. (1990) suggested that target strength estimates of schooling fish may not accurately reflect the actual size of fish insonified because the equipment measures fish on the periphery of the schools. Fish on the periphery of schools may not be the same size as fish in the center of the school or may be exhibiting different behavior (orientation).

Although Love's equation was the primary means of scaling echo integrator data, we calculated dual-beam target strength as well. Target strength estimated from Love's equation included schooling fish. Dual-beam analysis, however, included only nonoverlapping echoes, i.e. those fish not in a school. At stations with few schools, the back-scattering cross sections obtained from dual-beam analysis were almost identical to the back-scattering cross sections derived from the mean length of observed fishes (Table 4). At station 2, where large schools of juvenile rockfishes occurred, the back-scattering cross section estimated from dual-beam methods was 4.8 times higher than estimates from Love's equation. When the mean length of only nonschooling fishes was used in Love's equation at station 2, the dual-beam estimate and Love's equation estimate of target strength were more similar.

In this study, a combination of two survey methods provided a better estimate of the distribution and relative abundance of rockfishes than did either method alone. Submersible surveys yielded estimates of fish density near the bottom as well as information used to provide ground truth for acoustic surveys and to scale echo integrator values. Acoustic equipment enabled portions of the water column not observed on submersible transects to be surveyed and provided additional information on the vertical and horizontal distribution of fishes.

Acknowledgments

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Age and growth of yellowfin tuna, *Thunnus albacares*, from the western Indian Ocean, based on otolith microstructure*

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Abstract.—Microincrements of otoliths of 151 yellowfin tuna, *Thunnus albacares*, caught in the western Indian Ocean by French and Mauritian purse seiners were used to establish growth curves. On the basis of comparisons among several otolith preparations (transverse or oblique sections, acetate replicas of the external face) and two methods of examination (light microscopy and scanning electron microscopy), we chose to observe transverse otolith sections in light microscopy to estimate age in days.

The von Bertalanffy growth curve, $FL = 272.7\,(1 - e^{-0.176(t + 0.266)})$, where FL = fork length in cm and t in years, is very similar to those obtained by other investigators. It does not support the hypothesis that yellowfin tuna of the eastern Atlantic Ocean and the western Indian Ocean have two growth stanzas. Back-calculated dates of spawning show that yellowfin tuna spawn successfully throughout the year, but principally between November and March.

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Numerous studies have been conducted on the age and growth of yellowfin tuna, *Thunnus albacares*, in the tropical oceans using three techniques: 1) length-frequency analyses (Moore, 1951; Hennemuth, 1961; Davidoff, 1963; Le Guen and Sakagawa, 1973; Marcille and Stéquert, 1976; Fonteneau, 1980; Gascuel et al., 1992; Marsac[1]); 2) tagging (Bard, 1984; Bayliff, 1988); and 3) observation and interpretation of marks on calcified structures such as scales (Yabuta et al., 1960; Huang et al., 1973), vertebrae (Aikawa and Kato, 1938; Romanov and Korotkova[2]), dorsal spines (Shabotiniets, 1968), or otoliths (Wild and Foreman, 1980; Uchiyama and Struhsaker, 1981; Wild, 1986; Yamanaka[3]).

Only a few age and growth studies have been conducted in the Indian Ocean, and the results have been contradictory. There are presently two hypotheses concerning yellowfin tuna growth. The first suggests that growth follows a von Bertalanffy model (von Bertalanffy, 1938), with growth rates from 2.9 to 3.4 cm per month for individuals between 60 and 70 cm. These studies were based on the analysis of length-frequency distributions

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[1] Marsac, F. 1991. Growth of Indian Ocean yellowfin tuna estimated from size frequencies data collected on French purse seiners. FAO, Indo-Pacif. Tuna Prog., Workshop on stock assessment of yellowfin tuna in the Indian Ocean, Coll. Vol. of Working Documents TWS/91/17, 8 p.

[2] Romanov, E. V., and L. P. Korotkova. 1988. Age and growth rates of the yellowfin tuna (*Thunnus albacares*) (Bonnaterre, 1788) (Pisces, Scombridae) in the northern part of the Indian Ocean, determined by counting the rings of vertebrae. FAO, Indo-Pacif. Tuna Prog., Coll. Vol. of Working Documents TWS/88/38, p. 68–73.

[3] Yamanaka, K. L. 1990. Age, growth, and spawning of yellowfin tuna in the southern Philippines. FAO, Indo-Pacif. Tuna Prog. Working Paper 90/WP/21, 87 p.

(Marcille and Stéquert, 1976; Maldeniya and Joseph[4]; Anderson[5]) or seasonal growth marks on calcified structures (Yabuta et al., 1960; Huang et al., 1973). The second hypothesis, also based on length-frequency analysis, suggests that there are two different growth periods, a slow period for young fish (1.5 cm/month for fork length [FL] below 60 cm) and a faster period for larger fish with FL >60 cm (Marsac and Lablache[6]; Marsac[1]). The objective of the present study is to test these two hypotheses by estimation of the ages (based on counting daily microincrements on otoliths) of yellowfin tunas in the Indian Ocean.

Materials and methods

Sampling

Sagittal otoliths were collected from fish caught in the western Indian Ocean (between lat. 5°N to 15°S and long. 42°E to 72°E). Otoliths were extracted either directly on board French purse seiners based in Mahé (Seychelles) or at the Port Louis tuna cannery (Mauritius) from fish caught by Mauritian purse seiners. A total of 674 yellowfin between 28 and 154 cm fork length (measured to the nearest half centimeter from the tip of the snout to the fork of the tail) were collected between May 1989 and November 1990. The sagittae were removed with forceps, rinsed, dried, and then stored in heat-welded, numbered plastic bags.

Otolith preparation

A subsample of 170 otolith pairs were chosen on the basis of fish-size frequency. Otoliths were cleaned in sodium hypochlorite (household bleach), rinsed with distilled water, and dried. They were then prepared according to the methods described in Secor et al. (1992). All terminology corresponded with that of the otolith glossary in Kalish et al. (1994). The right otolith was embedded in polyester resin (Embed 812), and a transverse section (Fig. 1) was made with a low-speed Buehler Isomet saw to obtain a slice containing the primordium. For 33 individuals, the left otolith was also embedded and sectioned in an oblique plane (Fig. 1). In each case, the slice was attached to a microscope slide with Crystalbond thermoplastic glue and then ground with wet sandpaper (400, 600, and 1,200 grit) and polished on a polishing plate with water and aluminium powder (0.3 μm) until the primordium was reached. The microscope slide was then placed on a hot plate for a few seconds to soften the glue and to turn the section: the primordium was then in direct contact with the microscope slide. The section was polished on the other side until a thin section of 75–100 μm maximum was obtained. The surface of this section was partially decalcified with 5–7% EDTA (tri-sodium-ethylenediaminetetraacetic acid, pH=7.2–7.6) to emphasize the increments used to estimate the age.

For 33 individuals ranging from 28.5 and 135 cm, we counted with the aid of light microscopy the number of daily increments on the transverse section of one otolith and the number of daily increments on the oblique section of the other. The results were compared to determine whether the interpretation of transverse sections tended to underestimate age as suggested by Wild and Foreman (1980). For 10 individuals ranging from 30 and 130 cm, we estimated age by counting the microincrements on acetate replicas of the external surface of the otoliths as in Wild and Foreman (1980). The results of the acetate replica counts were then compared with those of the transverse sections.

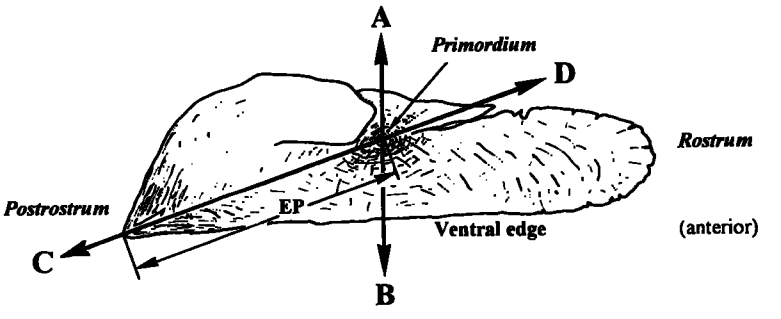

Figure 1

Drawing of a typical right yellowfin tuna, *Thunnus albacares*, sagitta. (**A–B**) Transverse section axis. (**C–D**) oblique section axis. EP = external path.

[4] Maldeniya, R., and L. Joseph. 1985. On the distribution and biology of yellowfin tuna from the western and southern waters of Sri Lanka. FAO, Indo-Pacif. Tuna Prog., Coll. Vol. of Working Documents TWS/85/21, p. 51–61.

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[6] Marsac, F., and G. Lablache. 1985. Preliminary study of the growth of yellowfin estimated from purse seiner data in the western Indian Ocean. FAO, Indo-Pacif. Tuna Prog., Coll. Vol. of Working Documents TWS/85/22, p. 91–110.

Age reading

Microincrements were counted on transverse sections of yellowfin tuna otoliths under a light microscope (1,000×) with an Olympus microscope BX 40 with a MPL 100× dry objective. Only 151 preparations were readable from the 170 fish because some were broken during grinding or too deeply etched by EDTA. The reading of microstructures was always made on the external part of the transverse sections along the ventral limb.

Each transverse section was chosen randomly and microincrements were counted at three different times by the same reader without knowledge of the sample identification or previous counts. After the readings, 16 sections were prepared for observation on a scanning electron microscope (SEM). A photographic series was made along each section (800×) to obtain the whole reading area and to count the number of microincrements. These results were then compared with those obtained from the light microscope reading.

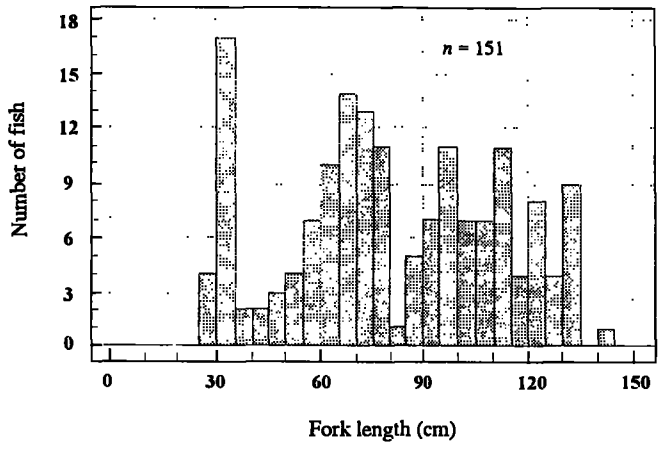

Figure 2

Length frequencies of yellowfin tuna, *Thunnus albacares*, for which otolith transverse sections were readable.

Growth

Several growth models exist to describe the relationship between fish size (FL in cm) and age (t in year = number of increments/365). Among the most used models, three of them (von Bertalanffy, Gompertz, and Richards) were tested. The equations of these models are as follows:

von Bertalanffy model: $FL_t = FL_\infty (1 - e^{-K(t-t_0)})$

Gompertz model: $FL_t = FL_\infty \exp(-ae^{-Kt})$

Richards model: $FL_t = FL_\infty/(1 + e^{(-Kt+b)})^m$

when FL_t = fork length at age t;
FL_∞ = asymptotic fork length;
K = coefficient of growth;
t_0 = theoretical age for $FL = 0$; and
a, b, and m = parameters.

Results

The fork lengths of the fish that had readable otoliths are shown in Figure 2. On the transverse section (Fig. 3), we observed that the microstructures are more visible in the layer (50–60 μm of thickness) which is located immediately under the otolith surface and that interpretation on the internal face is difficult because the microstructures tend to be obscure (Fig. 4).

Comparison of methods

The relationship between the numbers of microincrements on the transverse section and on the oblique section was highly significant (r=0.992, P<0.05, n=33) (Fig. 5). The slope of the regression was not different from one (t=–0.943, P>0.05, df=31), and the intercept was not different from zero (t=0.266, P>0.05, df=31). Therefore, transverse sections were used for the age readings.

Counts of microincrements on the transverse section under a light microscope (400×) compared to counts from SEM on the same section were significantly different for fish larger than 100 cm fork length (t=–4.643, P>0.05, df=18). To determine whether the difference was the result of the magnification used, we compared counts for 16 transverse sections under a light microscope (1,000× magnification) and a SEM with a comparable magnification (1,000×) (Fig. 6). The slope of the relationship was not different from one (t=–0.426, P>0.05, df=14), and the intercept was not different from zero (t=0.246, P>0.05, df=14). These results suggest that these two techniques give comparable counts. Therefore, subsequent analyses were based on counts from the light microscope (1,000×).

As the relationship between microincrement counts from acetate replicas and transverse sections could not be established for the same otolith, we plotted the results (age versus fork length) obtained from 10 individuals for which age was determined by replicas directly on the age versus fork length relationship estimated on the 151 transverse sections (means

of 3 counts) corresponding to our sample (Fig. 7). For acetate replica readings, the standard error of the counts is quite small (Table 1), and for counts on transverse sections, the coefficient of variation of Chang (1982) is acceptable (CV=2.802%, n=151)..

Transverse sections observed with the SEM clearly show that some increments overlap inside the otolith (Fig. 4). These increments cannot be seen on the external face even after acid etching for acetate replication. This overlap does not seem to appear on oblique sections where increments are more evenly spaced. In addition, the plane of growth of the otolith changed when viewed in a transverse plane (Fig. 8). From this plane (Fig. 3), the ventral surface of the otolith grows at an angle of about 120° to the original plane of growth which contains the primordium. The direction of otolith growth changes before the fish reaches 28 cm fork length. For all individuals, the distance between the primordium and the top of this angle (D1, Figs. 3 and 8) has a stable value (D1=644 μm [±4 μm]). Then, the otolith growth depends only on the plane of growth of D2 (Figs. 3 and 8). This change in growth direction occurs, on average, 50 (±5) days after the date of hatching (n=151). Because of this change, the use of back-calculation can be complicated. Because ages obtained with the acetate replica technique were similar to those based on transverse sections, we used the ages based on transverse sections for this study. All the observations described above (comparisons between oblique and transverse sections, replicas, light microscope, and SEM) show that the observation of microstructures on transverse sections of yellowfin tuna otoliths with a light microscope are suitable to estimate age in days.

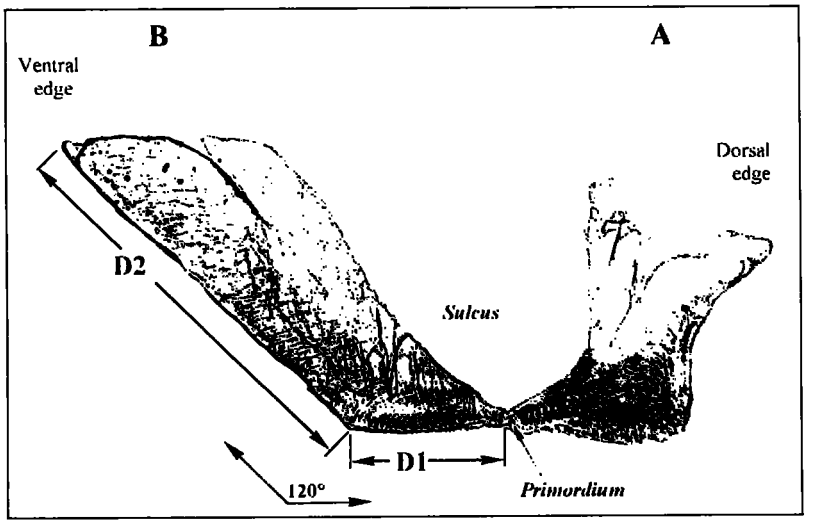

Figure 3

Transverse section (**A–B**) of a right yellowfin tuna, *Thunnus albacares*, sagitta (length of the section D = D1 + D2).

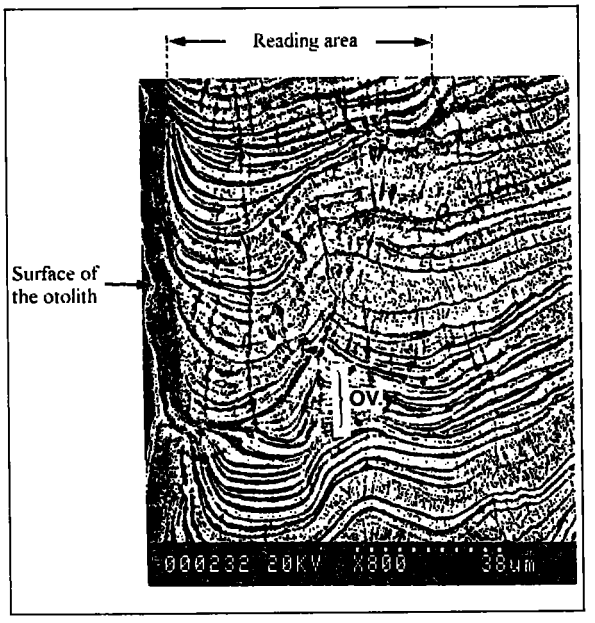

Figure 4

Daily microincrements on a transverse section of yellowfin tuna, *Thunnus albacares*, otolith (SEM, magnification = 800×, scale bar = 38 μm). ov = overlapping of increments.

Growth

The estimations of parameters were calculated by using the nonlinear regression procedure and are summarized in Table 2. The fits of each of these models are highly significant (P<0.01). For the three models, F-ratios of ANOVA (respectively 14,698, 14,799, and 10,960) and r^2 values (0.974 for each of them) are very similar to one another (Table 2). We used the von Bertalanffy growth curve to express our results and to compare with results obtained by other investigators because this model is the most widely used.

The model was also applied to males (n=63) and to females (n=61) separately. Males and females were similar in size at any given age (Table 3). ANCOVA

for both male and female adjusted relationships of fork length to age indicated no significant differences in the slope ($F_{(1, 120)}$=1.270, P>0.05) or intercept ($F_{(1, 121)}$=0.359, P>0.05).

The mean growth rate of yellowfin tuna in the Indian Ocean, based on this study, is approximately 2 mm/day for fish measuring 30 cm (FL), 1.3 mm·day^{-1} for length between 60 and 80 cm, and 1 mm·day^{-1} for fish larger than 110 cm.

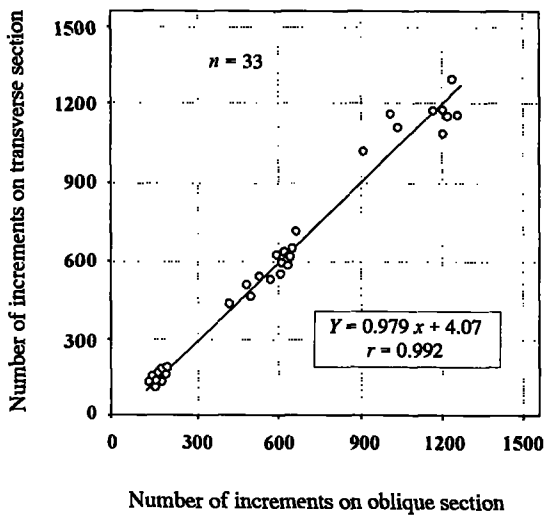

Figure 5

Comparison between the number of increments read on transverse and on oblique sections of yellowfin tuna, *Thunnus albacares*, otoliths.

Date of hatching

Spawnings occurred throughout the year, but mainly from October through March. If we compare the monthly development of the number of births (back-calculated from age estimations) and the variation of the gonad index (GI) established by Hassani and Stéquert,[7] there is a similarity in development for reproduction (Fig. 9). Analysis of correlation yields a significant correlation (r=0.997, P<0.05, n=12) between these two data sets. The months of hatching established from otolith estimations correspond to the months of the maximum reproductive activity determined from GI's.

Discussion

Choice of otolith preparation method

Age readings of yellowfin tuna previously have been made either directly on the external surface of the otolith or on the acetate replica of this surface (Wild and Foreman, 1980; Wild, 1986). Using the external surface of the otolith etched with 0.5N HCl, Wild and Foreman (1980) showed that the age reading should be done on the primordium–postrostrum axis (EP, Fig. 1) for interpreting the increments. They concluded that age was underestimated when the pri-

[7] Hassani, S., and B. Stéquert. 1990. Sexual maturity, spawning and fecundity of the yellowfin tuna (*Thunnus albacares*) of the western Indian Ocean. Document presented at the FAO expert consultation on stock assessment of tuna in the Indian Ocean; Bangkok, Thailand, 2–6 July 1990. FAO, Indo-Pacif. Tuna Prog., Coll. Vol. of Working Documents TWS/90/68, p. 91–104.

Table 1

Results of the microincrement readings on acetate replicas of the external otolith face of yellowfin tuna, *Thunnus albacares*, otoliths. I*n* = number of increments for the *n*th reading. I = mean of the increment numbers. SE = standard error

FL (cm)	I1	I2	I3	I4	I5	I6	I*n*	SE
35.0	195	197	198	194	197	196	196.2	0.60
49.5	310	307	311	308	306	310	308.7	0.80
59.5	405	406	401	403	405	407	404.5	0.88
66.0	518	532	522	515	523	526	522.7	2.44
75.0	561	559	550	551	557	552	555.0	1.88
78.5	623	644	635	627	631	624	630.7	3.23
99.0	809	814	802	804	803	818	808.3	2.67
99.5	852	861	848	850	860	872	857.2	3.67
118.0	1,148	1,155	1,137	1,151	1,143	1,132	1,144.3	3.56
130.5	1,211	1,224	1,208	1,220	1,222	1,233	1,219.7	3.71

mordium-ventral edge axis (Fig. 1) was used. This underestimation was as high as 17% for larger individuals. The irregularity of microincrement structure and its overlapping (Fig. 4) may explain the difference observed by Wild and Foreman (1980) between their readings on the surface of the otolith along the oblique and those on the transverse axis.

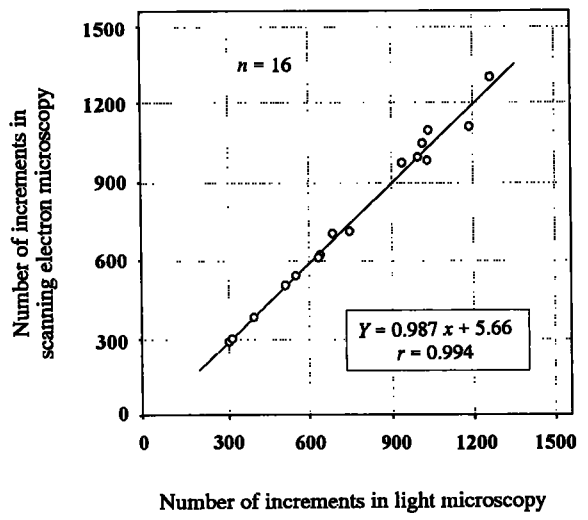

Figure 6

Comparisons between the number of increments estimated on transverse section of yellowfin tuna, *Thunnus albacares*, otoliths with the light microscope and the SEM.

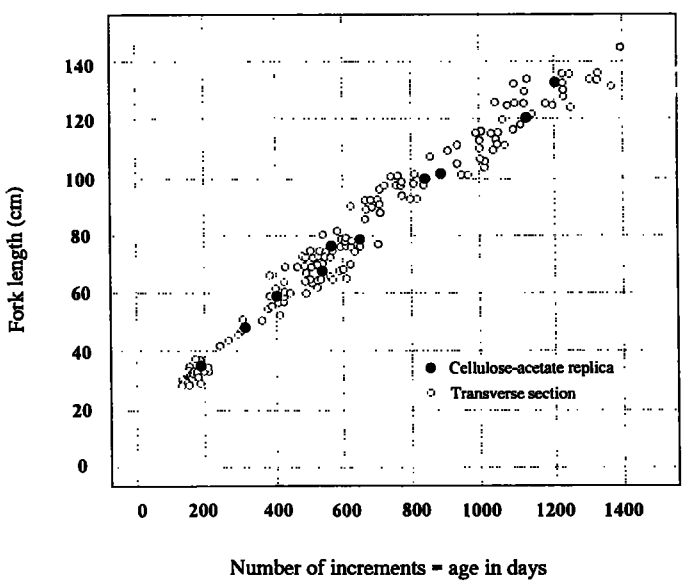

Figure 7

Comparison between the number of increments on yellowfin tuna, *Thunnus albacares*, otoliths estimated from acetate replicas and the number of increments estimated from transverse sections.

The results of the present study show that the microincrements can also be counted on a transverse or oblique otolith section which crosses the primordium. We obtained similar results with all three techniques. Because transverse otolith sections are easier to prepare and have excellent statistical replicability (CV <5%), they were used to count the microincrements and estimate the age of yellowfin tuna from the Indian Ocean. However, our results suggest that under light microscopy, a magnification of 1,000× must be used.

Validation of the age estimations

Wild and Foreman (1980) have shown that one daily microincrement is formed each day on the otolith of the yellowfin tuna from the eastern Pacific. If the same phenomenon occurs in the western Indian Ocean, comparable results should be found in this area with other methods. In order to verify indirectly our age estimations, we used the results of mark-recapture studies (Cayré and Ramcharrun[8]; Yesaki and Waheed[9]) and of length-frequency analyses of young individuals for which cohorts are easily recognized (Marcille and Stéquert, 1976).

In a tagging experiment carried out in the southwest Seychelles Islands area and in the Mozambique channel (Cayré and Ramcharrun[8]), three individuals (FL=67, 73, and 67 cm) were recaptured after liberty at sea for 252, 411, and 613 days, respectively after marking. They presented a mean growth rate of 27.3 cm·yr^{-1}. A tagging experiment in the Maldives (Yesaki and Waheed[9]) resulted in a mean growth rate of 2.4 cm·mo^{-1} for the 37 recaptured fish that were at liberty for more than 29 days after marking. The growth rates obtained in these two experiments were similar to those of the present study. Following the young yellowfin tuna cohorts caught by Japanese pole-and-line tuna boats along the northwest coast of Madagascar (Marcille and Stéquert, 1976), the mean growth rate of 40

[8] Cayré, P., and B., Ramcharrun. 1990. Results of the tagging operations conducted within the Regional Tuna Project (Indian Ocean Commission) in 1988 and 1989. FAO, Indo-Pacif. Tuna Prog. Coll. Vol. of Working Documents TRW/90/61, p. 63–85.

[9] Yesaki, M., and A. Waheed. 1992. Results of the tuna tagging program conducted in the Maldives during 1990. FAO, Indo-Pacif. Tuna Prog. Working Paper 92/WP/24, 18 p.

to 70 cm individuals was about 34 cm·yr^{-1}. The slopes corresponding to those growth rates, when plotted against the growth curve of the present study, show close agreement (Fig. 10). These comparisons demonstrate that 1) the microincrements on otoliths are deposited on a daily basis and 2) the ages of young tuna (FL ≤100 cm) estimated from otoliths are correct.

Comparative study of yellowfin tuna growths

The growth curve obtained for yellowfin tuna from the western Indian Ocean is similar to those obtained by different investigators in other oceans and using other age estimation methods. The use of skeletal

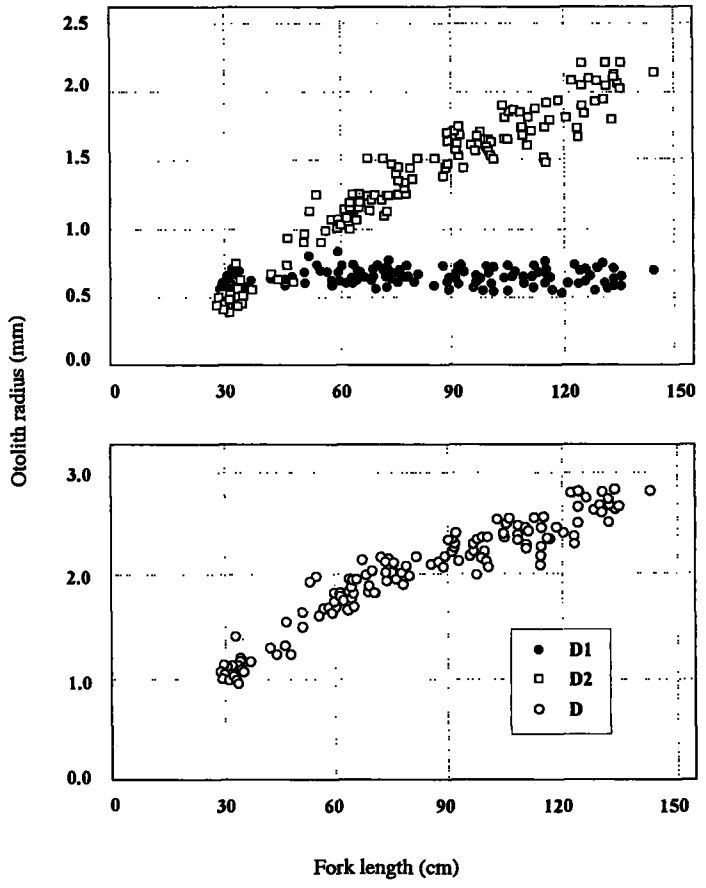

Figure 8

Relationships between different measurements on the transverse section of yellowfin tuna, *Thunnus albacares*, otoliths and fish length. The location of D1 and D2 are shown in Figure 3, where D = D1 + D2.

Table 2

Estimated parameters of the growth models for yellowfin tuna, *Thunnus albacares*, (all sexes, n=151) in the western Indian Ocean (FL in cm, t_0 in years). Est. = estimated value; SE = standard error.

	von Bertalanffy			Gompertz			Richards			
	FL_∞	K	t_0	FL_∞	a	K	FL_∞	K	b	m
Est.	272.7	0.176	−0.266	165.7	2.131	0.629	160.8	0.698	1.450	6.675
SE	28.9	0.027	0.050	5.2	0.039	0.033	13.1	0.204	5.269	19.604

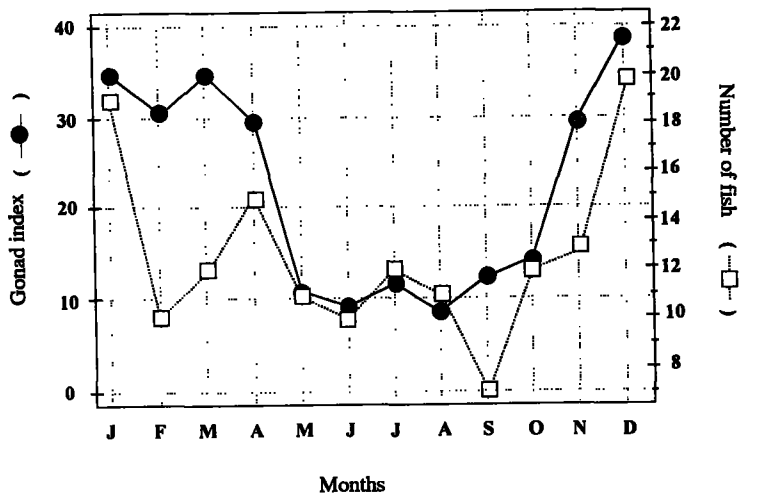

Figure 9

Comparisons between the monthly gonad index and the total number of yellowfin tuna, *Thunnus albacares*, hatched during the same month. The last number is determined from age and date of capture.

Table 3

Length (in cm) at different ages for yellowfin tuna, *Thunnus albacares*, predicted by the von Bertalanffy growth model.

	Age (yr)							
	0.5	1	1.5	2	2.5	3	3.5	4
All individuals	34.4	54.5	74.4	89.7	105.1	119.2	132.2	144.0
Females	—	54.3	73.1	90.1	105.2	118.0	131.2	142.2
Males	—	53.5	72.3	89.7	105.7	120.4	134.0	146.5

bony structures in the Pacific (Yabuta et al., 1960) or in the Indian Ocean (Huang et al., 1973) gave results similar to ours (Fig. 11A). Studies conducted on length-frequency analyses have also led to comparable results. The results for the Pacific yellowfin tuna of Hennemuth (1961) are close to those of the present study. The growth estimation of Le Guen and Sakagawa (1973) for the eastern Atlantic shows slight differences for young individuals: until 2 years of age, young yellowfin tuna grow more slowly than those from the Indian Ocean; however, after 2 years of age, growth is the same for eastern Atlantic and Indian Ocean populations. Two growth stanzas have been observed in the western Atlantic (Capisano and Fonteneau, 1991; Gascuel et al., 1992) and in the Indian Ocean (Marsac[1]), but we did not observe the accentuated inflection in the growth of juveniles reported by these studies.

A comparison of our results with other estimates based on otoliths yields similar growth models (Fig. 11B). Age estimates given by Yamanaka[3] for the smallest fish in the Philippines (FL between 25 and 50 cm) are equal to those of the small yellowfin tuna caught by the French purse seiners in the Indian Ocean. The length of our smallest fish (6 months old) is only a few centimeters larger than that proposed by Uchiyama and Struhsaker (1981) for the Pacific but is exactly the same for individuals older than 1 yr. The growth curve established by Wild (1986) for eastern Pacific yellowfin tuna shows growth rates slightly greater than those of the western Indian Ocean, but for 2-yr-old individuals, the lengths are equal (FL=90 cm).

For the Indian Ocean, however, studies of yellowfin tuna growth rates yield contradictory results. Growth rates calculated in the present study are similar to those obtained in the small-scale fisheries of the Maldives (Anderson[5]) and Sri Lanka (Maldeniya and Joseph[4]) but are significantly different from those obtained for the same Indian Ocean population landed by French purse seiners (Marsac[1]; Marsac and Lablache[6]). Differences in length are

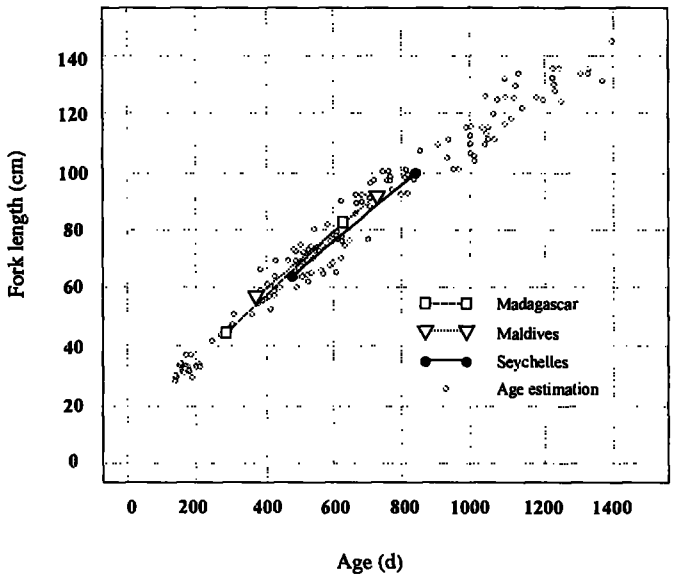

Figure 10

Comparisons between the ages estimated from otoliths and from different annual growth rates obtained by 1) small fish length-frequency analyses (Madagascar), and 2) tagging experiments (Maldives and Seychelles), for western Indian Ocean yellowfin tuna, *Thunnus albacares*.

observed for each age except for 1-yr-old and 2.5-yr-old individuals (Fig. 11C). That these studies assume there is only one period of reproduction that occurs annually during a short duration of time (November to March) and that individuals are sexually resting during the remainder of the year may explain the discrepancy. Recent hormone analyses (unpubl. data, senior author) and estimated dates of hatching show that yellowfin tuna of the western Indian Ocean spawn throughout the year. It is clear that the major reproductive period is between November and March, however some of the population spawns from July to September. A similar observation has been noted for the eastern Pacific populations of yellowfin tuna.[10] For the Indian Ocean population, there is agreement between the spawning period estimated from the otolith readings and the condition of the female gonad index during the year. This observation supports the assumption of daily deposition of microincrements.

The growth rates estimated in the present study are high at the beginning of the life cycle until 1 yr and regularly decrease with time to reach 1 mm·day^{-1}, which is consistent with growth estimates for most species of fish and other stocks of yellowfin tuna. This contradicts the growth model for the same stock landed by the French purse seiners presented by Marsac[1]: the young fish have linear growth, until they reach 60 cm, and then grow faster in accord with the von Bertalanffy growth model. A uniform growth model is also reasonable because yellowfin tuna from the Atlantic and Pacific oceans show no significant genetic differences (Scoles and Graves, 1993).

The present study introduces some new information about the growth of yellowfin tuna in the western Indian Ocean; that is to say, growth is regular, following a classical von Bertalanffy model without stanzas. Nevertheless, some problems remain unsolved. For example, we collected no fish smaller than 28 cm (from larvae until 28 cm size, i.e. for the first 5–6 months of life) and very few large individuals (>140 cm). The problem is more complex in collecting small fish: analysis of the stomach contents of more than 1,000 adult tunas or other predators did not yield any small individuals as has been possible for adult tunas in the Pacific Ocean (Uchiyama and Struhsaker, 1981). In fact, we do not know where the small Indian Ocean yellowfin tuna live or how to capture them in order to collect their otoliths. Once these otoliths are obtained, an important first study would concern otolith growth itself to determine the correspondence between life cycle

[10] Schaefer, K. 1993. Inter-American Tropical Tuna Commission, Scripps Institution of Oceanography, 8604 La Jolla Shores Drive, La Jolla, CA 92037-1508. Personal commun.

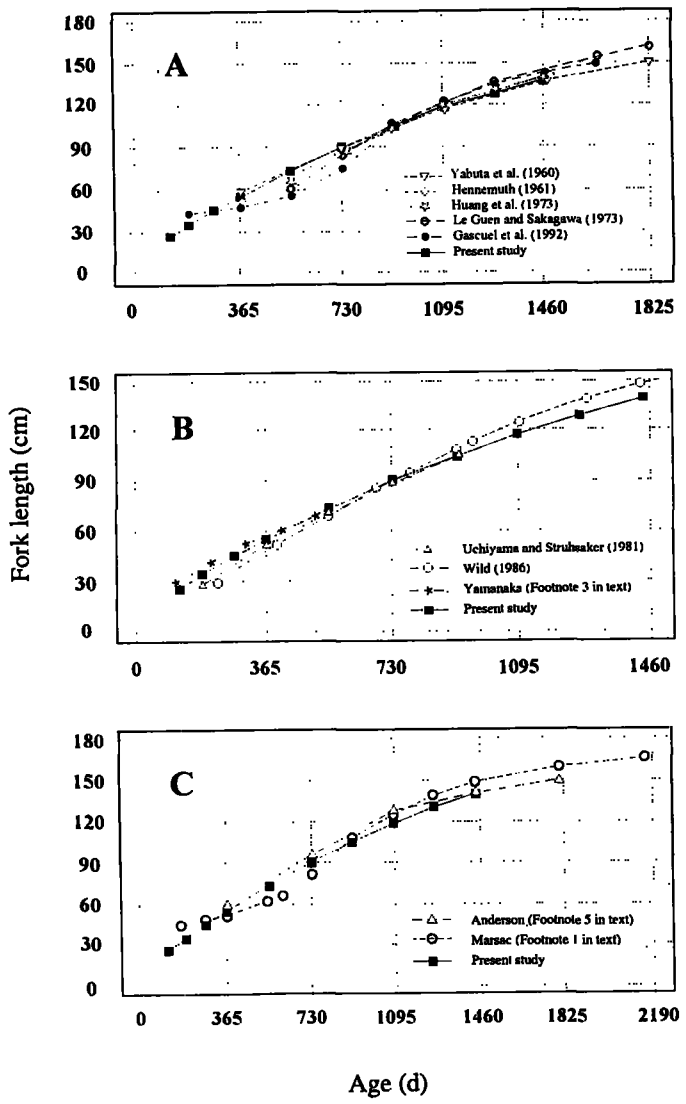

Figure 11

Comparisons of yellowfin tuna, *Thunnus albacares*, growth curves established by several investigators: (A) Atlantic and Pacific Oceans with different age estimation methods; (B) otolith daily increment readings; (C) Indian Ocean with different methods of age estimation.

events and the change in otolith growth direction (D1–D2 boundary). Regular samplings of small individuals and the analysis of daily microincrements could avoid difficult interpretations in the length-frequency analyses during the first months of growth.

Acknowledgments

The sampling in this study was financially supported by the Association Thonière (Indian Ocean Commission), and otolith preparation and data analysis by the Belle W. Baruch Institute for Marine Biology and Coastal Research (Univ. of South Carolina, SC). Special thanks are also due to Alex Wild of the Inter-American Tropical Tuna Commission, La Jolla, CA, for his assistance with the acetate-replica otolith preparations and age readings and to Charles Wilson at Louisiana State University, Baton Rouge, LA, for his hospitality. We wish to acknowledge the three anonymous reviewers for their constructive comments on our manuscript.

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Age and growth determination of the blacktip shark, *Carcharhinus limbatus*, from the east coast of South Africa

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Abstract.—Age and growth of the blacktip shark, *Carcharhinus limbatus*, from the east coast of South Africa were investigated by counting growth rings in vertebral centra. The vertebrae of 41 females (41–181 cm precaudal length [PCL]) and 51 males (42–182 cm PCL) were examined. Three methods successfully enhanced the visibility of growth rings: crystal violet staining of the centrum face, microscopic examination of the whole vertebra, with transmitted light and dark field, and "bow tie" sectioning of the vertebra. The results of the three methods were compared by using the average percentage error index and statistical means. Age and growth estimates were obtained from microscopic examination of the whole vertebra, the method which provided the most accurate ring counts and gave the second highest reproducibility.

The data for males and females were combined and the von Bertalanffy parameters obtained were L_∞= 193.6 cm PCL, K = 0.21 yr^{-1} and t_0 = –1.2 yr. Age at maturity was 7 years (156 cm PCL) for females and 6 years (150 cm PCL) for males. The oldest aged female was 11 years (179 cm PCL), the oldest aged male was 10 years (179 cm PCL) old. Mean calculated growth rates were 24 cm/yr for the first three years, 11–13 cm/yr through adolescence, and 5–6 cm/yr after maturity.

Back-calculated lengths were lower than observed lengths and Lee's phenomenon was apparent. In 83% of the vertebrae the band immediately after the change in angle was translucent. Opaque band deposition is assumed to occur in summer.

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Fishery Bulletin 94:135–144 (1996).

The Natal Sharks Board (NSB) operates a shark fishery on the east coast of South Africa that is aimed at protecting beach users against shark attack (Cliff et al., 1988a). The sharks are caught in large-mesh gill nets, which fish throughout the year off the more popular recreational beaches of KwaZulu-Natal. Concern has arisen over the possible impact of over 30 years of gillnetting on shark populations off this coast (Dudley and Cliff, 1993a). One of the 14 species contributing to the annual catch of about 1,440 sharks is the blacktip shark, *Carcharhinus limbatus*. Between 1978 and 1994 an annual average of 121 *C. limbatus* were caught in the nets. Information about the distribution, fecundity, size at maturity, diet, and movements of *C. limbatus* is given by Bass et al. (1973) and Dudley and Cliff (1993b).

Research on ageing is an integral part of life history studies of exploited species. This study estimates age and growth of *C. limbatus* from vertebral ring counts. Comparable information exists for this species from the Gulf of Mexico (Branstetter and McEachran, 1986; Branstetter, 1987a; Killam and Parsons, 1989).

Materials and methods

Sampling

Sharks were sampled in the NSB nets from 1985 to 1991. Each net was 214 m long, 6 m deep, had a 50-cm stretched mesh, and was set in water 10–14 m deep, parallel to and 300–400 m from the shore. For details of the netting operation see Cliff et al. (1988a).

Precaudal length (PCL) was measured in a straight line from the snout tip to the precaudal notch and was used throughout this study. For comparison with literature which reported total length (TL), as defined by Branstetter (1987b), the following equation was generated by Dudley and Cliff (1993b):

$$TL = 1.334 \times PCL + 4.27$$
$$[n=94,\ r=0.999;\ \text{range } 40.5\text{–}190.0 \text{ cm}]$$

Maturity was assessed on the basis of the criteria of Bass et al. (1973). Males were considered mature only if the claspers were fully calcified. Sperm is produced before claspers are fully calcified and was therefore not regarded as a criterion of maturity. Females were considered mature by the presence of a ruptured hymen and large eggs (>15 mm diameter) in the ovary. In addition, a uterus width of more than 5 cm indicated maturity (Dudley and Cliff, 1993b).

Vertebral samples were taken anterior to the origin of the first dorsal fin from 41 females (41–181 cm) and 51 males (42–182 cm). The vertebrae were stored in various ways: dry (71%); in 70% isopropyl

alcohol after fixing in 10% formalin for two weeks (15%); frozen (12%); or processed fresh (2%). Individual centra were soaked in a 5.25% solution of sodium hypochlorate for 10–40 minutes and the connective tissue was then removed with forceps.

Ring-enhancing methods

Five methods to enhance visibility of growth rings were tested. X-radiography[1] and silver nitrate staining[2] failed to clarify the rings and were discarded. The crystal violet staining technique (CV method) of Schwartz (1983) was modified in that the corpus calcareum was stained with a 0.01% solution of crystal violet for 2–10 minutes and then destained with 50% isopropyl alcohol until the desired color intensity was obtained. In the second (UT) method the entire cleaned, unstained vertebra was viewed through a dissecting microscope with transmitted light and a dark field. In the "bow tie" (BT) method, as described by Branstetter and McEachran (1986), a sagittal section was cut from the centrum and successively polished with 200-, 400-, and 600-grit sandpaper to a thickness of 0.5 cm. The section was mounted on a glass microscope slide with clear epoxy resin for viewing.

Ring counts

A growth ring was defined as a band pair, composed of one calcified, opaque band and of one less-calcified, translucent band. A change in angle on the centrum face, a result of the difference between fast intra-uterine and slower post-natal growth (Walter and Ebert, 1991), was regarded as the birth mark. Birth was defined as age zero and two embryos which were close to term, a 42 cm male and a 41 cm female, were included in establishing the von Bertalanffy growth curves (VBGC).

Three nonconsecutive ring counts for each method were made without knowledge of the animal's length and previous counts. Count reproducibility was determined by using the average percentage error (APE) and the APE index as described by Beamish and Fournier (1981). An upper limit in the APE was arbitrarily set at 20% for each vertebra. Samples were discarded if, after a single recount, they were still above this limit. For each method, a mean of the three counts was used as an age estimate. In the fourth (ALL) method, a mode of all nine readings was taken as an age estimate. This method was chosen to compensate for possible over- or under-counting tendencies of the different methods.

The von Bertalanffy growth parameters (VBGP) were computed with Marquardt's algorithm (Draper and Smith, 1981). The von Bertalanffy growth equation was fitted by using the nonlinear regression procedure of STATGRAPHICS®. The equation is

$$L_t = L_\infty(1-e^{-K(t-t_o)})$$

where L_t = length at age t in years, L_∞= maximum theoretical length, K = the rate at which L_∞ is reached, and t_o = the theoretical age at length zero.

The VBGC were then examined for their goodness of fit. A poor goodness of fit in all four methods may be due to a wide variation in the growth of individuals, whereas a poor fit in a single method would suggest inaccurate age estimates.

Centrum analyses

Confirmation of the annual periodicity of growth rings (Cailliet et al., 1983, a and b) was attempted with centrum analyses. The band immediately after the change in angle and the outermost band were classified as translucent or opaque. The nature of the last deposited band was related to the month of capture, and the observed and expected ratios of translucent to opaque last bands were compared.

Distance from the focus to the outer edge of the opaque band of each growth ring, marginal increments, dorsal diameter, and dorsal "birth diameter" were measured in a transverse plane along a straight line through the focus. A relationship between centrum diameter and animal length was investigated and the Dahl-Lea method of back calculation (Carlander, 1969) was used, in which

$$PCL_t = CD_t \times PCL_c/CD_c,$$

where PCL_t = length at age t, CD_t = centrum diameter at age t, PCL_c = length at capture, and CD_c = centrum diameter at capture.

Results

The APE indices were 8.1% for the CV method (n=87), 8.9% for the UT method (n=86), and 9.4% for the BT method (n=87). These results indicated that all three methods were of similar reproducibility. The APE index for the ALL method was 13.0% (n=80).

[1] Standard x-radiography, mammography, and a technique producing zerograms.

[2] A modification of the method of Stevens (1975).

The clarity of the growth rings seemed to be affected by storage method. The rings in fresh, frozen, or alcohol-stored vertebrae were clearer (especially with the UT method) than those stored dry. Fixation in formalin, despite its decalcifying properties, did not appear to affect band clarity adversely.

The growth curves obtained for males and females from each of the four methods were visually very similar; those obtained with the UT method are given in Figure 1. The VBGP for each sex are given in Table 1. Because no significant difference between the sexes was found with the UT, BT, CV, or ALL methods (ANCOVA, $P>0.52$, $P>0.95$, $P>0.43$, $P>0.91$, respectively), the data were combined. The growth curves for the four different methods were also visually very similar (Fig. 2). The BT method had the worst good-

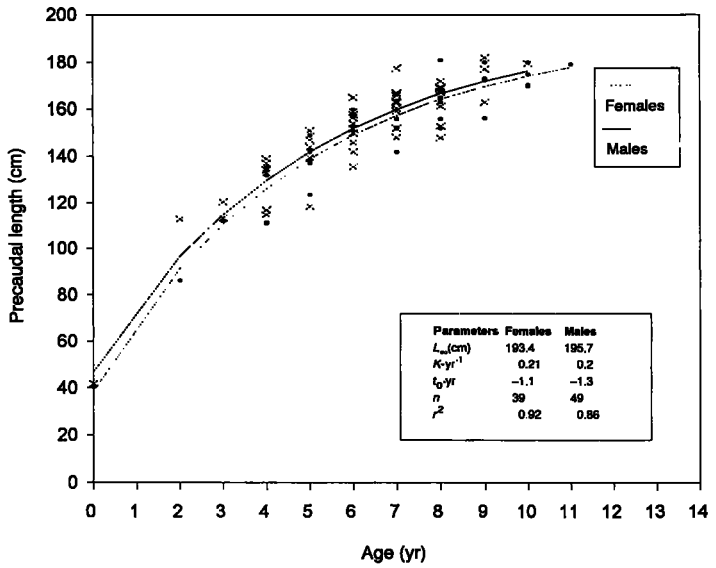

Figure 1

Von Bertalanffy growth curves for male (×) and female (·) blacktip shark, *C. limbatus*. Age estimates were obtained by examination of unstained vertebrae with transmitted light (UT method).

Table 1

Comparison of von Bertalanffy growth parameters for male and female *C. limbatus* and for sexes combined. Age estimates were obtained with four ageing methods. UT = unstained-vertebra technique; BT = "bow tie" technique; CV = crystal-violet–staining technique; and ALL = nine-readings technique.

	Method											
	UT			BT			CV			ALL		
	Male	Female	**Both**	Male	Female	**Both**	Male	Female	**Both**	Male	Female	**Both**
L_∞ (cm)	195.7	193.4	**193.6**	184.2	174.3	**177.7**	191.0	194.0	**192.2**	191.8	190.4	**190.7**
SE	10.9	7.8	**6.3**	9.1	4.9	**4.4**	10.9	8.7	**6.8**	10.0	9.4	**6.6**
K (yr^{-1})	0.20	0.21	**0.21**	0.21	0.28	**0.25**	0.19	0.18	**0.19**	0.21	0.21	**0.21**
SE	0.04	0.03	**0.02**	0.04	0.04	**0.03**	0.04	0.03	**0.02**	0.04	0.04	0.03
t_0 (yr)	−1.3	−1.1	**−1.2**	−1.6	−0.9	**−1.2**	−1.3	−1.2	**−1.3**	−1.2	−1.1	**−1.1**
SE	0.4	0.3	**0.3**	0.5	0.3	**0.3**	0.5	0.4	**0.3**	0.4	0.4	**0.3**
n	49	39	**88**	49	39	**88**	49	40	**89**	45	35	**80**
r	0.86	0.92	**0.89**	0.81	0.97	**0.84**	0.83	0.92	**0.87**	0.85	0.89	**0.87**

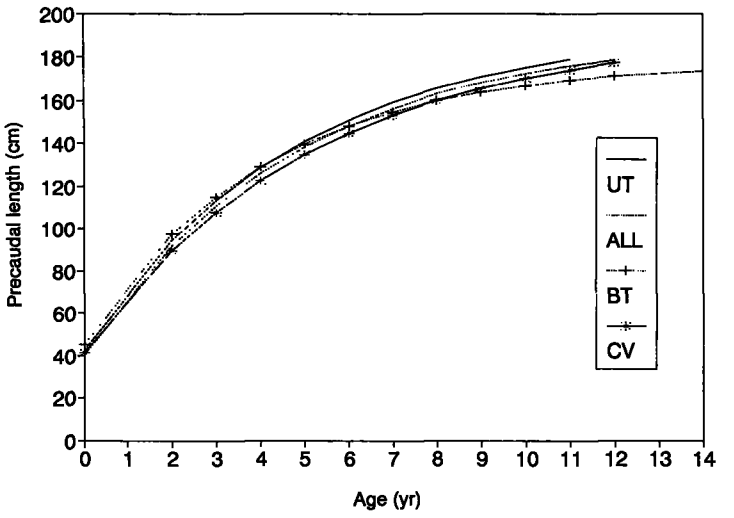

Figure 2

Von Bertalanffy growth curves for the blacktip shark, *C. limbatus*. Age estimates were obtained with four different methods: UT = unstained-vertebra technique; BT = "bow tie" technique; CV = crystal-violet-staining technique; and ALL = nine-readings technique.

ness of fit and the greatest difference between the L_∞ value and the observed maximum length. The best goodness of fit was found for the UT method, which was therefore used to obtain age estimates.

Centrum analyses

A distinct prebirth mark, a translucent band appearing before the birth mark, was found in 20% of the vertebrae but in none of the embryonic vertebrae. In 83% of the vertebrae, the first band immediately after the change in angle was a narrow translucent one.

The first three growth rings were all clearly visible in each of the three ring-enhancing methods. Difficulty was experienced in resolving bands at the centrum edge in older specimens; therefore, accurate marginal increment measurements could be obtained only for the five specimens younger than four years, and the marginal increment analysis was omitted. The observed ratio of translucent to opaque last bands differed significantly from the expected ratio (χ^2 test, $P<0.001$, $n=89$); consequently, annual periodicity of the growth rings could not be confirmed.

A linear relationship was found between centrum diameter and PCL (Fig. 3). As there was no significant difference between the sexes (Student's t-test, $P>0.2$), the data were combined. The intercept of the linear regression was very close to zero (–0.039 cm), and we felt that any correction, such as the Fraser-Lee method (Branstetter, 1987a; Carlander, 1969), was unnecessary.

Mean back-calculated lengths were lower than observed values, except at age zero, where back-calculated birth size was 42 cm and the observed value was 41 cm (Table 2). Lee's phenomenon, a tendency for back-calculated lengths of older fish in the earlier years of life to be systematically lower than those of younger fish at the same age (Carlander, 1969; Smith, 1983), was apparent (Fig. 4). For example, in a shark aged 10 years, there was a 33.6 cm difference between observed and back-calculated length at age four; whereas an animal aged five had only a 21.6 cm difference at age four.

Age and growth estimates

The smallest female (86 cm) was two years, the largest (181 cm) was eight years old (Fig. 5). The two smallest mature females, one of which was pregnant, measured 156 cm and were both seven years old. The smallest (113 cm) and largest (182 cm) males were two and nine years old, respectively. The smallest mature male (150 cm) was six years old. The oldest female (179 cm) was 11 years and the oldest male (179 cm) was 10 years old. Size at birth was calculated to be 43 cm.

Growth rates calculated from mean observed lengths were lower, especially for immature sharks,

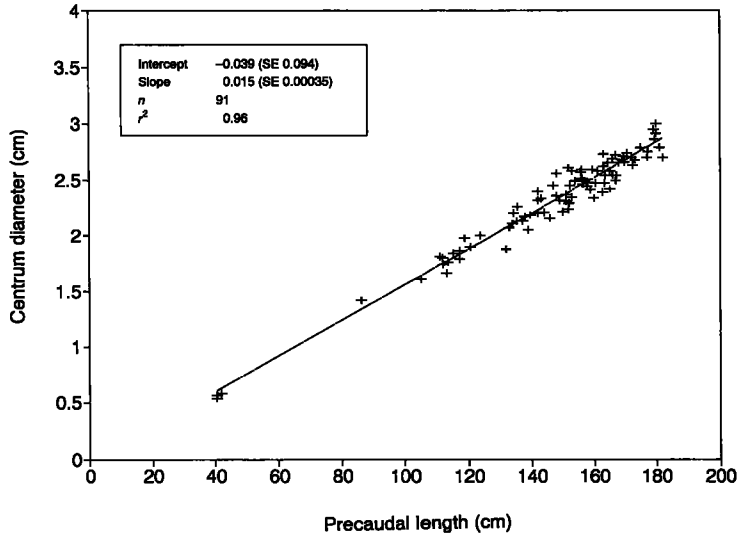

Figure 3

Relationship of length to centrum diameter for combined sexes of the blacktip shark, *C. limbatus*.

Table 2

Observed and back-calculated lengths at age for *C. limbatus*. Age estimates were obtained by examination of the unstained vertebrae with transmitted light.

	Observed PCL (cm)				Back-calculated PCL (cm)			
Age	Min	Max	Mean	*n*	Min	Max	Mean	*n*
0	41	42	41	3	36	55	42	89
1	—	—	—	0	44	81	62	89
2	86	113	100	2	60	103	79	89
3	105	121	113	4	72	132	94	86
4	111	152	128	13	84	158	109	81
5	119	151	139	11	96	159	122	69
6	136	165	153	15	106	162	135	55
7	142	177	160	17	118	177	144	41
8	148	181	164	14	130	182	154	24
9	156	182	172	7	137	193	160	10
10	170	180	175	5	150	185	162	7
11	—	—	179	1	—	—	—	0

than those calculated from mean predicted lengths (Fig. 6). The mean growth rate for predicted lengths over the first three years was 24 cm/yr. Adolescent sharks, until age six or seven, grew an average of 11–13 cm/yr. After maturity the growth rate dropped to 5–6 cm/yr.

Discussion

The APE index for each of the three different ring-enhancing methods (8.1–9.4%) was higher than that of Brown and Gruber (1988), who used alizarin-red-S–stained and unstained "bow tie" sections of

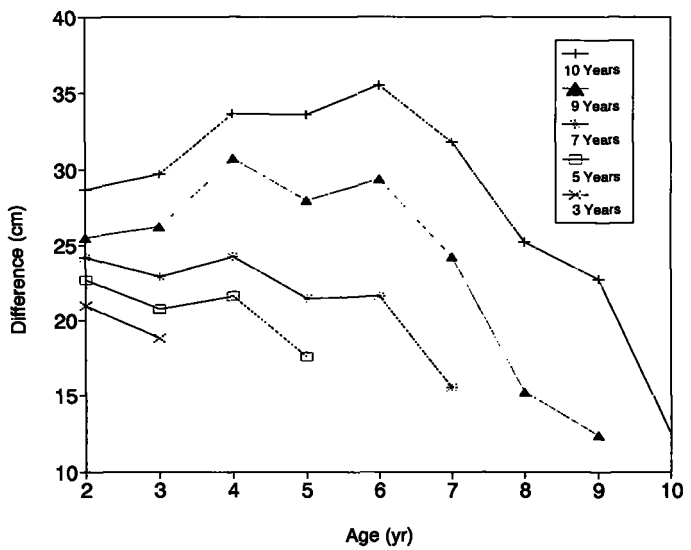

Figure 4

Differences between mean observed and mean back calculated lengths at age for the blacktip shark, *C. limbatus*, aged 3,5,7,9, and 10 years.

Negaprion brevirostris and had an APE index of 3.4% (n=55). Their high level of reproducibility is probably a result of counting monthly circuli, where the higher frequency and number of these rings inherently results in a low APE. The statistical differences among our three ring-enhancing methods, assessed by comparing APE indices and goodness of fit of the growth curves, were small, and it is was difficult to decide which of the three produced both the most accurate and the most reproducible results. The UT method, although having the second best reproducibility, was chosen because of its best goodness of fit.

Centrum analyses

A prebirth mark, a translucent band, was found in only 20% of the vertebrae. Branstetter (1987a) found that at least one growth ring formed in *C. limbatus* during embryonic development, but Killam and Parsons (1989) found none. Prebirth marks have also been found in *Carcharhinus plumbeus* (Casey et al., 1985), *C. leucas* (Branstetter and Stiles, 1987), *C. brevipinna* (Branstetter, 1987a), and *C. brachyurus* (Walter and Ebert, 1991). None of these authors, however, indicated whether the prebirth marks were present in all vertebrae examined.

In 83% of the vertebrae, the band immediately after the change in angle was a narrow, translucent one. Bass et al. (1973) and Dudley and Cliff (1993b) sampled pregnant females with well-developed embryos between September and February, suggesting that birth takes place in summer. If the assumption made earlier, that the change in angle is formed at birth is correct, then the translucent band is associated with summer growth. This is contrary to most other ageing studies using vertebral growth rings. Branstetter (1987a) noted that in *C. limbatus*, band calcification occurred in the northern hemisphere summer. He also found that "the first growth band, bordered by the birth annulus and the first postnatal annulus, represented approximately 6 months growth." Killam and Parsons (1989) found that translucent ring deposition occurred during December and January but referred to a translucent "birth" ring, although the sharks are born in May and June, the northern hemisphere summer. In the only other study of this nature in southern Africa, Walter and Ebert (1991) found that in *C. brachyurus* opaque bands are deposited in spring or summer.

Brown and Gruber (1988) found that the change in angle in *Negaprion brevirostris* was not laid down

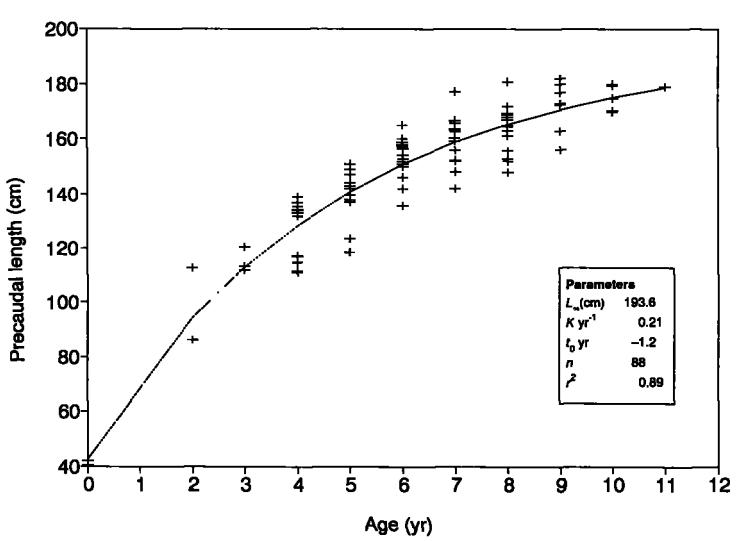

Figure 5

Von Bertalanffy growth curve for the blacktip shark, *C. limbatus*, sexes combined. Age estimates were obtained by examination of the unstained vertebrae with transmitted light.

at birth, but during the first summer growth. This provides a more plausible explanation for the nature of initial band deposition found in *C. limbatus* from southern Africa. The narrow, translucent band found immediately after the change in angle is deposited during the first winter growth, and subsequent opaque bands are the result of summer growth. Clearly, the relationship between change in angle and birth requires investigation.

Centrum edge analysis (where the ratio of translucent to opaque last bands differed significantly from the expected ratio) and the inability to perform marginal increment analysis did not shed light on the periodicity of band deposition. The inability to perform the latter on sharks older than four years is not unique to the present study. Killam and Parsons (1989) used only sharks with two or three growth rings for this analysis. In our study, the shark nets tended to select for large sharks; consequently few small *C. limbatus* were sampled and only five animals younger than four years were available.

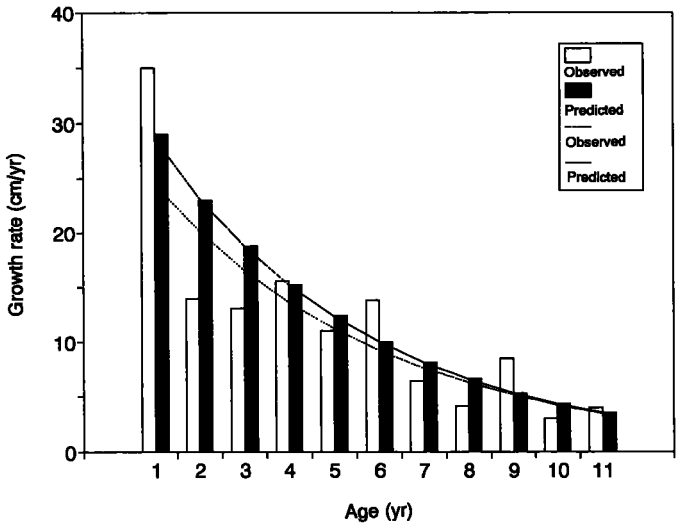

Figure 6

Observed and predicted annual growth of the blacktip shark, *C. limbatus*, in each age class.

All age estimates from vertebral growth rings are based on the assumption of an annual growth-ring deposition. According to Cailliet (1990), the annual periodicity of calcified growth zones has been proven for only five species and partly confirmed for 25 species, including *C. limbatus* (Branstetter, 1987, a and c; Killam and Parsons, 1989). A project was initiated recently in which all shark species, including *C. limbatus*, found alive in NSB nets were injected with oxytetracycline. In this study, growth ring periodicity for *C. limbatus* from southern Africa could not be confirmed, owing to a lack of holding facilities for large sharks and to the absence of any recaptured sharks injected with oxytetracycline.

A linear relationship between vertebral diameter and animal length was also found in *C. limbatus* by Branstetter (1987a) and Killam and Parsons (1989) and has been found in several other shark species (Cailliet et al., 1983b; Schwartz, 1984; Branstetter, 1987b). The existence of this relationship in the present study justified the use of the Dahl-Lea method of back calculations. These back calculations were not used to confirm growth-ring periodicity, because this method is based on several assumptions and has inherent problems (Smith, 1983) but was used to test for Lee's phenomenon and to derive a comparison with observed values. Unfortunately, the use of mean age estimates in this study created discrepancies in back calculations. The number of observed lengths per age class, plus the number of back-calculated lengths in the next age class, does not always add up to the total number of observed lengths. This phenomenon is evident in Table 2.

Mean back-calculated lengths were lower than observed values, as was found by Killam and Parsons (1989). Branstetter (1987a) found that observed lengths were slightly greater than back-calculated values. Lee's phenomenon was encountered in the present study. Even the exclusion of slow-growing individuals in age classes with few individuals did not affect the phenomenon. Killam and Parsons (1989) noted that it appeared to occur at some ages, but no consistent trend was identified. Branstetter (1987a) found no evidence of Lee's phenomenon in *C. limbatus*.

Age and growth estimates

The mean back-calculated birth size was slightly lower than the size of the neonates, as found by Branstetter (1987a) and Killam and Parsons (1989) (Table 3). On the basis of neonate sizes, *C. limbatus* from KwaZulu-Natal is born at a slightly larger size than are those from the Gulf of Mexico. Branstetter (1987a) remarked that in general *C. limbatus* is smallest in the northwestern Atlantic and largest in the Indian Ocean. This is not only evident in birth sizes but also in sizes at maturity and maximum sizes (Table 3).

On the KwaZulu-Natal coast, *C. limbatus* of both sexes mature at similar ages, males at six years and females at seven years. They mature at similar

Table 3

Comparison of life history and von Bertalanffy growth parameters for *C. limbatus* from different regions.

Parameters	Northwestern Gulf of Mexico, Branstetter (1987a)	Tampa Bay, Florida, Killam and Parsons (1989)	KwaZulu-Natal, east coast of South Africa
L_∞ (cm)	128.7	121.6 ♂ 142.9 ♀	193.6
K (yr^{-1})	0.274	0.276 ♂, 0.197 ♀	0.21
t_0 (yr)	–1.2	–0.88 ♂ –1.15 ♀	–1.2
Age at maturity (yr)	4–5 ♂ 7–8 ♀	4–5 ♂ 6–7 ♀	6 ♂ 7 ♀
Length at maturity (cm)	94 ♂ 109–113 ♀	97–99 ♂ 115–118 ♀	150 ♂ 156 ♀
Oldest animal (yr)	5.8 ♂ [1] 9.3 ♀	9 ♂ 10 ♀	10 ♂ 11 ♀
Length of oldest animal (cm)	108 ♂ 125 ♀	117 ♂ 131/132 ♀	179 ♂ 179 ♀
Observed maximum length (cm)	108 ♂ 125 ♀	117 ♂ 134 ♀	182 ♂ 181 ♀
Mean back-calculated birth length (cm)	39	37 ♂ 36 ♀	42
Mean neonate length (cm)	43 (n=33)	42 (n=1)	47[2] (n=3)
n	13 ♂, 34 ♀, 7 unknown	54 ♂, 86 ♀	51 ♂, 41 ♀

[1] This value does not reflect the attainable age (Branstetter, 1987a).
[2] Converted from Bass et al. (1973).

lengths (males: 146–150 cm, n=728; females: 151–155 cm, n=615) and attain the same maximum size of 190 cm (Dudley and Cliff, 1993b). The calculated L_∞ of 193.6 cm is close to these observed maximum lengths which were far greater than those reported by Killam and Parsons (1983) and Branstetter (1987a), in which males mature at less than 100 cm and females at 110–120 cm, with females attaining a greater maximum length than did males (Table 3).

Immature *C. limbatus* from KwaZulu-Natal grew more rapidly than those from other areas. Juveniles grew an average of 24 cm/yr and adolescents 11–13 cm/yr. Appropriate conversion of the growth rates obtained by Killam and Parsons (1989) reveals adolescent growth of 7–8 cm/yr. Branstetter (1987a) found that juveniles grew 15 cm/yr, which slowed down to 8 cm/yr through adolescence. While individuals from the two blacktip shark populations mature at similar ages, especially females, their corresponding lengths are markedly different (Table 3). After maturity, the difference in growth rates were less marked: 5–6 cm/yr in our study, 4–5 cm/yr (Branstetter, 1987a), 2–3 cm/yr (Killam and Parsons, 1989), but maximum lengths showed a marked difference at similar ages (Table 3).

The differences in growth rates between the populations appear to be large. It is tempting to attribute the differences to factors such as sample size and sampling bias, preparation techniques, and reader accuracy and precision (Cailliet et al., 1990). A comparison of two ring-enhancing methods revealed that with the BT ageing method, the growth rate for juvenile sharks from KwaZulu-Natal was about 23 cm/yr and for adolescents 10–11 cm/yr. These values are

similar to those obtained with the UT method and higher than those from the Gulf of Mexico. With the BT method, mature sharks grew at a rate of 3 cm/yr, which is slower than the 5–6 cm/yr of the UT method, but similar to the values obtained by Killam and Parsons (1989).

It is therefore possible that the UT method, by overestimating the growth of mature animals, may underestimate the age of these sharks. Nevertheless, given the large differences in size at birth and maturity and in maximum size between sharks of the two populations (Table 3), there is no apparent reason to question the large differences in growth rates between immature sharks of the two populations.

Dudley and Cliff (1993b) found that 66% of *C. limbatus* caught in NSB nets were mature. If age at maturity of females is taken at seven years, maximum age at 11 years, the gestation period as 14 months, and the median litter size as six (Dudley and Cliff, 1993b), the maximum fecundity of a female is about 24 pups. Most carcharhinids have a two-year reproductive cycle (Branstetter, 1981), but there is evidence for a three-year reproductive cycle in *C. limbatus* from South Africa (Dudley and Cliff, 1993b). Catch rates for this species since 1978, the earliest period for which accurate catch data are available, have shown no trend (Dudley and Cliff, 1993b) and can be interpreted as reflecting a relatively constant annual harvesting of immigrants (Wallet, 1973; Cliff et al., 1988b). Despite its low fecundity, catches are sustained by the wide distribution of *C. limbatus* in the western Indian Ocean, in which the small netted region falls largely outside the nursery grounds of this species (Dudley and Cliff, 1993a).

Acknowledgments

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An alternative approach to estimating growth parameters from length-frequency data, with application to green tiger prawns

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Abstract.—An alternative approach, Central Location Measure, to estimating the growth parameters from length-frequency data was proposed and applied to green tiger prawns, *Penaeus semisulcatus*, from Kuwait waters. The proposed method estimates mean length at age by defining a central location around the mode of the length-frequency distribution for a cohort and then estimates the growth parameters by using the method of the nonlinear least squares. The variances and covariances for the growth parameters derived from the nonlinear-fitting technique enable statistical comparisons of growth performance between sexes, cohorts, or populations. Bootstrap simulations indicated that the proposed method was satisfactory in estimating the growth parameters for green tiger prawns, and that, therefore, it may be applied to other short-lived crustacean species with discontinuous recruitment. Significant differences in growth between male and female green tiger prawns in Kuwait waters were detected by using a multivariate test ($P<0.005$), and annual variations in growth were more obvious in males than in females, indicating that growth of males may be more vulnerable to environmental changes.

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Growth parameters for crustacean populations are usually estimated from length-frequency data because of the lack of reliable methods for ageing decapods. Pauly and David (1980) integrated Petersen's method (Petersen, 1891) and Modal Class Progression Analysis (George and Banerji, 1964) into a single approach named ELEFAN I, which has been implemented in the computer software of Compleat ELEFAN (Pauly, 1987; Gayanilo et al., 1989). It has been widely applied in growth studies, especially in the tropical and subtropical areas. Shepherd (1987) proposed the SLCA method which performs a similar analysis to ELEFAN I in that both methods estimate the growth parameters by detecting the peaks and troughs in the length-frequency data; SLCA, however, applies a different goodness-of-fit function in model estimation (Holden and Bravinton, 1992). Harding (1949), Cassie (1954), Tanaka (1956), Hasselblad (1966), Bhattacharya (1967), MacDonald and Pitcher (1979), and Sparre (1987a) developed methods for analysis of length-frequency distributions based on the normal distribution assumption of the length-frequency for each cohort. McNew and Summerfelt (1978) discussed the case when the length distribution at each age was not normal. Some computer programs (Abramson, 1971; Young and Skillman, 1975; Sparre, 1987b; Sparre et al., 1989) were developed for implementing these parametric methods. A difficulty in applying probability distributions to separate each age group is that the breaking points between age groups can be quite ambiguous owing to the problems of overlapping distributions. Schnute and Fournier (1980) proposed an approach using biological structure as constraints to eliminate the ambiguity.

All the above methods are based on information on the central location of the length-frequency data. There are many ways to measure the central location of a distribution, such as the mode if the distribution is symmetric, the median, the mean, and the trimmed mean. The mean is sensitive to outlying values in a sample, whereas the mode and median are insensitive to these outliers. The trimmed mean is a compromise between the mean and median in the sensitivity to outliers (Devore, 1987) and might be preferred in order to obtain a representative location of the length distribution of an animal by a sample. For a species with multiple overlapping cohorts in length distribution, however, it is impossible to estimate the mean, median, and trimmed mean without an assump-

tion of the mixture of the components in the distribution. Following the idea of the trimmed mean and the idea of the mode, one is able to define a central location which is located around the mode with a certain amount of spread. A central value can be estimated from this spread and used to represent the mean length for the cohort at time i. The estimated mean length from several length intervals around the mode should be more robust than the mode in representing the growth of a cohort, especially when the length distribution is skewed, which is often the case for small-size samples. In this study, an approach using the mean length, estimated from the central part of the distribution, for estimating the parameters of a seasonal von Bertalanffy growth equation was proposed and applied to green tiger prawns, *Penaeus semisulcatus*, in Kuwait waters. With the proposed method, which might be termed the Central Location Measure, one is able to apply the methods of the linear or nonlinear least squares in order to estimate the growth parameters with variances and covariances and thus to study the statistical differences in growth performance between sexes and between cohorts.

Materials and methods

The seasonal growth model and the fitting technique

Various versions of the seasonal growth models which incorporate some parameters defined by season into the von Bertalanffy model (von Bertalanffy, 1938) have been proposed (Ursin, 1963; Pitcher and MacDonald, 1973; Cloern and Nichols, 1978; Pauly and Gaschütz[1]). Among these models, Pauly-Gaschütz's model is the most widely used:

$$L_t = L_\infty \left\{ 1 - \exp^{\left[-K\left(t - t_0 + \frac{C}{2\pi}\sin 2\pi(t - t_s)\right)\right]} \right\} \qquad (1)$$

where L_t = the length at age t; L_∞ is the asymptotic length; K = the intrinsic growth rate; t_0 = the age at which the length of the animal is 0; and t_s and C are the parameters defining the seasonal growth patterns.

The seasonal growth model (Eq. 1) was fitted by using the nonlinear least squares method with SAS Proc NLIN (SAS, 1992). A SAS program for fitting the seasonal growth model with the method of the nonlinear least squares is available upon request. A multivariate test, Hotelling's T^2 statistic (Johnson and Wichern, 1992), was used to test the hypothesis of no differences in growth between two populations, i.e. H_0: $\beta_1=\beta_2$, if the assumption of the equality of the two covariance matrices holds; otherwise, an alternative statistic, T_v^2, for unequal covariance case (Johnson and Wichern, 1992; Hanumara and Hoenig, 1987) was used:

$$T_v^2 = (\hat{\beta}_1 - \hat{\beta}_2)'(D_1 + D_2)^{-1}(\hat{\beta}_1 - \hat{\beta}_2), \qquad (2)$$

where $\hat{\beta}$ and D_i = the vectors of the estimated growth parameters and the estimated covariance matrix of the growth parameters, respectively, for population i. The null hypothesis, H_0: $\beta_1=\beta_2$, is rejected if $T_v^2 \geq \chi^2_{\alpha;p}$, where p is the dimension of multinormal populations. The hypothesis of equality of m covariance matrices, H_0: $\Sigma_1 = \Sigma_2 = \ldots = \Sigma_m$, was tested by using an approximate chi-squared statistic MC^{-1} modified from Morrison (1990, p. 297), for which

$$M = \sum_{i=1}^{m}(n_i - 1)\ln|S| - \sum_{i=1}^{m}(n_i - 1)\ln|S_i|$$

and

$$C^{-1} = 1 - \frac{2p^2 + 3p - 1}{6(p+1)(m-1)}\left(\sum_{i=1}^{m}\frac{1}{n_i - 1} - \frac{1}{\sum_{i=1}^{m}(n_i - 1)}\right),$$

where n_i is the sample size for population i; ln indicates natural logarithm; S_i (the estimate of Σ_i) is set as $S_i=n_i D_i$ in this study as suggested by Hanumara and Hoenig (1987); S is the pooled estimate of the common covariance matrix of the estimated growth parameters; and $|S|$ represents the determinant of the matrix S.

Bernard (1981) and Hanumara and Hoenig (1987) discussed the application of Hotelling's T^2 in comparing the growth of fish; however, the statistics proposed by Bernard (1981) and Hanumara and Hoenig (1987) were different by a constant multiple, because they treated the covariance matrix of the growth parameters differently. In this study, the estimated covariance matrix of the growth parameters has the same form as that proposed by Hanumara and Hoenig (1987), therefore the latter was used.

The approach to obtaining length-at-age data

To estimate the parameters in model 1 (Eq. 1), one needs a set of length-at-age data. The method pro-

[1] Pauly, D., and G. Gaschütz. 1979. A simple method for fitting oscillating length growth data, with a program for pocket calculators. Int. Coun. Explor. Sea, Council Meeting 1979/G:24, 26 p.

posed in this study to obtain length-at-age data includes the following steps: 1) arrange the monthly length-frequency samples in sequential order (the data series should begin with the month in which the new recruitment is first detected); 2) identify the mode representing the newly recruited cohort in the length-frequency distribution of the first month (this should be the smallest in size in the length distribution); 3) follow the movement of this mode from month to month to find its location in the time series; 4) define the width of the central location spreading from the mode in each month; 5) use the length data in the range of the central location to calculate the mean length weighted by the frequencies (this mean length is considered to be the mean length at month i); and 6) according to the information on the spawning season, define the birth-month, a, for the cohort (then the age for that cohort in month i can be estimated by $age = i - a$). A length-at-age data set is then established. Like that in other length-frequency analysis methods such as ELEFAN I (Pauly et al., 1984), age here should be considered relative age instead of true age. One might be able to adjust it if information on the observed spawning season for each year was available. The change of relative age, however, would only change the location but not the shape of the growth curve. Note that step 3 might be difficult for a long-lived species with highly overlapping cohorts at old ages or for species with continuous recruitment and thus result in multiple peaks in the length-frequency distribution (Brothers, 1979). For a species with distinct modes and discontinuous recruitment in one year, like green tiger prawns in Kuwait waters, the modal progression of a cohort can be easily followed from month to month. This will be shown below. Step 4 involves making subjective decisions regarding the width of the central location. If the length distribution is fairly symmetric around the mode and the cohorts in the length distribution do not highly overlap, the estimates of growth parameters should not be sensitive to the subjective selection of the width. The overlap index proposed by McNew and Summerfelt (1978) can be applied as a guideline to define the degree of overlap among the adjacent age-class distributions. The Cental Location Measure should work like the trimmed mean for a single cohort case.

Data collection

In order to obtain a series of monthly length-frequency samples that are representative of the population, monthly research vessel surveys were carried out from May 1986 to July 1990 in Kuwait waters with RV *Bahith*, a stern trawler (679 tons in gross tonnage) of the Kuwait Institute for Scientific Research. Surveys were interrupted in June 1986 and December 1988 because of logistical problems. Each monthly survey included 7 to 10 fixed stations in Kuwait waters and each tow lasted from 30 to 50 min. All shrimp were sorted and weighed prior to examination of the entire catch (or a 3- to 6-kg subsample) to determine species composition and length frequencies. Carapace length, rear margin of the orbit to the posterior edge of the carapace (Dall et al., 1990), was measured to the nearest 1 mm.

Kuwait waters were partitioned into three areas (Kuwait Bay, Middle Area, and Southern Area) on the basis of species distribution and geographical considerations (Xu et al., 1995). The relative size ratios of the three areas of Kuwait Bay: Middle Area: Southern Area were 3: 4: 5, respectively. These ratios were used as weighting factors in the compilation of monthly length frequencies from the data of each sampled station.

Results

Length at age

The monthly carapace length (CL) frequency showed distinct modes and clear modal progression for the 1986, 1987, 1988, and 1989 spring cohorts of male and female green tiger prawns. The central location of the length distribution in each month was defined by spreading the distribution from the mode up and down for 2–3 mm. Tables 1 and 2 provide part of the monthly length-frequency data for male and female shrimp, respectively, to show the central locations (bold numbers) used to calculate the mean length. For a length distribution with a mode located in one interval, three intervals from the mode to each side were selected. Otherwise, for a mode located in more than one interval, two intervals from the mode to each side were selected. The number of sampled shrimp was usually small for the new recruits owing to gear selectivity, and for the oldest shrimp owing to low abundance. The width of the central location in these cases was defined by recognizing a breaking point at which the smallest number was observed, e.g. 20 mm in May 88 and 32 mm in August 89 for males (Table 1). If two peaks are located closely (e.g. June and July 1988 for females), a moving average over three intervals was used to define the mode. For example, the mean numbers of shrimp over 22–24, 23–25, 24–26, and 25–27 mm were 59, 62, 62, and 58, respectively, for July 1988 females; therefore the mode was defined from 23–26 mm. If two peaks from the same cohort were located far from each other (e.g. September 1988), they were consid-

Table 1

Monthly carapace length (CL) frequency of male green tiger prawns, *Penaeus semisulcatus*, in Kuwait waters sampled by RV surveys in 1988 and 1989. The bold numbers indicate the range of the central location used to calculate the mean length.

CL (mm)	1988							1989							
	May	Jun	Jul	Aug	Sep	Oct	Nov	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug
12	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0
13	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
14	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0
15	**4**	0	0	0	0	0	0	0	0	0	0	12	0	1	0
16	**2**	0	3	0	0	0	0	0	0	0	0	17	0	0	0
17	**4**	1	7	0	0	0	0	0	0	0	0	19	0	0	0
18	**3**	3	7	0	2	0	0	0	0	0	0	23	5	0	0
19	**3**	8	24	0	0	0	0	0	0	0	0	9	6	3	6
20	0	**28**	**24**	3	2	0	0	0	0	0	0	6	3	6	8
21	1	**48**	**46**	4	15	0	0	0	0	0	0	9	25	12	25
22	1	**52**	**59**	13	51	0	0	0	0	0	0	9	24	17	35
23	1	**59**	**66**	29	59	0	0	0	0	0	0	4	52	30	70
24	1	**43**	**59**	44	99	2	0	0	0	0	0	0	75	42	96
25	1	**35**	**55**	**78**	75	4	1	1	0	0	0	2	159	34	173
26	0	**26**	**21**	**72**	**68**	4	3	0	0	0	0	0	32	23	255
27	2	6	31	**94**	**120**	**8**	6	1	0	0	1	0	16	22	343
28	4	6	10	**110**	**180**	**27**	6	1	1	1	3	1	10	12	127
29	5	7	1	**56**	**230**	**48**	**12**	**2**	1	2	4	1	18	3	46
30	6	6	1	**21**	**169**	**83**	**27**	**4**	**5**	**3**	**5**	**1**	3	3	1
31	5	6	1	**12**	**37**	**54**	**40**	**19**	**9**	**16**	**14**	**2**	2	3	1
32	3	2	0	1	**10**	**12**	**42**	**16**	**19**	**24**	**48**	**7**	**4**	**3**	**1**
33	5	2	0	3	1	**4**	**17**	**14**	**17**	**25**	**46**	**7**	**4**	**3**	**1**
34	3	1	0	1	0	0	**11**	**6**	**3**	**6**	**25**	**4**	**5**	**7**	**2**
35	1	1	0	1	0	1	2	4	**2**	**4**	**7**	**2**	**4**	**5**	**3**
36	2	1	7	1	3	0	1	0	1	2	4	3	1	**1**	**3**
37	0	0	0	0	3	0	0	0	2	1	4	1	0	**1**	0

ered to represent different recruitments, and only the one that could be followed based on biological grounds was used in growth parameter estimation (Schnute and Fournier, 1980). Recruitment was usually first detected in May or June for the spring cohort and a minor recruitment in September or October in some years (Tables 1 and 2). The birthday of the spring cohort, based on the spawning study of Mohammed et al. (1981) was considered to be January 1. The age of the 1986 spring cohort on 18 May which was the survey date was then calculated to be 4.58 months or 0.38 yr. The ages of the cohort in the following months were calculated in the same way, and the weighted mean carapace length for the cohort at each month or age was then calculated by using the defined central range (Table 3).

Estimation of the seasonal growth parameters

The growth parameters, L_∞, K, t_0, C, t_s, were estimated for males and females of the 1986, 1987, 1988, and 1989 spring cohorts (Table 4). The hypothesis of equality of the covariance matrices between sexes or cohorts was rejected in all cases except for the comparison of 1986 and 1987 females (Tables 5 and 6). Therefore, the differences between vectors of the growth parameters were tested by using Equation 2 for all the pairs except for the 1986 and 1987 females which were tested with Hotelling's T^2. Significant differences in growth between male and female shrimp were detected ($P<0.005$) for all four cohorts (Table 5). The differences in growth of female shrimp between cohorts were not significant except for the 1986 and 1988 cohorts ($P<0.05$). The vectors of growth parameters for male shrimp differed significantly between 1986, 1987, and 1988 cohorts, but the growth of the 1989 cohort was not found to be significantly different from the others.

Discussion

Accuracy of the proposed method

The bootstrap technique (Efron, 1982) was applied to examine the effects of variations in length fre-

Table 2

Monthly carapace length (CL) frequency of female green tiger prawns, *Penaeus semisulcatus*, in Kuwait waters sampled by RV surveys in 1988 and 1989. The bold numbers indicate the range of the central location used to calculate the mean length.

CL	1988							1989								
(mm)	May	Jun	Jul	Aug	Sep	Oct	Nov	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
12	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
13	2	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0
14	1	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0
15	**2**	2	0	0	0	0	0	0	0	0	0	10	2	0	0	0
16	**2**	1	3	0	0	0	0	0	0	0	0	15	0	0	0	0
17	**3**	2	7	0	0	0	0	0	0	0	0	11	0	0	0	0
18	**4**	5	17	0	0	0	0	0	0	0	0	23	0	0	0	0
19	**3**	6	13	0	0	0	0	0	0	0	0	15	0	0	0	0
20	**2**	10	7	1	0	0	0	0	0	0	0	6	1	3	11	1
21	**1**	**20**	**28**	1	3	0	0	0	0	0	0	2	0	6	6	1
22	0	**43**	**46**	0	7	0	0	0	0	0	0	10	3	11	18	1
23	0	**53**	**68**	3	21	0	0	0	0	0	0	6	2	20	20	1
24	1	**37**	**65**	8	16	0	0	0	0	0	0	6	1	26	46	3
25	0	**51**	**53**	31	37	0	0	0	0	0	0	2	23	28	70	17
26	0	**33**	**69**	25	44	0	0	0	1	0	0	2	5	22	47	13
27	1	**22**	**53**	37	63	1	0	0	1	0	0	0	18	23	94	16
28	1	15	**51**	**50**	42	1	1	0	0	0	0	0	39	28	131	17
29	0	8	23	**41**	33	3	1	0	0	0	0	0	0	23	92	29
30	0	10	24	**60**	**67**	4	3	0	1	0	0	0	8	25	107	38
31	0	4	18	**52**	**84**	10	2	0	0	0	0	0	3	17	115	83
32	0	1	12	**58**	**75**	9	6	0	0	0	0	1	0	14	107	140
33	0	1	14	**34**	**99**	14	9	1	1	1	1	0	0	10	77	128
34	1	0	0	**31**	**81**	25	7	2	1	1	2	0	0	14	50	166
35	0	2	0	29	**81**	**36**	13	4	1	0	3	0	0	4	23	110
36	1	1	0	16	**63**	**30**	9	4	1	2	1	2	1	1	18	138
37	1	1	0	10	74	**42**	**15**	4	2	3	3	1	1	1	7	82
38	2	2	4	8	40	**49**	**24**	6	2	4	3	0	0	2	2	66
39	1	1	1	3	20	**31**	**34**	**3**	4	3	3	0	0	5	2	20
40	1	1	0	3	19	**16**	**36**	**8**	**4**	3	3	1	0	1	2	25
41	1	3	0	2	0	**21**	**31**	**10**	**4**	**10**	7	1	4	1	5	16
42	3	0	0	0	3	10	**29**	**10**	**6**	**14**	**9**	**2**	**3**	1	17	0
43	1	0	0	1	4	0	**20**	**7**	**7**	**15**	**12**	**2**	**4**	**1**	0	0
44	4	1	1	2	0	4	13	**5**	**4**	**17**	**16**	**4**	**3**	**1**	1	0
45	2	3	1	1	0	2	9	3	**3**	**15**	**18**	**5**	**5**	**2**	**1**	**0**
46	2	1	1	1	0	1	5	2	3	**12**	**11**	**4**	**3**	**4**	**0**	**0**
47	4	2	7	1	1	1	0	1	3	**7**	**9**	**4**	**4**	**2**	**0**	**0**
48	2	1	7	0	0	0	1	0	0	4	5	**3**	**2**	**2**	**2**	**2**
49	1	0	0	1	2	0	1	0	0	1	1	1	0	**1**	**0**	**0**
50	1	0	0	0	1	1	0	0	0	1	1	1	0	1	**0**	**0**
51	0	0	0	0	1	0	0	0	0	0	0	0	0	0	**1**	**0**

quency on the growth estimates by the proposed method. The monthly length-frequency data in Table 1 were resampled 100 times with replacement and thus 100 length-frequency data sets were generated which were used to estimate the growth parameters with the proposed method in this study. The bias caused by the variations in length-frequency distributions was estimated from 100 bootstrap estimates compared to the true value, i.e. *bias* = *estimate* − *true* for K, t_0, C, and t_s, and *bias* = (*estimate* − *true*)/10 for L_∞. The boxplot (Fig. 1) showed that the bias distributions were fairly symmetrical, and the medians of the biases in bootstrap estimates for growth parameters, shown as a bar in the box of the boxplot, were located very close to the center of the box and to the horizontal zero line. The means of L_∞, K, t_0, C, and t_s from 100 bootstrap estimates were 35.88 mm, 1.98 yr^{-1}, −0.06 yr, 0.73, and −0.41 yr which were very close to the true values (Table 4). The bootstrap simulations indicated no trend of over- or under-estimation of the growth parameters by the proposed method. The proposed method works well for green

tiger prawns in Kuwait waters because this species is short lived and has only one main recruitment (van Zalinge, 1984) so that different cohorts can be recognized clearly and the central location of the length distribution for each cohort can be defined easily. This method may be used for other short lived species with discontinuous recruitment.

The sensitivity of the growth estimates to the subjective selections of the spread width of the central location was investigated with the length-frequency

Table 3

Carapace length (CL) at age of male and female green tiger prawns, *Penaeus semisulcatus*, in Kuwait waters for cohorts 1986–89.

	1986			1987			1988			1989		
Month	Age (yr)	CL ♂ (mm)	CL ♀ (mm)	Age (yr)	CL ♂ (mm)	CL ♀ (mm)	Age (yr)	CL ♂ (mm)	CL ♀ (mm)	Age (yr)	CL ♂ (mm)	CL ♀ (mm)
May	0.38	19.39	21.11	0.36	—	15.23	0.39	16.91	17.71	0.39	17.55	17.54
Jun	—	—	—	0.44	23.26	24.22	0.49	22.86	23.94	0.44	23.57	23.58
Jul	0.55	25.04	27.92	0.55	24.41	25.54	0.53	23.02	24.72	0.52	24.26	25.02
Aug	0.61	26.95	30.02	0.61	27.16	30.74	0.63	27.24	30.77	0.60	26.36	28.39
Sep	0.73	28.11	32.65	0.69	27.84	33.33	0.70	28.57	32.98	0.70	28.40	33.97
Oct	0.78	29.32	37.41	0.78	29.67	36.80	0.78	29.84	37.64	0.83	30.28	39.09
Nov	0.86	30.07	39.28	0.86	29.26	40.04	0.85	31.38	40.11	0.89	31.67	42.63
Dec	0.94	30.65	40.60	0.97	31.57	42.70	—	—	—	0.95	31.47	41.99
Jan	1.03	31.42	40.90	1.05	32.30	41.94	1.03	31.92	41.59	1.04	31.89	41.37
Feb	1.11	30.35	40.29	1.12	32.33	43.03	1.12	32.16	42.48	1.11	31.71	42.91
Mar	1.19	31.41	43.44	1.20	32.10	43.14	1.21	32.36	43.89	1.19	31.93	43.27
Apr	1.28	30.69	44.82	1.28	32.73	44.53	1.29	32.64	44.47	1.29	32.43	44.03
May	1.36	31.32	45.28	1.39	33.15	46.77	1.39	32.73	45.30	1.37	32.48	45.05
Jun	1.44	32.75	45.33	1.49	33.46	45.76	1.44	33.69	44.82	1.48	33.41	45.39
Jul	1.55	34.31	45.40	1.53	34.45	47.37	1.52	33.99	46.13	1.52	33.33	45.06
Aug	1.61	33.86	46.34	1.63	34.23	47.13	1.60	34.76	47.86	1.58[1]	34.63	45.68
Sep	1.69	—	46.71	1.70	—	49.24	1.70	—	47.78	—	—	—

[1] The survey date was 28 July 1990.

Table 4

Growth parameters of green tiger prawns, *Penaeus semisulcatus*, in Kuwait waters estimated by using the proposed method. SE represents the standard error. L_∞ is the asymptotic length; K is the intrisic growth rate; t_0 is the age at which the length of the animal is 0; and t_s and C are the parameters defining the seasonal growth patterns.

	L_∞	SE	K	SE	t_0	SE	t_s	SE	C	SE
Cohort	(mm)		(yr^{-1})		(yr)		(yr)			
♂	37.83	1.92	1.15	0.26	–0.39	0.13	–0.43	0.03	0.96	0.18
1986										
♀	49.71	2.53	1.75	0.48	0.04	0.11	–0.22	0.12	0.25	0.23
♂	37.51	3.02	1.26	0.57	–0.39	0.30	–0.30	0.06	0.45	0.31
1987										
♀	51.13	2.30	1.81	0.41	0.10	0.08	–0.34	0.08	0.30	0.25
♂	35.88	0.76	1.95	0.27	–0.05	0.07	–0.42	0.03	0.75	0.16
1988										
♀	51.60	1.51	1.62	0.21	0.05	0.05	–0.32	0.03	0.54	0.14
♂	34.63	1.27	2.33	0.78	–0.01	0.16	–0.48	0.10	0.49	0.36
1989										
♀	47.95	3.44	2.15	0.98	0.09	0.16	–0.25	0.09	0.55	0.36

data in Table 1 by using five scenarios, i.e. modes, 1–2 mm, 2–3 mm, 3–4 mm, and as wide as possible to spread from the mode to each side. Scenario 1 is similar to the modal progression analysis (George and Banerji, 1964) and scenario 3 is the selection used in this study. The growth estimates for the five scenarios were very similar, and the growth curve estimated with scenario 3 was located in the middle of the five curves (Fig. 2). The insensitivity of the proposed method to the subjective selection of the spread width, as mentioned in the Material and Methods section, may be due to the fairly symmetrical length distribution around the distinct mode of the cohort. The spread from the mode can only go up and down for 2–3 mm for the old age classes (e.g.

Table 5

Test of equality of covariance matrices of growth parameters between sexes using the statistic MC^{-1} and test of differences in growth between sexes of green tiger prawns, *Penaeus semisulcatus*, in Kuwait waters using the statistic T^2_v.

Cohorts		1986	1987	1988	1989
H_0:$\Sigma_♂=\Sigma_♀$	Statistic	91.45	95.55	57.95	74.14
	v	15	15	15	15
	$P<$	0.005	0.005	0.005	0.005
	$\chi^2_{0.005;15}$	32.8	32.8	32.8	32.8
H_0:$\beta_♂=\beta_♀$	Statistic	392.53	664.87	445.76	281.05
	v	5	5	5	5
	$P<$	0.005	0.005	0.005	0.005
	$\chi^2_{0.005;5}$	16.7	16.7	16.7	16.7

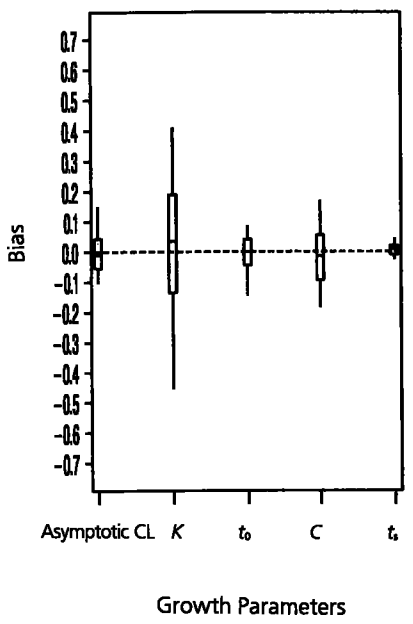

Figure 1

Boxplot of the bias in the estimates of seasonal growth parameters, based on 100 bootstrap simulations compared with true values.

Table 6

Test of equality of covariance matrices of growth parameters between cohorts using the statistic MC^{-1} and test of differences in growth between cohorts of green tiger prawns, *Penaeus semisulcatus*, in Kuwait waters using Hotelling's T^2 for the pair of 1986 and 1987 cohorts of female and T^2_v for the rest.

Cohorts			1987	1988	1989
H_0:$\Sigma_i=\Sigma_j$	♂	1986	47.09 ($P<0.005$)	99.20 ($P<0.005$)	124.79 ($P<0.005$)
		1987	—	115.99 ($P<0.005$)	122.66 ($P<0.005$)
		1988	—	—	69.48 ($P<0.005$)
	♀	1986	18.92 ($P>0.1$)	47.37 ($P<0.005$)	67.96 ($P<0.005$)
		1987	—	46.94 ($P<0.005$)	52.74 ($P<0.005$)
		1988	—	—	81.85 ($P<0.005$)
H_0:$\beta_i=\beta_j$	♂	1986	16.19 ($P<0.01$)	26.73 ($P<0.005$)	6.26 ($P>0.25$)
		1987	—	37.49 ($P<0.005$)	8.02 ($P>0.1$)
		1988	—	—	6.46 ($P>0.25$)
	♀	1986	1.45 ($P>0.1$)	12.30 ($P<0.05$)	6.59 ($P>0.25$)
		1987	—	1.50 ($P>0.9$)	4.28 ($P>0.5$)
		1988	—	—	4.54 ($P>0.25$)

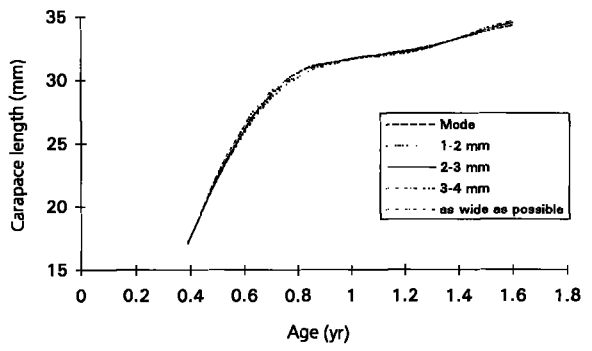

Figure 2

Growth curves estimated with five scenarios of width selection of the central locations by using the proposed method with the data in Table 1. The legend indicates the width of the spread from the mode to each side.

June and July 1989) in order to avoid the overlapping part with other cohorts; therefore, the ranges of the central locations for these length distributions were the same for scenarios 3, 4, and 5. This may reduce the variations in growth parameters estimated by the five scenarios and indicates that the spread of 2–3 mm is a reasonable choice.

Comparison between the ELEFAN I, Bhattacharya, and proposed methods

Statistical tests with the modified Hotelling's T^2 statistic (Hanumara and Hoenig, 1987) and Equation 2 indicated no significant difference (P>0.1) in growth parameters estimated by the proposed method and the Bhattacharya method (Table 7) with the same length-frequency data. The Bhattacharya method estimates the population density function of the length-frequency distribution for a cohort on the basis of the normal assumption; therefore, the method requires very complicated calculations and involves a subjective selection of the estimated population density function (Pauly and Caddy, 1985). The proposed method, however, avoids the tedious calculations. Therefore, the sophisticated computer packages for length-frequency analysis are not necessary with the proposed method. Moreover, at least for the oldest age class of green tiger prawns, to define the width of the central location is more objective than to define the population density function. The Bhattacharya method has an advantage over the proposed method in that it estimates the mean length at age with standard deviation, which can be used to estimate the degree of overlap among cohorts (McNew and Summerfelt, 1978).

It is impossible to compare the proposed method with ELEFAN I by an analytical approach because ELEFAN I cannot estimate the variances of the growth parameters. The growth parameters estimated by using ELEFAN I (Table 8) with the same length-frequency data were similar to those estimated by the proposed method, although the parameter K estimated by ELEFAN I tends to be lower (six out of eight) and the parameter C tends to be higher (six out of eight). The simulation studies by Rosenberg and Beddington (1987) and Isaac (1990)

Table 7

Growth parameters of green tiger prawns, *Penaeus semisulcatus*, in Kuwait waters estimated by using Bhattacharya method. SE represents the standard error.

	L_∞	SE	K	SE	t_0	SE	t_s	SE	C	SE
Cohort	(mm)		(yr^{-1})		(yr)		(yr)			
♂	39.01	1.87	1.08	0.22	–0.39	0.12	–0.45	0.03	0.80	0.15
1986										
♀	48.91	1.77	1.85	0.39	0.04	0.08	–0.21	0.06	0.43	0.17
♂	36.20	2.59	1.43	0.68	–0.36	0.31	–0.27	0.06	0.57	0.34
1987										
♀	51.29	2.60	1.49	0.36	–0.07	0.11	–0.23	0.03	0.69	0.20
♂	35.42	0.62	2.16	0.27	–0.01	0.06	–0.44	0.03	0.76	0.16
1988										
♀	51.00	1.76	1.68	0.26	0.06	0.06	–0.32	0.03	0.51	0.17
♂	34.39	1.10	2.89	1.06	0.11	0.16	–0.57	0.15	0.47	0.32
1989										
♀	47.02	2.83	2.48	1.16	0.14	0.16	–0.22	0.12	0.52	0.33

Table 8

The growth parameters of green tiger prawns, *Penaeus semisulcatus*, in Kuwait waters estimated by using ELEFAN I. WP represents winter point.

Cohort	L_∞ (mm)	K (yr^{-1})	WP (yr)	C
♂	36.13	1.5	0.50	0.7
1986				
♀	49.87	1.6	0.40	1.0
♂	36.83	1.5	0.10	0.6
1987				
♀	52.13	1.6	0.45	0.5
♂	37.13	1.6	0.10	0.8
1988				
♀	50.88	1.6	0.20	0.6
♂	36.13	1.4	0.20	0.8
1989				
♀	49.00	1.7	0.20	0.5

suggested that ELEFAN I underestimates the true value of K, and Rosenberg and Beddington (1987) concluded that ELEFAN I estimated K reliably only if the true value of K was known within about 25%. ELEFAN I also tends to have multiple maxima of the score function (Rosenberg and Beddington, 1987; Isaac, 1990), as found for the SLCA method (Basson et al., 1988; Isaac, 1990), which makes it difficult to select the best set of growth parameters from the multiple solutions. The proposed method has the advantage over ELEFAN I in that it applies a nonlinear least-squares technique with the Gaussian iterative method (SAS, 1992) for solution searching, which is more sensitive in defining the best set of growth parameters and which estimates variances and covariances for the growth parameters so that the growth between cohort and sexes can be compared statistically.

Castro and Erzini (1988) studied the effect of different recruitment patterns on ELEFAN I (Pauly and David, 1980) and modal progression analysis implemented in LFSA (Sparre, 1987b) with simulated length-frequency data. The results were generally encouraging, and ELEFAN I produced better estimates than did modal progression analysis for the case of multiple recruitment per year. However, for both methods, multiple recruitment makes it difficult to estimate growth parameters (Castro and Erzini, 1988). The recruitment pattern of green tiger prawns in Kuwait waters is relatively simple and the degree of overlap between cohorts is low. It would be worthwhile to test the performance of the proposed method for species with more complicated recruitment patterns and high overlapping cohorts with real or simulated data.

Implication of the variations in growth

The highly significant differences in growth between sexes of green tiger prawns is not surprising because female shrimp grow to be much larger than males. Female and male green tiger prawns in Kuwait waters are distributed in the same area and experience the same environmental changes, but the annual variations in growth curves between cohorts are more obvious for males than for females (Table 6). These variations suggest that the responses of the female and male shrimp to environmental factors might be different, and that the growth of males may be more vulnerable to environmental changes. A possible reason that females are less sensitive to environmental change is that they have more energy reserves that can be utilized to maintain homeostasis by shifting from anabolism to catabolism (Pickering, 1981). Female shrimp grow faster and become larger than males, have lower natural mortality, but with a higher market demand suffer higher fishing mortality (Xu et al., 1995) compared with males. All these differences between female and male shrimp should be taken into consideration when monitoring the shrimp fisheries, estimating the population abundance and biomass, and formulating management policy.

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Natural mortality of blue rockfish, *Sebastes mystinus*, during their first year in nearshore benthic habitats

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Much of the variation in year-class strength among marine fishes has been attributed to high mortality during the egg and larval stages (Ricker, 1954; Cushing, 1973; Beverton, 1984). However, for groundfish species that migrate from a pelagic to a benthic juvenile stage, there has been increasing suggestion that natural mortality during the early benthic juvenile stage may control year-class strength (Beverton, 1984; Sissenwine, 1984). These arguments stem from the following: 1) demonstration of density-dependent natural mortality of juvenile groundfish (Lockwood, 1980; Meyers and Cadigan, 1993); 2) cases where larval abundance and later year-class strength are uncorrelated (Bakun and Parrish, 1980; Saville and Schnack, 1981; and Fogarty et al., 1987); and 3) the reasoning that total natural mortality during the juvenile stage may be greater than during the egg or larval stage, because the juvenile stage lasts much longer (Sissenwine, 1984). These arguments were reviewed specifically for rockfish (*Sebastes* spp.) by Love et al. (1991), but the results were inconclusive.

Materials and methods

Off northern California, young of blue rockfish, *Sebastes mystinus*, released in the winter spend three to five months offshore as pelagic larvae and early juveniles and then settle to the benthos. During the course of monitoring annual recruitment of these benthic nearshore juveniles, data were collected from which mortality rates could be estimated for juvenile blue rockfish during their first year in the benthic stage. Annual population density estimates were the averaged counts made between July (when recruitment to nearshore habitats was complete) and mid-September of each year. The mortality estimates were based on counts from July through the following April. Exceptionally high or low counts were excluded when the distribution of juveniles was influenced by unusual oceanic conditions. Because the sampling began after settlement was complete, these estimates do not include mortality that occurs during or immediately following settlement.

First-year juvenile blue rockfish were counted along strip transects at three northern California sites during different years. Dark Gulch was sampled from 1985 to 1989, Salmon Point in 1987 and 1988, and Horseshoe Point in 1988 (Fig. 1). Each site covers approximately 10,000 m^2 and consists of high-relief rocky reefs surrounded by lower reefs and boulders with occasional sand patches interspersed. Rock surfaces shallower than 15 m were covered with benthic algae and bull kelp (*Nereocystis luetkeana*) from July through November, after which time the bull kelp was ripped up by winter storms.

One-minute strip-transect counts were made by two observers using SCUBA over bottom depths between 5 and 22 m (Fig. 2). Transects always began in the offshore portion of the study site and moved inshore. Direction changes were made perpendicular to the previous course, usually after one to three counts on the same heading. Observers swam 2 m off the bottom and counted first-year juvenile blue rockfish within 3 m in any direction during one-minute transects. Counts were made only when horizontal visibility was greater than 4 m. Twenty counts were made at each site (average total counts=19, range 10–35). All counts were made between 1000 and 1400 hours.

Results and Discussion

Natural mortality was estimated by using a catch-curve analysis based on the exponential decrease in fish abundance with age (Ricker, 1975; Vetter, 1988). Juvenile blue rockfish density during each one-minute count was transformed to $\ln(x+1)$ and plotted against age (days). The slope of the least-squares regression through the decreasing portion of the log-transformed density was the instantaneous rate of decrease, or natural mortality, provided there was no significant movement either into or out of the area. The mortality coefficients were calculated from the transformed one-minute counts rather than from daily averages in order to demonstrate the patchy nature of the data where a large portion of zero counts occurred ran-

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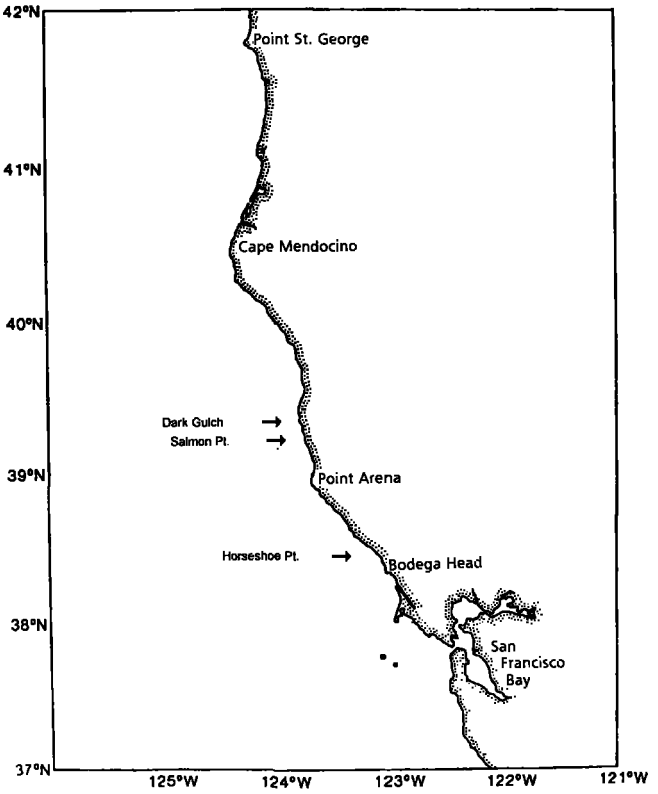

Figure 1

Northern California study sites: Dark Gulch and Salmon Point in Mendocino County, and Horseshoe Point in Sonoma County.

domly throughout each day's sampling. Mortality coefficients from individual counts and daily averages are nearly identical (because the daily sample size is consistent). For the individual counts, the coefficients of determination (r^2) are very small (because counts range from zero to a maximum number each day). However, if the daily averages were used, the coefficients of determination would be high (because the daily variation has been removed), but the probabilities of the tests of regression lines would be much lower (because of fewer degrees of freedom).

Estimates of daily natural mortality for first-year juvenile blue rockfish range from 0.001 to 0.008 day^{-1} (Table 1; Fig. 3) over the three sites and four years. The fit of data to the mortality model was good; five of the seven regressions were significant at the 99% level, and a sixth significant at the 92% level. The coefficients of determination were low owing to the large variability in the dependent variable (log-transformed density, ranging from zero to the maximum number) on each sampling date. The consistency of all the estimates, ranging over only a narrow span, from different years and locations, despite the large variance within the daily sampling, was probably the strongest validation of the mortality estimates.

Our estimates of natural mortality of juvenile blue rockfish are much lower than published values of natural mortalities for other juvenile fishes (Table 2). The values in Table 2 include all juvenile fish mortality coefficients estimated from catch-curve analysis and represent both different types of fishes (i.e. flatfish and roundfish) and different types of habitats (marine, estuarine, and freshwater). The low juvenile natural mortality is consistent with the estimates of low adult natural mortality based on the extreme longevity of this species (Leaman, 1991).

Mortality estimates were higher during years with stronger juvenile recruitment (Fig. 4). There was a positive relationship between mortality estimates and the strength of the annual population density estimates, with an eight-fold difference in mortality rate estimates corresponding to a twenty-four-fold difference in density. The relationship of natural mortality with population density seems to increase

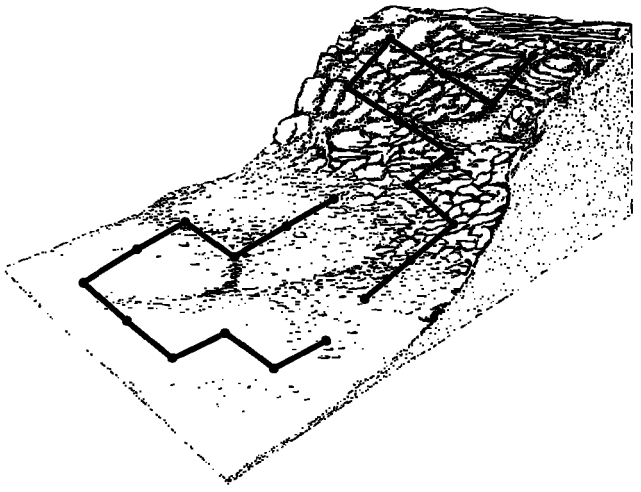

Figure 2

A sampling diagram depicting the 20 one-minute transects where juvenile blue rockfish, *Sebastes mystinus*, were counted. Counts began offshore and ended inshore.

to a certain point and then levels off to an asymptote. We feel that the asymptotic level-off is real, but because of the large variability in the daily counts (see Fig. 3), it may be a sampling artifact. Both Lockwood (1980) and Meyers and Cadigan (1993) found that density-dependent mortality occurred in juvenile marine fishes. Lockwood (1980) proposed a two-stage density-dependent mortality mechanism for juvenile plaice where normally piscivorous predators cause a baseline level of natural mortality and, in years when juvenile numbers are high, other predators switch to preying on juveniles. We feel that a similar process may occur with juvenile blue rockfish and that the natural mortality asymptote is the point at which these secondary predators are saturated.

For blue rockfish, density-dependent mortality in the benthic juvenile stage would reduce the interannual variation between subsequent adult year classes. An example of how density-dependent mortality would reduce interannual variation can be made by using the 1986 (a weak year class, see Fig. 4) and 1987 (a strong year class) data from Dark

Table 1

Instantaneous daily natural mortalities (M) for juvenile blue rockfish, *Sebastes mystinus*, during the period of July to April from three northern California sites by year. The analysis of variance of the fit of the estimate (F), degrees of freedom (df), probability (P), and coefficient of determination (r^2) are also included.

Site	Year class	M	F	df	P	r^2
Mendocino County						
Dark Gulch	1985	0.004	3.08	1,69	0.084	0.029
	1986	0.001	2.77	1,121	0.429	0.003
	1987	0.005	11.97	1,63	0.001	0.149
	1988	0.007	10.08	1,116	0.002	0.022
Salmon Point	1987	0.008	29.78	1,36	0.001	0.438
	1988	0.008	40.77	1,85	0.001	0.316
Sonoma County						
Horseshoe Point	1988	0.006	8.95	1,102	0.003	0.072

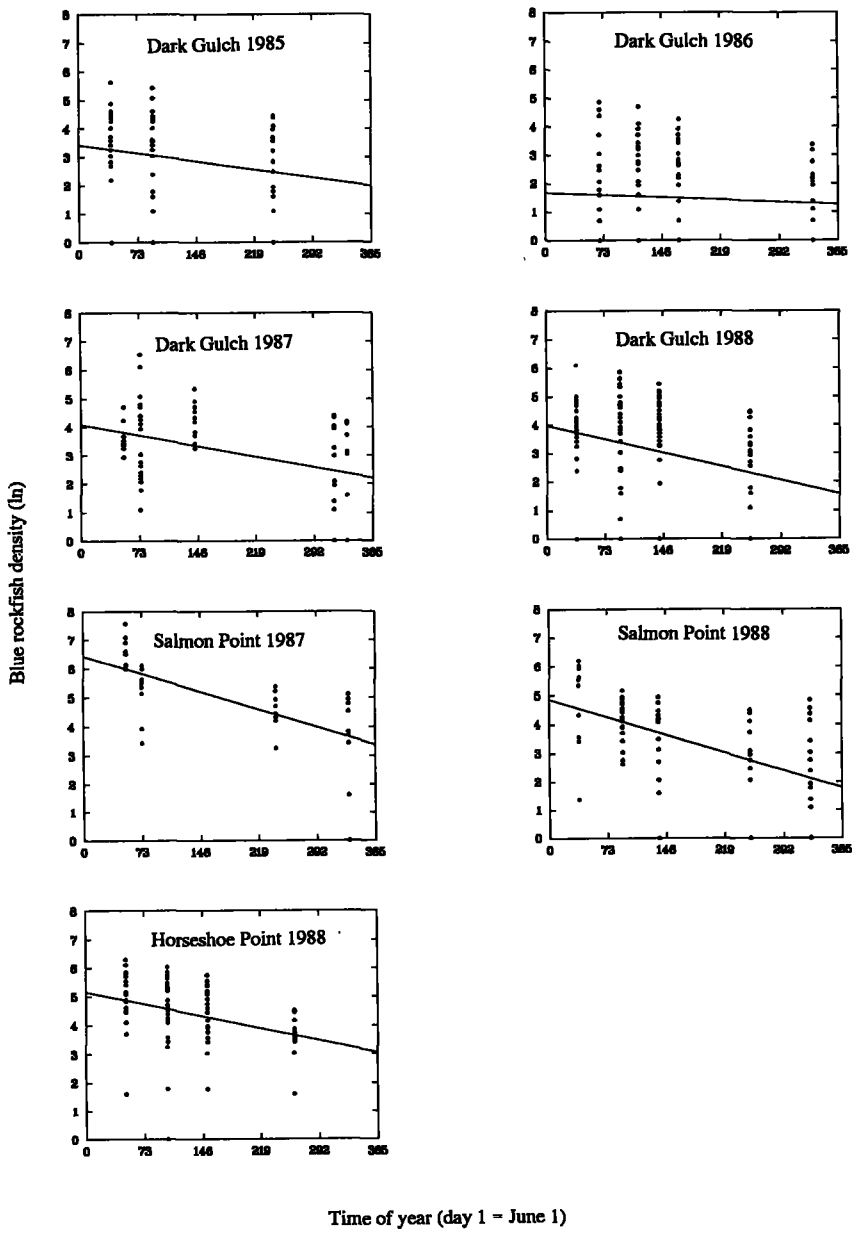

Figure 3

Natural mortality estimates from linear regressions of density (ln x+1) versus age (days) for first-year juvenile blue rockfish, *Sebastes mystinus*, for three northern California sites (Dark Gulch and Salmon Point in Mendocino County and Horseshoe Point in Sonoma County) for periods of one to four years. Sampling was undertaken from July to April, and each dot represents one or more one-minute counts.

Gulch. At the beginning of the benthic stage in mid-July, the ratio between the 1986 and 1987 Dark Gulch annual density estimates is 1/23. After these two year classes experience their respective mortality rates (0.001·day^{-1} for 1986, 0.005·day^{-1} for 1987, Table 1) from mid-July until the following April, the ratio between the year classes is reduced to 1/7.7. Although there are no published values for variability in adult blue rockfish year-class strength, the 1/7.7 ratio in the example is consistent with ratios between small and large adult year classes in other rockfish species. For example, Hightower and Lenarz (1989)

found a 1/6.5 ratio between the smallest and largest year classes of widow rockfish (*S. entomelas*).

Density-dependent natural mortality during the benthic juvenile stage reduces interannual variation in numbers but does not change the rank order of abundance between years. Since year-class strength ratios at the end of year one are similar to those of adults, we feel that year-class strength is set before this period. However, by removing some of the variation in estimates caused by year-class strength, density-dependent mortality increases the relative contribution to variation from the underlying patchiness and reduces one's ability to distinguish between different estimates (i.e. reduces statistical power).

Table 2

Published values of instantaneous daily natural mortalities in juvenile fishes. This also includes fishes that are estuarine and freshwater species. Mortalities are either a single value or a mean if followed by a range in parentheses.

Species	Instant. daily mortality	Reference
Blue rockfish (*Sebastes mystinus*)	0.006 (0.001–0.008)	This study
Shad (*Alosa sapidissima*)	0.019	Crecco et al. (1983)
Winter flounder (*Pseudopleuronectes americanus*)	0.012	Pearcy (1962)
Atlantic herring (*Clupea harengus*)	0.017	Dragesund (1969)
Plaice (*Pleuronectes platessa*)	0.018 (0.007–0.052)	Bannister et al. (1974) Lockwood (1980), Zijlstra et al. (1982) Iles and Beverton (1991)
Dab (*Limanda limanda*)	0.019 (0.011–0.035)	Iles and Beverton (1991)
Turbot (*Scophthalmus maximus*)	0.025	Iles and Beverton (1991)
Atlantic cod (*Gadus morhua*)	0.023 (0.012–0.038)	Sundby et al. (1989)
Largemouth bass (*Micropterus salmoides*)	0.029	Timmons et al. (1981)
Striped bass (*Morone saxatilis*)	0.015	Dey (1981)
Spot (*Leiostomus xanthurus*)	0.042	Currin et al. (1984)
Atlantic croaker (*Micropogonias undulatus*)	0.023	Currin et al. (1984)
Northern anchovy (*Engraulis mordax*)	0.015	Smith (1985)
Pink salmon (*Oncorhynchus gorbuscha*)	0.030	Parker (1968)

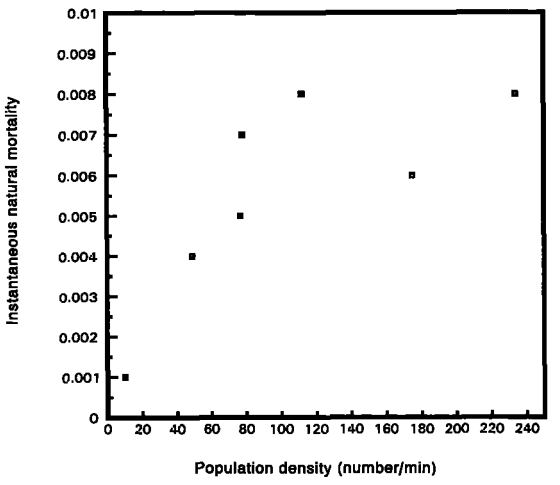

Figure 4

Natural mortality estimates and population density estimates for juvenile blue rockfish, *Sebastes mystinus*, at Dark Gulch during 1985–88, at Salmon Point during 1987–88, and at Horseshoe Point during 1988.

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Is the first annulus on the otolith of the Atka mackerel, *Pleurogrammus monopterygius*, missing?

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Atka mackerel, *Pleurogrammus monopterygius*, is a semidemersal, shallow-water species distributed along the Northern Pacific Ocean from the Kamchatka Peninsula to Southeast Alaska. Resource surveys show that the largest concentration of this species is along the Aleutian Islands chain where it sustains an important and growing commercial fishery.

Few studies (Gorbunova, 1962; Lee, 1985) have described the life history of Atka mackerel. Adults migrate to coastal areas from the open ocean before the July to October spawning season (McDermott and Lowe.[1]). Hatching occurs about 40–45 days after spawning. Gorbunova (1962) reported that newly hatched larvae are about 8–10 mm long (whether measurements were standard or fork lengths was not indicated); whereas fish 60–70 mm and 170–190 mm long are 1 and 2 year olds, respectively. However, the smallest Atka mackerel observed with a single translucent zone on their otoliths were May-captured 180-mm-FL fish caught during bottom trawls in the Northwestern Pacific (Fig. 1). Because there are no other translucent zones visible on the otoliths, convention dictates that the one formed along the otolith margin represents the first-year annulus and that the fish is assumed to be one year old. The contrast in lengths at age between otolith-determined ages and Gorbunova's data has long vexed fisheries scientists.

The purpose of this study is to determine whether Atka mackerel form an annulus during the first year of life. Annuli are also referred to as translucent zones (or dark zones), observed on the otolith when viewed with reflected light. To accomplish this, we 1) identified the season of translucent-zone formation for Atka mackerel; 2) compared characteristics between otoliths from spring-captured Atka mackerel larvae and otoliths observed with at least one translucent zone; and 3) examined average seasonal lengths of Atka mackerel during the first four years of life.

Methods

Seasonality of translucent-zone formation

A monthly series of Atka mackerel otoliths was selected from a collection maintained by the Age and Growth Unit at the Alaska Fisheries Science Center (AFSC). Young fish otoliths (observed with 2 to 3 translucent zones) were chosen to minimize affects of age-related factors on the marginal increment formation. A lack of fall and winter collections limited our samples to 19 or 20 otoliths per month. Otoliths meeting our criteria of less than four translucent zones were available from all months except November and December.

The sample was assigned to an age reader to determine the marginal increment stage of each otolith. Otoliths were prepared by snapping each one along the dorsal-ventral plane and by passing the broken surface over a flame. The burnt surface was examined with a dissecting microscope and illuminated by reflected light. Marginal increment determination was made along the ventral proximal edge of the broken surface at 50× magnification.

The stages of marginal increment development were defined as follows: stage 1 = a translucent zone is forming along the otolith growth margin; stage 2 = area of opaque growth between the otolith growth

[1] McDermott, S. F., and S. A. Lowe. 1995. The reproductive cycle and sexual maturity of Atka mackerel (*Pleurogrammus monopterygius*) in Alaskan waters. Alaska Fisheries Science Center, Resource Ecology and Fisheries Management, 7600 Sand Point Way NE, Seattle, WA 98115. Unpubl. manuscr., 30 p.

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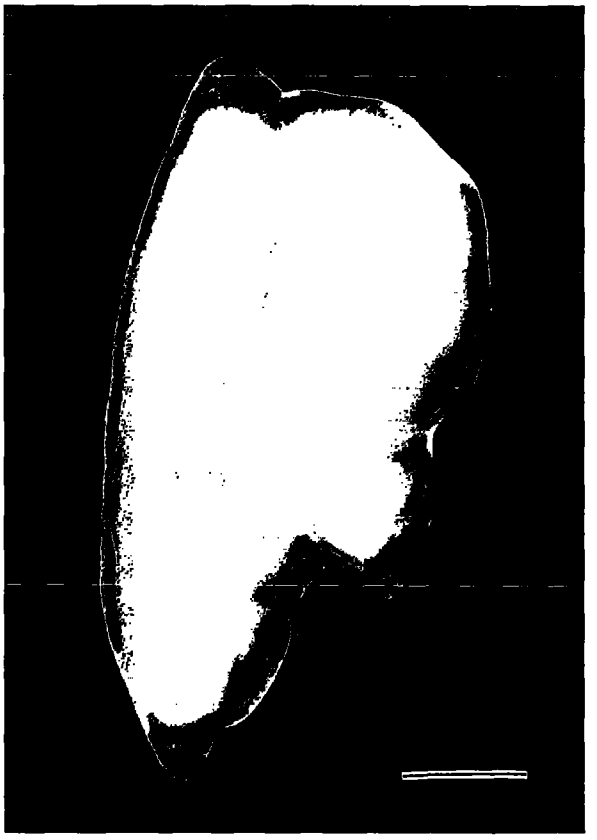

Figure 1
Distal surface of a whole Atka mackerel otolith (25× magnification) from a 180-mm-FL fish captured in May 1985. A single translucent zone is apparent along the otolith margin. Bar = 500 μm.

margin and adjacent translucent zone is nearly one-fourth the size of the previously deposited opaque zone; stage 3 = area of opaque growth between the otolith edge and adjacent translucent zone is nearly one-half the size of the previously deposited opaque zone; and stage 4 = area of opaque growth between the otolith edge and adjacent translucent zone is nearly equivalent in size to the previously deposited opaque zone.

Larval otoliths

In April 1993, the AFSC's Fisheries-Oceanography Coordinated Investigations (FOCI) scientists made a special collection of 88 larval Atka mackerel from one neuston-net trawl in the Akutan Pass region of the Aleutian Islands. Larval standard lengths were measured. Owing to the protocols of the different surveys, lengths cited in this study for fish smaller than 180 mm are standard length (SL) measurements and lengths cited for fish equal or greater than 180 mm are fork length (FL) measurements.

Sagittal otoliths were extracted from 30 larvae and otolith diameters were measured. Each otolith was ground along one side of the sagittal plane until the otolith core was clearly visible through a compound light microscope at 1,000× magnification. Unvalidated but presumed daily increments were counted from the otolith core to the edge with a compound light microscope at 1,000× magnification.

Adult otoliths

To help distinguish between the larval and older fish samples in our discussion, we will refer to Atka mackerel >180 mm FL as adult fish. Otoliths observed with at least one translucent zone (250 mm FL–390 mm FL) were ground from both lateral sides until the core was visible on the surface when examined through a light microscope. Some otoliths were ground along the transverse plane and others along the sagittal plane. Unvalidated but presumed daily increments were counted from the core to the first translucent zone on 25 prepared otoliths with the clearest incremental patterns.

Five adult fish otoliths were prepared for viewing with a scanning electron microscope (SEM). These otoliths came from fish that were 250 mm FL to 280 mm FL and that had two translucent zones. Each otolith was ground from both lateral sides along the frontal plane until the core was visible on the surface when viewed through a light microscope. The samples were coated with platinum-palladium and examined with a Hitachi S-2300 SEM.

Seasonal length data

FOCI larval data Most larvae from this collection were captured in neuston nets (some from bongo-net tows) along coastal shelf zones around Kodiak Island (a few specimens were collected from the eastern Bering Sea). The survey years spanned from 1977 to 1986 and yielded larval length data from 1,545 specimens (Table 1) from September to November and from February to June.

The average seasonal lengths for northeastern Pacific larval Atka mackerel, calculated from FOCI data, were compared with Gorbunova's (1962) reported seasonal lengths for Atka mackerel larvae captured near the Kamchatka Peninsula. Gorbunova (1962) cited only monthly minimum and maximum lengths (assumed to be standard lengths) from September to May; therefore, for comparative purposes, we used the monthly midpoints.

Table 1

Standard length at catch date of FOCI Atka mackerel, *Pleurogrammus monopterygius*, larvae from 1977 to 1986.

Month	Year(s)	Sample size	Min length (mm)	Max length (mm)	Average length (mm)
Sep	1978	32	7.9	9.0	8.6
Oct	1977, 1978	171	7.8	14.7	10.0
Nov	1977, 1978	631	7.5	13.8	10.5
Feb	1979, 1986	198	9.1	19.6	14.4
Mar	1978, 1979, 1981	307	10.1	23.2	16.7
Apr	1978, 1981, 1984, 1986	198	11.2	32.8	19.2
May	1983, 1985	2	33.0	34.5	33.8
Jun	1979	10	27.9	44.6	34.7

NRIFSF offshore larval survey Twenty-five Atka mackerel, collected from 15-minute surface tows with larval nets (1.3-m diameter and 0.333-mm mesh size) in the central Bering Sea from 23 June to 20 August 1991 were provided by the National Research Institute of Far Seas Fisheries (NRIFSF) of Japan. Standard lengths were measured. These fish were stored in formalin; therefore all otoliths from this sample were partially dissolved and unusable.

AFSC-RACE bottom trawl survey Average lengths of Atka mackerel observed with 1, 2, and 3 otolith translucent zones were calculated from data compiled by the AFSC's Resource Assessment and Conservation Engineering (RACE) division and taken from samples collected during the 1991 Aleutian Islands summer bottom trawl survey at depths ranging between 100 and 200 meters.

Results

Seasonality of translucent-zone formation

Translucent-zone formation along the otolith growth margin (stage 1) was the dominant edge-type observed on otoliths collected from January to June, reaching a 75% frequency peak in April (Fig. 2). Most otoliths exhibited the stage-2 pattern in July (90%) and the stage-3 pattern in August (65%). Stage-4 otoliths were most common in February (50%) and May (40%).

Larval otoliths

The April collection of larval Atka mackerel ranged in lengths from 10 mm SL to 23 mm SL and averaged 17 mm SL. Average otolith diameter was 240 μm. No evidence of accessory primordia was observed in any larval otoliths. Daily increments surrounding the otolith core were narrowly spaced and many daily increments could easily have been missed. In some areas, distinction between increments was not clear (owing to poor contrast) so that estimating the number of increments in these areas was necessary. The ring intervals widened as the daily increments approached the otolith edge. Total increment counts from the core to the edge of the larval fish otoliths ranged from 60 to 136 and averaged 90 increments.

Adult otoliths

As with the larval otoliths, enumerating daily increments surrounding the core of adult otoliths proved difficult because of the dense arrangements of increments. SEM micrographs revealed increments narrowing and becoming indistinguishable around 90 μm distal to the core along the frontal plane (Fig. 3A). At about 380 μm, the increments gradually widened so that about 200 increments were clearly observed with a regular periodicity. The distance between increments reached a maximum width of 3 to 4 μm in the first opaque zone (Fig. 3B) before narrowing again at about 1,000 μm. The increments became obscure even at high magnifications and were observed to merge into a deeply etched groove (about 1,400 μm from the nucleus), presumably the site of a translucent zone viewed under light microscopy (Fig. 3C). Toward the next opaque zone the increments widened and became easy to identify again. A similar sequential pattern was observed through the light microscope in both transverse and sagittal sections though distances varied owing to the different viewing axes.

Accessory primordia were clearly evident in the adult fish otoliths. These structures created disrup-

tions along the counting axis, adding to the difficulty of making reliable daily increment estimates. Total minimum daily increment counts (many increments were probably missed) from light microscope observations ranged from 190 to 353 increments, averaging 250 increments from the core to the first translucent zone.

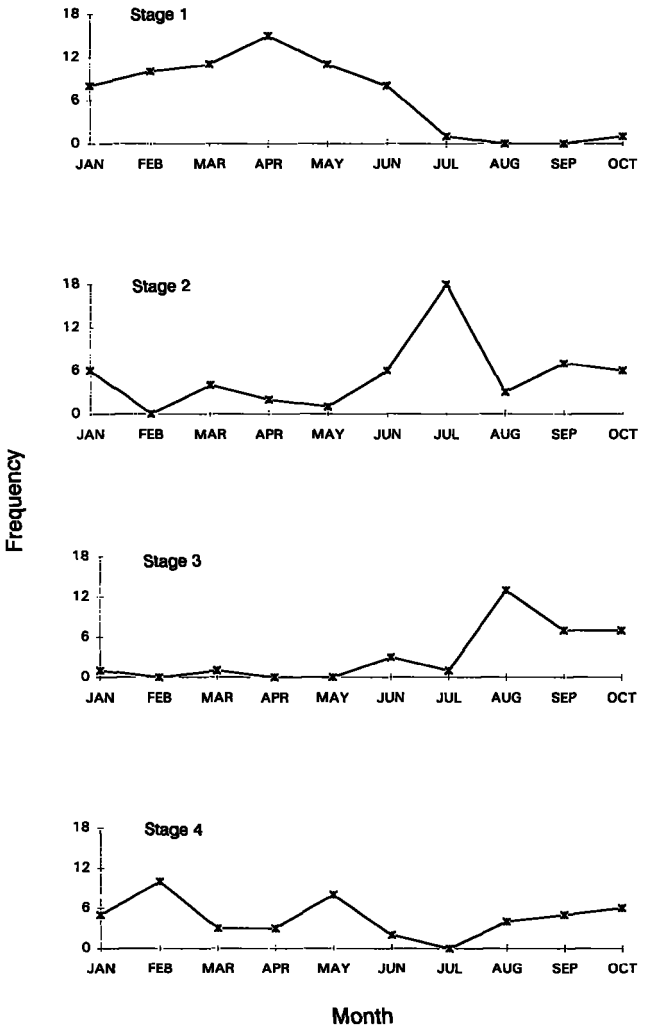

Figure 2

Results of marginal increment stage determination from otoliths with 2–3 translucent zones. Stage 1 = a translucent zone along the otolith growth margin; stage 2 = area of opaque growth between the otolith growth margin and adjacent translucent zone that is nearly one-fourth the size of the previously deposited opaque zone; stage 3 = area of opaque growth between the otolith edge and adjacent translucent zone that is nearly one-half the size of the previously deposited opaque zone; and stage 4 = area of opaque growth between the otolith edge and adjacent translucent zone that is nearly equivalent in size to the previously deposited opaque zone.

Seasonal length data

FOCI larval data FOCI data showed relatively small increases in Atka mackerel larval lengths from September to April, averaging about 1.5 mm per month. A more rapid increase in mean length appeared to occur after April. However, FOCI data for May and June were sparse; only two specimens were caught in May and 10 in June (Table 1). Lengths from Gorbunova (1962) also showed relatively small monthly increases in size for larval Atka mackerel and closely resembled lengths from FOCI larval data (Fig. 4).

NRIFSF offshore larval survey Average summer lengths (minimum and maximum lengths and sample size are in parentheses) of Atka mackerel caught from the NRIFSF offshore survey are 49 mm SL in June (39 mm SL–59 mm SL; n=8), 54 mm SL in July (46 mm SL–67 mm SL; n=15), and 101 mm SL in August (99 mm SL–104 mm SL; n=2).

AFSC-RACE bottom trawl survey The average summer length for one-translucent-zone fish was 250 mm FL (210 mm FL–290 mm FL; n=43), for two-translucent-zone fish it was 306 mm FL (240 mm FL–410 mm FL; n=286), and for three-translucent-zone fish it was 358 mm FL (310 mm FL–440 mm FL; n=38).

Discussion

Seasonality of translucent-zone formation

The highest frequencies of translucent-zone formation (stage 1) occurred around April. The period during which most otoliths exhibited the stage-1 pattern spanned at least 6 months, whereas the period exhibiting stage-2 and stage-3 patterns was relatively short but intense. In other words, the frequency of a relatively small opaque growth beyond the translucent zone (stage 2) peaked in July, and opaque growth doubled in size (stage 3) by August. This rapid otolith growth appeared to coincide with the spurt in somatic growth observed in summer-caught NRIFSF Atka mackerel. The bimodal appearance of the stage-4 pattern was probably due to the reader's confusion with the pseudo-translucent nature of the otolith edge (North, 1988) with the result that some stage-1 otoliths were classed as stage-4 otoliths. Nev-

ertheless, it appears evident that translucent-zone formation (stage 1) is most common in late winter to spring.

Comparisons of larval and adult otoliths

The increase in size between otoliths of spring-caught larvae and otoliths of adults with at least one translucent zone suggests that the first translucent zone is formed considerably later than the first April after fall hatching. Because study on the marginal increment identified late winter to spring as seasons of translucent-zone formation, it appears that the first translucent-zone is probably formed during the fish's second spring (after two winter seasons). Results from the daily increment counts did not conclusively support our hypothesis. Some support may be gleaned from the deposition pattern of the otolith daily increments viewed with light and SEM micrography where two regions of narrow increments were observed between the otolith core and the first translucent zone, suggesting two periods of slow growth, probably during the first two winters.

Seasonal length data

Seasonal larval length frequencies from FOCI data and Gorbunova (1962) were very similar, suggesting that the growth characteristics of the Kamchatka Atka mackerel do not differ greatly from those of the Northeastern Pacific fish during the first nine months of life. Therefore it would seem that length at age in the early years should be similar between Atka mackerel from the two regions.

When seasonal lengths from FOCI, NRIFSF larval surveys, and the AFSC-RACE summer bottom trawl survey are combined (Fig. 5), it becomes very apparent that spring-captured Atka mackerel at lengths of 180 mm FL (the smallest fish observed with a translucent zone) must have already lived through two winters, further supporting the hypothesis of a missing first-year translucent zone.

The various sites where Atka mackerel were found may provide clues to the early life history of this species. Life history changes, such as metamorphosis or

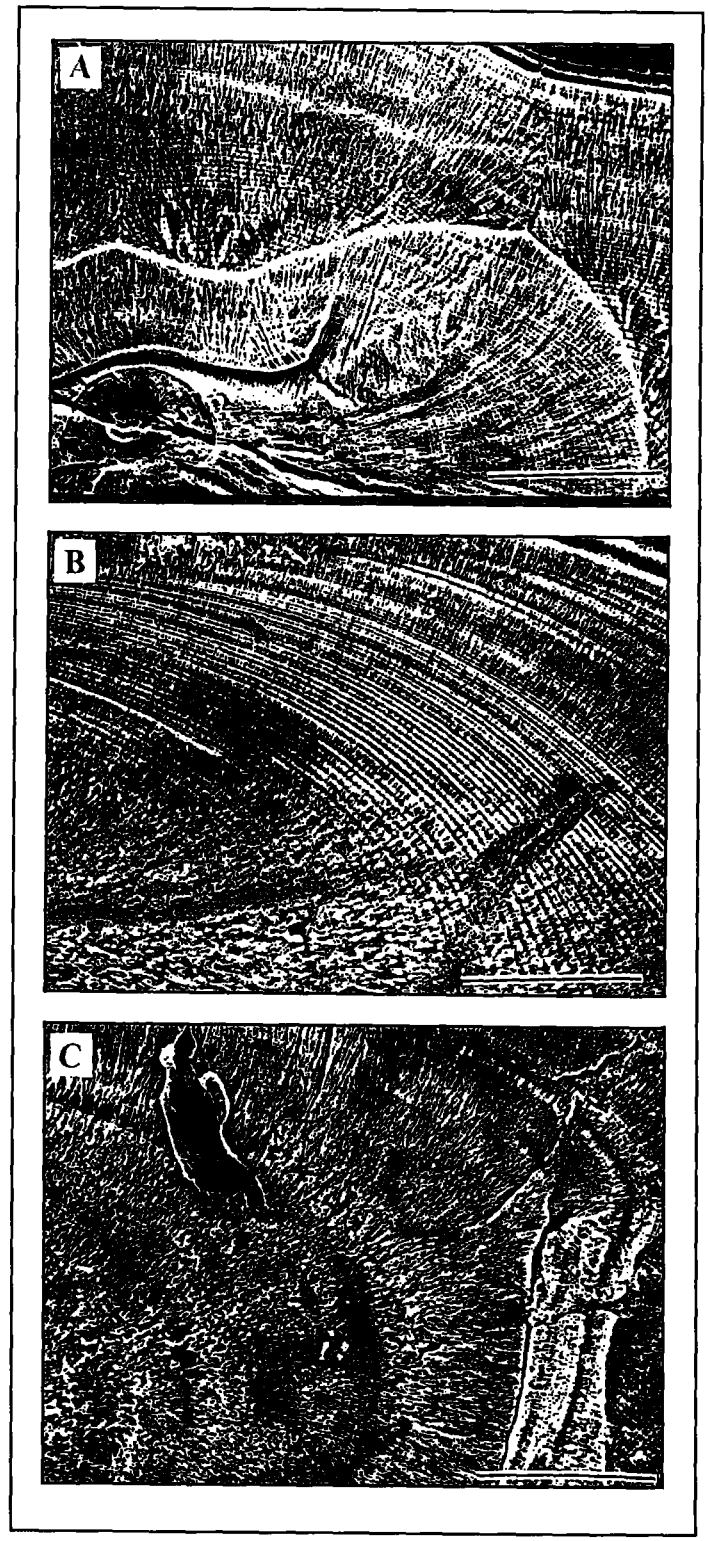

Figure 3

The following SEM micrographs were taken along frontal sections of otoliths with two translucent zones that came from fish 250 mm–280 mm FL captured during summer bottom trawls in 1991. (**A**) This panel shows a zone of very narrow increments surrounding the otolith core. Increments radiating from several accessory primordia are clearly evident. (**B**) Well-defined increments are observed with regular periodicity in the opaque zone proximal to the first translucent zone. (**C**) The increments narrow in width until they become obscure and disappear into the groove structure that is the first translucent zone. Bars = 50 μm.

habitat changes, have been associated with accessory primordia formation in the otoliths of other fish species (Gartner, 1991; Sogard, 1991; Toole et al., 1993). Atka mackerel accessory primordia were found proximal to the first translucent zone in adult otoliths but none were observed in larval otoliths, suggesting that these structures were formed after their first April and before the following spring. The appearance of the accessory primordia coincides with a time in the life history of Atka mackerel when young fish may be undergoing migration and habitat changes within the water column. Catch data from the three scientific surveys described in this study seemed to indicate that Atka mackerel migrate from nearshore surface waters, where larvae are found between fall hatching and the following spring, to offshore sur-

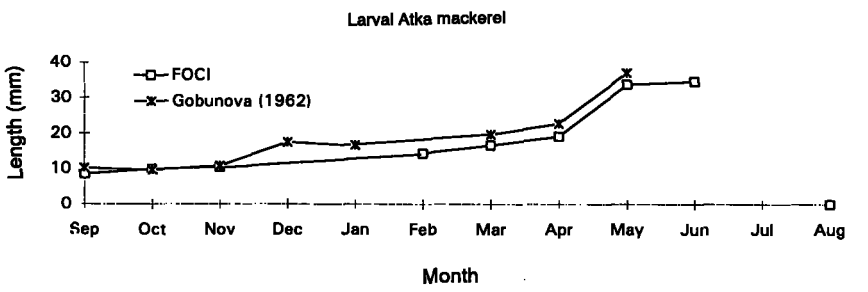

Figure 4

Comparison between the average monthly length of larval Atka mackerel collected from the northeastern Pacific Ocean (FOCI) and the monthly midpoint of the larval length range from northwestern Pacific Ocean Atka mackerel (Gorbunova, 1962).

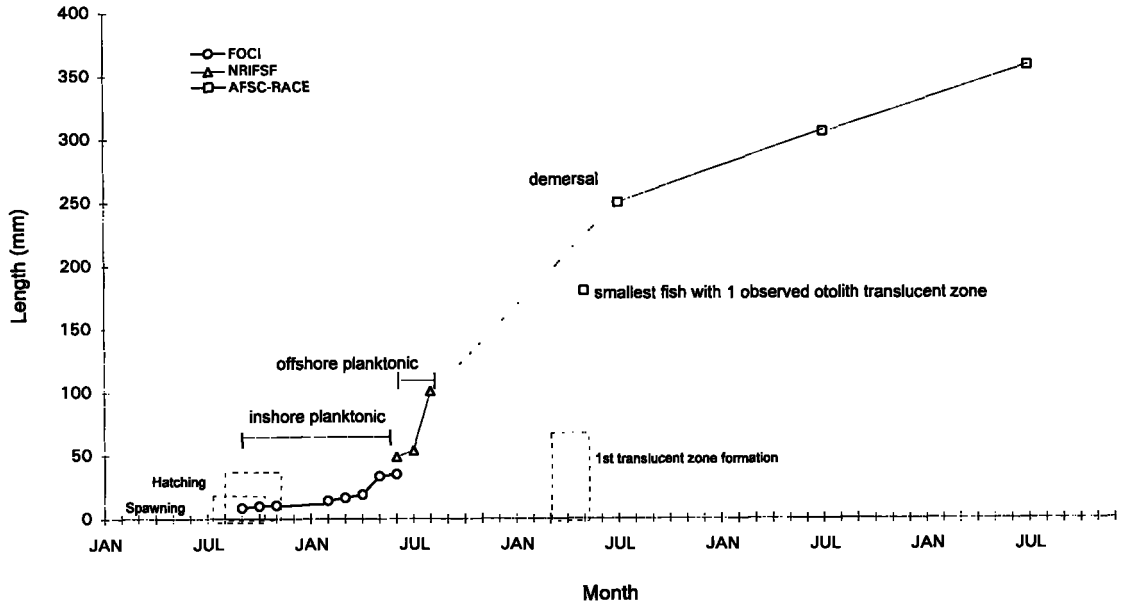

Figure 5

Combined average seasonal lengths of Atka mackerel larvae collected from nearshore surface waters from September to June 1977–86 by FOCI and of young fish collected both from offshore larval surface tows from June to August 1991 by NRIFSF and from the 1991 nearshore summer bottom trawls (100–200 meters) by AFSC-RACE scientists. The smallest fish (180 mm FL) observed with a single translucent zone were captured in May from nearshore bottom trawls. FOCI = Fisheries-Oceanography Coordinated Investigations; NRIFSF = National Research Institute of Far Seas Fisheries; AFSC-RACE = Alaska Fisheries Science Center's Resource Assessment and Conservation Engineering division.

face waters in the summer. Between their first summer and their second spring, the young fish return to nearshore waters, settling to a semidemersal existence. It is during this second spring that the first translucent zone appears on the otolith. Perhaps the translucent zone does not form during the first spring because the larvae are still planktonic. The translucent zone in Atka mackerel otoliths may be a manifestation of changes in temperature and food availability along the ocean bottom.

Conclusions

When all available evidence regarding otolith characteristics and seasonal changes in size and habitat are combined, the most parsimonious explanation of these data is that Atka mackerel have survived two fall–winter periods prior to formation of the first translucent zone.

Acknowledgments

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The use of otolith microstructure in resolving issues of first year growth and spawning seasonality of white hake, *Urophycis tenuis*, in the Gulf of Maine–Georges Bank region

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White hake, *Urophycis tenuis*, has become an increasingly important commercial species in the northeastern United States. Landings from the Gulf of Maine–Georges Bank region steadily increased from less than 1,000 metric tons (t) in the late 1960's to approximately 7,500 t in 1984, averaged about 5,800 t during 1986–91, and increased to an average of 9,300 t during 1992–93 (NEFSC, 1995; Burnett et al.[1]). An assessment of white hake conducted in 1984 indicated that landings above 6,000 t would probably not be sustainable. However, a lack of information regarding the biology of the species and the fishery (e.g. catch-at-age data) left the evaluation uncertain (Burnett et al.[1]). Recent analyses have estimated the long-term potential catch to be about 6,500 t (NEFSC, 1995).

The stock structure of white hake in the Gulf of Maine–Georges Bank region is uncertain. While previous assessments of the population in U.S. waters have assumed a single stock inhabiting the waters of the Gulf of Maine south to the mid-Atlantic Bight (Burnett et al.[1]), the existence of two reproductively isolated stocks in the northwest Atlantic has been revealed, and their spawning seasonality determined by Fahay and Able (1989).

Fahay and Able (1989) concluded that the southern stock of white hake spawns along the continental slope, primarily south of Georges Bank, but also on the Scotian Shelf and off southern New England in the spring. The northern stock reportedly spawns in the shallow waters of the southern Gulf of St. Lawrence and Scotian Shelf in the summer (Fahay and Able, 1989). These conclusions were based on the distribution and abundance of early life history stages as well as known circulation patterns throughout the region. Their results also indicated that there is negligible successful spawning of the species within the Gulf of Maine (Fahay and Able, 1989). Further, on the basis of circulation patterns between the Gulf of St. Lawrence and southern New England waters, Fahay and Able (1989) provided support for the hypothesis of Musick (1969) that pelagic juveniles actively migrate across Georges Bank into the Gulf of Maine.

Accurate age data on the adult component of the stock greatly enhance estimates of spawning stock size and predictions of future catch and abundance. Several ageing studies have been conducted for white hake (Nepzky, 1968; Beacham and Nepzky, 1980; Hunt, 1982; Clay and Clay, 1991). Ages determined by counting the number of hyaline zones visible on transverse sections of the sagittal otoliths have been validated for white hake inhabiting the Gulf of St. Lawrence by comparing mean lengths at age with observed length-frequency modes (Hunt, 1982). However, the results of a preliminary analysis of age data collected from the Gulf of Maine–Georges Bank region indicated that there is still uncertainty about the first hyaline zone and therefore the location of the first annulus.

Researchers ageing white hake have noted the presence of a hyaline zone between the nucleus and what has been regarded as the first annulus (Hunt, 1982; Clay and Clay, 1991). This hyaline zone varies in intensity and in distance from the nucleus. Most experienced age readers believe that this zone is located too close to the nucleus to be the first annulus and have assumed that it is a check formed either when pelagic larvae settle into a

[1] Burnett, J., S. H. Clark, and L. O'Brien. 1984. A preliminary assessment of white hake in the Gulf of Maine–Georges Bank area. Natl. Mar. Fish. Serv., Northeast Fisheries Science Center, Woods Hole Lab. Ref. Doc. 84-31, 33 p.

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demersal habitat (Hunt, 1982) or during the first winter when the fish are about six months of age (Clay and Clay, 1991).

The hyaline check observed on white hake otoliths is probably analogous to checks that have been documented on the otoliths of other gadoid species such as Barents Sea cod, *Gadus callarias* (Trout, 1954); silver hake, *Merluccius bilinearis* (Hunt, 1980; Dery, 1988a); and red hake, *Urophycis chuss* (Dery, 1988b). Timing of the check on silver hake otoliths was resolved by Nichy (1969), whose back-calculated lengths at the time of check formation corresponded well with the size at which silver hake become demersal. A similar check on the otoliths of capelin, *Mallotus villosus*, was also shown to be formed when the fish undergoes metamorphosis (Bailey et al., 1977). These studies support the assumption that the first hyaline zone observed on white hake otoliths is a check, probably formed when pelagic juveniles settle into a demersal lifestyle. To date, however, there has been no direct determination of the timing of this check.

The objectives of this study are to determine the timing and nature of the check on white hake otoliths, to estimate the daily growth rates of juvenile white hake, and to estimate spawning dates of these juveniles in order to evaluate Fahay and Able's (1989) theory that there are two distinct spawning stocks of white hake in the Gulf of Maine–Georges Bank region.

Methods

Juvenile white hake were obtained from archived specimens collected from several locations off the northeast coast of the United States throughout the mid-Atlantic Bight, Georges Bank, and Gulf of Maine (Fig. 1). Collection dates ranged from June 1986 through September 1992. Sampling gears that successfully captured white hake included MOCNESS (multiple opening-closing net and environmental sensing system), otter trawl, and beach seine (Table 1).

In the laboratory, fish were measured to the nearest 0.1 mm TL and all otoliths were removed. Sagittae were stored whole and dry and were examined with a dissecting microscope for the presence of hyaline zones. Each pair of lapilli and asterisci were mounted whole on glass slides and examined with a compound microscope to enumerate daily rings. Both the sagittae and asterisci of the juveniles were irregularly shaped and difficult to age. Lapilli, which had

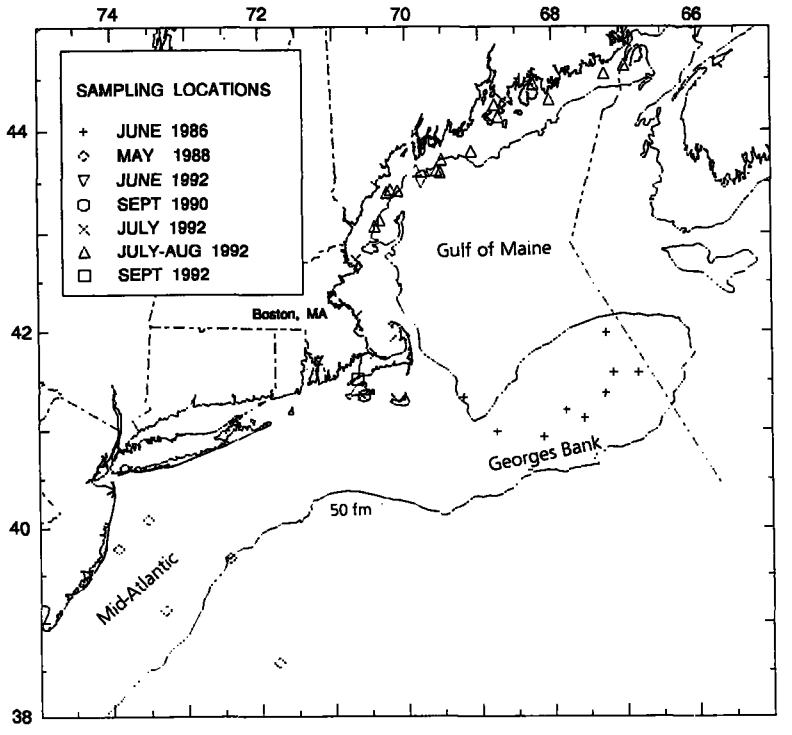

Figure 1

Locations of juvenile white hake, *Urophycis tenuis*, samples by year of collection.

Table 1

Dates, locations, and sampling gears that collected juvenile white hake, *Urophycis tenuis*, utilized in growth analyses.

Date	Region	Sampling program/Gear	Sample size
Jun 1986	Georges Bank	NEFSC/MOCNESS	22
May 1988	Mid-Atlantic	MARMAP/MOCNESS	5
Sep 1990	Coastal Massachusetts	MA State Bottom Trawl Survey	6
Jun 1992	Gulf of Maine	NEFSC–Maine DMR Bottom Trawl Survey	1
Jul 1992	Woods Hole, MA	Beach seine	4
Jul–Aug 1992	Coastal New England	NEFSC Bottom Trawl Survey	40
Sep 1992	Coastal Massachusetts	MA State Bottom Trawl Survey	45

more discernible rings, were polished with 1,200-grit paper and surface viewed at magnifications ranging from 500 to 1,000× by two readers. The 500× magnification was subsequently chosen as appropriate for these otoliths.

A Gompertz growth model was fitted to the daily increment data and the Y intercept taken as an estimate of the time of formation of the lapilli. Spawning dates were estimated for each individual by subtracting the increment count from the date of capture.

Results

A total of 123 juvenile white hake were available from seven sampling programs (Table 1). Fish ranged in size from 28 to 187 mm TL, and in age from 40 to 146 days. A hyaline check was found on the sagittal otoliths of fish collected from inshore estuarine locations. The check was on the edge of the otoliths of the juveniles collected from Woods Hole, Massachusetts, in July 1992. These fish were 70–104 mm TL and 59–73 days old.

Juvenile white hake distribution varied by size and age. The smallest fish were collected in very deep water (>100 m) offshore in the mid-Atlantic Bight in May and still had pelagic countershading, whereas the largest fish were collected in shallow waters off Martha's Vineyard, Massachusetts, in September. Smaller fish were generally caught earlier in the year (May) (Fig. 2) and farther south (mid-Atlantic Bight, Georges Bank), whereas larger individuals were taken later in the year (July–September) from locations farther north (Cape Cod, Gulf of Maine). Younger fish were collected only from May to July, whereas older fish were collected only from August to September (Fig. 3).

During July–August 1992, juvenile hake of two size classes were collected. Smaller individuals (40 to 57 mm TL) were collected off New Hampshire and southwestern Maine (Biddeford Pool) and larger individuals (86 to 186 mm TL) were taken from locations off eastern Maine. Only one small fish (41 mm) was taken off eastern Maine during this period.

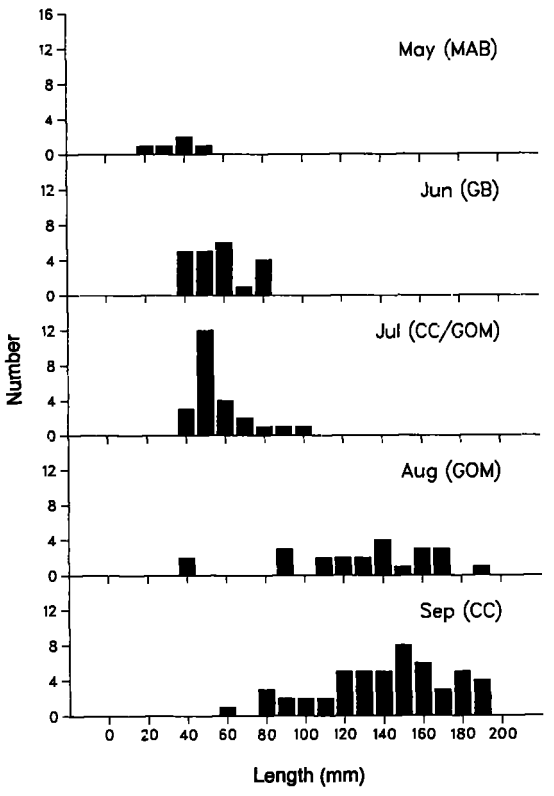

Figure 2

Size distribution of juvenile white hake, *Urophycis tenuis*, by month of collection. (MAB=mid-Atlantic Bight; GB=Georges Bank; CC=Cape Cod; and GOM=Gulf of Maine.)

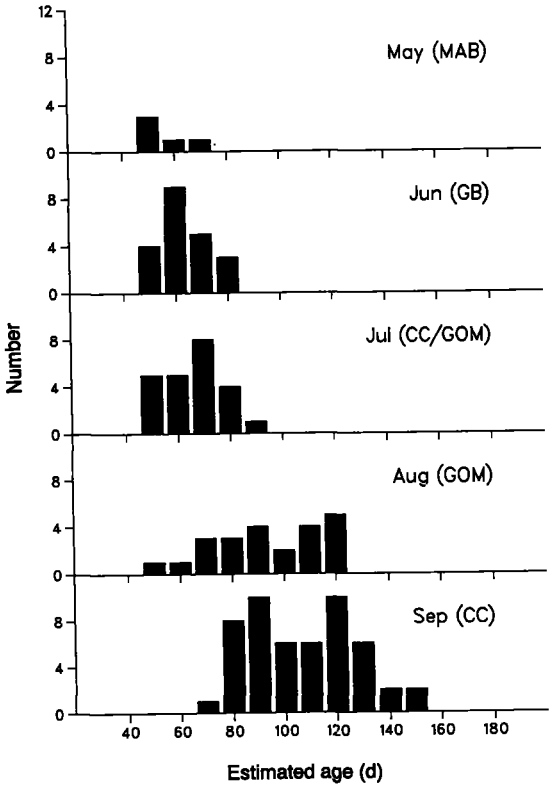

Figure 3

Age distribution of juvenile white hake, *Urophycis tenuis*, by month of collection. (MAB=mid-Atlantic Bight; GB=Georges Bank; CC=Cape Cod; and GOM=Gulf of Maine.)

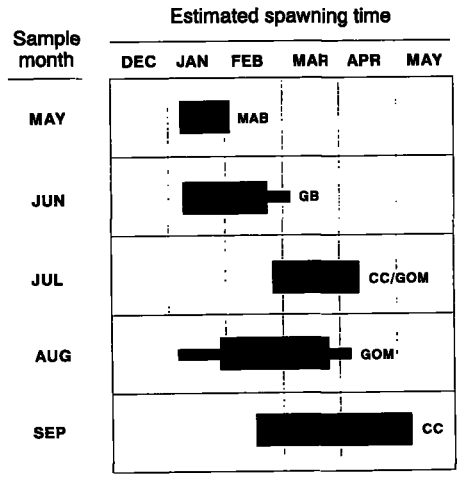

Figure 4

Back-calculated spawning times of juvenile white hake, *Urophycis tenuis*. Narrow bars indicate single observations. (MAB=mid-Atlantic Bight; GB=Georges Bank; CC=Cape Cod; and GOM=Gulf of Maine.)

Back-calculated spawning dates indicated that peak spawning occurred in the late winter for fish collected from the mid-Atlantic Bight and Georges Bank (smaller, younger individuals), whereas peak spawning occurred in late spring (March–April) for fish collected along coastal New England (larger, older individuals) (Fig. 4).

Age-length data of the juvenile hake (all data combined) were best described by a Gompertz curve (Fig. 5):

$$LEN = 210.760e^{-19.9812e^{-0.0303(AGE)}}, \quad [r^2=0.883, n=123]$$

where LEN = total length in mm, and
AGE = number of days (increments) from spawning.

Evident in the distribution of data presented in Figure 5 is the observation that small white hake (28–77 mm) collected in May–June grew at the same

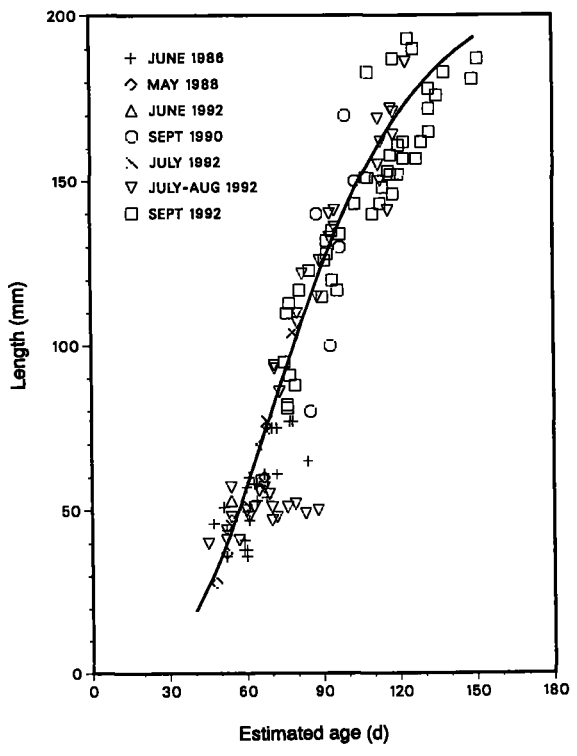

Figure 5

Gompertz growth curve fitted to total length vs. age data for white hake, *Urophycis tenuis*.

rate during each of the three years for which we obtained samples (1986, 1988, and 1992). Likewise, fish collected during July–September grew at similar rates during 1990 and 1992. An average growth rate of 1.01 mm/day for the first 200 days was estimated from the equation. When the data were analyzed by time of collection (and consequently by separating smaller, younger fish from larger, older fish), the equation for the June 1986 samples was

$$LEN = 167.193e^{-6.2611e^{-0.0184(AGE)}}, \quad [r^2=0.588, n=22]$$

with an estimated growth rate of 0.71 mm/day, and the equation for July–September (1992) samples was

$$LEN = 206.980e^{-17.7158e^{-0.2299(AGE)}}, \quad [r^2=0.877, n=89]$$

with an estimated growth rate of 0.99 mm/day.

Discussion

A hyaline zone, or check, can form on fish otoliths in response to a significant change in environmental conditions such as temperature or food availability, or both (i.e. by the transition from a pelagic to a demersal lifestyle). Our samples of juvenile white hake reflect the dramatic change in habitat experienced by this species because the smallest, youngest fish (pelagic juveniles) were collected from deep offshore areas and the largest, oldest fish (demersal juveniles) were collected from shallow inshore locations.

The juveniles collected in Woods Hole, Massachusetts, in August, 1992 (70–104 mm TL) had hyaline edges on their sagittal otoliths which would have appeared as a check on adult otoliths. Previous studies suggest that juvenile white hake "settle out" from a pelagic to demersal lifestyle at about 50 to 80 mm TL (Musick, 1974; Markle et al., 1982). They may also actively migrate to inshore areas at this time because juvenile hake in this size range have often been collected from shallow inshore areas (Bigelow and Schroeder, 1953; Musick, 1969; Markle et al., 1982; Comyns and Grant, 1993). The ages of the juveniles collected in Woods Hole (59–73 days) confirm that this hyaline zone was a check rather than the first annulus.

Daily ages were also used to calculate growth rates for the juvenile hake. We found that juveniles grew about 0.99 mm/day in June and September (1992), a rate that coincides with Fahay and Able's (1989) estimate of 1.02 mm/day for demersal juveniles collected during June–October 1986, which they calculated by means of length-frequency progression. This relatively fast growth rate may reflect the benefit to juvenile fish of moving into warm, shallow areas where prey abundance can be high.

Our results also support Fahay and Able's (1989) hypothesis that juvenile white hake are recruited northward along the east coast of the United States. As mentioned above, only smaller, younger individuals were collected from southern locations (in the mid-Atlantic Bight) and only larger, older fish were collected from areas farther north (in the Gulf of Maine). Whereas only cruises with positive catches of white hake were utilized for this study, Fahay and Able (1989) obtained similar results after an extensive series of surveys conducted during 1984–87, using various sampling gear and covering areas from Cape Fear, North Carolina, to the Scotian Shelf (Tables 1 and 2 in Fahay and Able, 1989). Fahay and Able (1989) also reviewed the results of other researchers which documented the absence of eggs and larvae in Georges Bank–Gulf of Maine waters and the northward progression of juvenile stages in the study area (Chenowith, 1973; Colton and St. Onge, 1974; Bolz et al., 1981; Laroche, 1982; Townsend, 1984).

In light of the northward recruitment theory, and given the northward progression of sizes and ages, all of the fish in this study probably came from one spawning population located offshore from the mid-Atlantic Bight and Georges Bank region. Our collections from the Gulf of Maine in July and August 1992 may indicate that there were two successful spawning periods (or one very protracted spawning period) that year because they included two size classes of juvenile hake. We found no evidence of a summer-spawning Scotian Shelf stock, possibly because of the timing of our sampling of the northernmost stations (in July–August 1992). These results again support Fahay and Able's (1989) hypothesis that there is no significant spawning within the Gulf of Maine.

In summary, our results confirm details of the early life history of white hake. Pelagic juveniles settle into a demersal existence at 50 to 80 mm TL, when they are approximately 50 to 60 days old. Many individuals settle in shallow estuarine nursery areas which results in the formation of a hyaline check on their sagittal otoliths. We therefore support previous ageing studies in which the check on adult otoliths was not counted in ageing. We also confirm with daily ageing a growth rate of about 1 mm/day for juvenile white hake. Finally, we provide additional evidence that there is apparently a major spawning population of adults located offshore of the mid-Atlantic Bight–Georges Bank region, and that juvenile hake spawned from this group are recruited northward into the Gulf of Maine.

Acknowledgments

We thank Lisa Hendrickson, NMFS, Woods Hole, Massachusetts, for preparing Figure 1.

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Counts of northern elephant seals, *Mirounga angustirostris*, from large-format aerial photographs taken at rookeries in southern California during the breeding season

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Various techniques have been used to count northern elephant seals, *Mirounga angustirostris*, at rookeries in the United States and Mexico. Individuals are customarily counted by observers stationed in observation blinds or on walks atop cliff-tops, along the beach, or among the seals (Le Boeuf, 1974; Stewart, 1989; Stewart et al., 1994; DeMaster et al.[1]). Some rookeries are counted from skiffs nearshore (Stewart et al., 1994). Large-format (228-mm) black-and-white or small-format (35-mm) color-transparency aerial photographs also have been used to count northern elephant seals (Bartholomew and Boolootian, 1960; Carlisle and Aplin, 1966, 1971; Odell, 1971; Antonelis et al., 1981; Stewart, 1989). In addition, counts from aerial photographs have been combined with information on the phenology of haulout behavior to estimate elephant seal abundance when they are not censused at peak haulout periods (Antonelis et al., 1981; Stewart et al., 1994).

In 1985, scientists of the National Marine Fisheries Service began to count northern elephant seals from vertical, color-transparency photographs taken with a large-format camera. A 228-mm-format (cartographic) camera was used in 1985 and 1986, but an improved system was adopted in 1987 which used a 126-mm-format (military reconnaissance) camera adjusted for low altitude photography. This paper describes equipment and procedures used for counting northern elephant seals from photographs taken with these cameras. Counts of northern elephant seals are presented for San Miguel Island (1985–95), San Nicolas Island (1988–95), Santa Rosa Island (1990–95), and Santa Barbara Island (1993–95) off the coast of southern California. The method used to obtain these counts was validated by comparing the precision of counts of northern elephant seals made by biologists on the ground with counts made from large-format aerial color-photographs. The counts of pups that were obtained from photographs taken at each island were then used to estimate the number of births for each year. These birth estimates were then compared with published estimates where other techniques were used in order to evaluate the results obtained by each technique.

Methods

Photography equipment

In 1985 and 1986, vertical photographs of northern elephant seals were taken with a 228-mm-format RC-10 cartographic camera equipped with a 152-mm focal length lens. The resolution of these photographs allowed us to count seals, but the image smear caused by the forward motion of the aircraft reduced image resolution slightly. This problem was solved in 1987 with a 126-mm-format KA-45A or KA-76A (military reconnaissance) camera equipped with a 152-mm focal length lens and image motion compensation (IMC). The IMC and camera firing sequence varied according to ground speed and altitude information to achieve a 66% overlap between adjacent frames (i.e. an object on the ground was photographed three times per pass). In addition, the hyper focal distance of the KA-45A and KA-76A cameras was adjusted to focus at an altitude as low as 129 meters.

The RC-10 camera was mounted in a Cessna 207 aircraft (1985–86) and the KA-45A or KA-76A camera

[1] DeMaster, D. P., R. L. DeLong, B. S. Stewart, P. K. Yochem, and G. A. Antonelis. 1984. A guide to censusing pinnipeds in the Channel Islands National Marine Sanctuary and Channel Islands National Park. Southwest Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, P.O. Box 271, La Jolla, CA. Admin. Rep. LJ-84-44, 22 p.

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was mounted in a Partenavia P-68 aircraft (1987–95). Both aircraft were flown at an altitude between 244 and 366 meters (typically 259 meters) and at a ground speed of 90 to 110 knots. Kodak Aerochrome MS Film 2448, a very fine-grain, medium-speed, color-reversal film suitable for aerial photography, was used. Photographs also were taken at an altitude of 1,219 meters (at San Miguel Island in 1985) and 1,372 meters (at San Nicolas Island and the western end of Santa Rosa Island in 1989). These high-altitude photographs were used 1) to determine the geographic location of seals shown in low-altitude photographs, 2) to prevent counting the same seals twice that were visible along segments of the coastline in photographs taken during two or more photographic passes (double counting), and 3) to identify segments of coastline that were not photographed during low altitude flights.

Surveys

Two aerial photographic surveys were conducted during the northern elephant seal breeding season (December through February) each year from 1985 to 1995, except 1987 and 1994, when only one survey was conducted. For each year, the first survey occurred when the maximum number of adults was expected to occupy rookery sites (between 18 and 30 January [Stewart, 1989]). These surveys were scheduled for the later part of that period to maximize the number of pups present, but winter storms or scheduling conflicts sometimes resulted in a later starting date (Table 1). The second survey was made late in the breeding-season, between 13 and 22 February, after all pups were born, but before weaned pups had left the beaches (see Odell, 1974; Le Boeuf and Bonnell, 1980; Stewart and Yochem, 1984; Stewart, 1989).

Aerial photographic surveys were conducted off southern California at San Miguel Island (34°02'N, 120°21'W) in 1985–95, San Nicolas Island (33°15'N, 119°30'W) in 1988–95, the western end of Santa Rosa Island (34°00'N, 120°14'W) in 1990–95, and Santa Barbara Island (33°29'N, 119°02'W) in 1993–95. A peak breeding-season survey was not conducted at San Nicolas Island in 1988 nor at Santa Rosa Island in 1990. The southern shorelines of San Miguel Island (≈16 km) and San Nicolas Island (≈18 km) were photographed during all surveys. Portions of the northern shorelines of San Miguel Island (≈12 of ≈20 km) and San Nicolas Island (≈4 of ≈16 km) were included in the surveys in 1988 and 1989, respectively. At the western end of Santa Rosa Island, ≈4 km of coastline were photographed, and at Santa Barbara Island ≈0.75 km of 8 km of coastline were photographed. A mosaic of overlapping photographs taken from multiple photographic passes over the hauling grounds at Point Bennett and Cardwell Point (located on the western and eastern ends, respectively, of San Miguel Island) was made to prevent double counting seals that appeared in more than one photograph.

Counts

We counted six categories of elephant seals: 1) pups that were alive or of unknown status (not decomposed, Fig. 1); 2) decomposed carcasses of pups; 3) juveniles; 4) subadult and adult males; 5) adult females; and 6) seals of unknown age and sex category. Color, shape, and behavior (i.e. their tendency to be away from water) distinguished pups from harbor seals, *Phoca vitulina*. No attempt was made to locate decomposed pups in the late breeding-season photographs that were found earlier in peak breeding-season photographs. Juveniles were yellowish in color and generally were not found in the same vicinity as the harems. Adult females were smaller than adult males, were located within a harem, and either attended a pup or appeared parturient. Subadult and adult males were identified as nonparturient animals with a penile opening or proboscis, or as nonparturient animals stationed along the periphery of harems (see Le Boeuf, 1974; Cox, 1983; and McLaren, 1993). Those that could not be classified were included in the "unknown" category. Adult and subadult males were included in the same category because we could not distinguish between them.

Our count of adult females may have contained males that were three to seven years old that (on the basis of our criteria) were not detected in large harems. We believe that the probability of counting males as females when the photographs were taken is very low. Studies of northern elephant seals at Año Nuevo Island indicate that ≤1% of our count of adult females could include young males. (Le Boeuf[2]).

The color-transparency photographs were illuminated with a light table and inspected with a 7–70× zoom binocular microscope. The seals were counted according to each age and sex class category and their numbers were tabulated on a transparent acetate sheet when ten or more were in the photograph to prevent under- or double-counting them. After counting and marking the acetate sheet, the acetate sheet was then placed on an adjacent photograph at the exact location where the count terminated previously.

[2] Le Boeuf, B. J. 1994. Department of Biology and Institute of Marine Sciences, Univ. California at Santa Cruz, CA 95064. Personal commun.

Table 1

Counts of northern elephant seals, *Mirounga angustirostris*, at San Miguel, San Nicolas, Santa Rosa, and Santa Barbara Islands, California, obtained from 228-mm-format (1985–86) or 126-mm-format (1988–95) aerial color transparency photographs (augmented with visual counts from sites that were not photographed during the survey). Juveniles were not counted in 1985 and 1986. No counts are provided for the peak breeding-season survey at San Miguel Island in 1987 and 1992 owing to partial survey coverage that resulted in an incomplete count.

		Pups			Subadults and Adults		
Survey date	Survey coverage[1]	Alive and unknown	Decomposed carcasses	Juveniles	♀[2]	♂	Unknown sex
San Miguel Island							
Peak breeding season							
31 Jan 1985	Partial[3]	9,102	71		8,748	1,512	0
1 Feb 1986	Near total	9,622	71		8,651	1,607	0
1–2 Feb 1987	Partial						
1 Feb 1988	Near total	10,146	168	3	10,266	1,705	0
28 Jan 1989	Total	10,114	147	20	10,461	1,663	7
3 Feb 1990	Total	12,185	158	6	10,048	1,990	0
1 Feb 1991	Total	12,883	180	7	11,898	2,065	0
2 Feb 1992	Partial						
29 Jan 1993	Total	13,096	257	22	13,145	2,310	0
28 Jan 1995	Total	10,947	258	25	13,282	2,713	0
Late breeding season							
22 Feb 1985	Partial[3]	9,585	80		1,241	1,308	0
21 Feb 1986	Near total	9,555	67		1,338	1,410	0
15 Feb 1988	Near total	10,901	182	0	4,842	1,493	3
16 Feb 1989	Total	11,117	175	3	3,772	1,648	0
19 Feb 1990	Total	12,241	183	1	2,320	1,779	3
18 Feb 1991	Total	13,029	162	1	3,358	2,084	0
17 Feb 1992	Total	13,116	227	6	4,282	2,272	1
15 Feb 1993	Total	13,720	180	5	5,489	2,292	0
13 Feb 1994	Total	14,616	222	3	8,010	2,403	2
15 Feb 1995	Total	13,012	450	3	7,556	2,411	0
San Nicolas Island							
Peak breeding season							
28 Jan 1989	Total	4,124	50	16	4,313	549	3
3 Feb 1990	Total	4,092	55	5	3,439	475	3
2 Feb 1991	Total	4,053	67	2	4,019	502	0
3 Feb 1992	Total	5,482	78	5	4,745	634	1
29 Jan 1993	Total	4,940	63	23	4,878	554	0
28 Jan 1995	Near total	5,218	62	27	6,232	724	0
Late breeding season							
15 Feb 1988	Near total	3,120	34	0	1,732	430	0
16 Feb 1989	Total	4,688	63	0	1,649	537	0
19 Feb 1990	Total	4,079	52	2	976	425	2
18 Feb 1991	Total	4,547	51	3	1,316	469	0
17 Feb 1992	Partial[4]	5,387	63				
15 Feb 1993	Total	5,171	37	8	1,973	602	0
13 Feb 1994	Total	5,727	63	7	2,998	648	3
15 Feb 1995	Total	6,486	89	2	3,590	673	0
Santa Rosa Island							
Peak breeding season							
2 Feb 1991	Total	86	0	0	86	37	0
3 Feb 1992	Total	67	0	0	68	52	0
29 Jan 1993	Total	110	0	0	119	72	0
28 Jan 1995	Total	143	0	2	175	69	0
Late breeding season							
19 Feb 1990	Total	23	0	0	4	14	0
18 Feb 1991	Total	83	0	0	24	45	0
17 Feb 1992	Total	64	0	0	29	40	0
15 Feb 1993	Total	123	0	0	48	57	0
13 Feb 1994	Total	315	0	0	173	141	0
15 Feb 1995	Total	186	0	0	114	81	0
Santa Barbara Island							
Peak breeding season							
29 Jan 1993	Total	53	0	0	109	9	0
28 Jan 1995	Total	28	0	0	113	18	0
Late breeding season							
15 Feb 1993	Total	34	0	0	21	14	0
13 Feb 1994	Total	47	0	0	45	21	0
15 Feb 1995	Total	27	0	0	113	10	0

[1] Survey coverage: Total = all sites were photographed or visually inspected; Near total = sites not photographed or visually inspected were estimated to have trivial numbers of seals relative to the total count; and Partial = sites inhabited by large numbers of seals were not photographed.
[2] The count of adult females may contain an extremely small percentage (estimated to be ≤1%) of males that are of similar size as adult females.
[3] The counts of pups, adult females, and subadult or adult males include counts made from high-altitude photographs for sites not photographed at low altitude.
[4] Counts of pups from the peak breeding-season survey were substituted for sites, or portions of sites, that were not photographed.

Elephant seals were counted in this manner until the entire photographed coastline was examined.

A subjective evaluation was used to determine the degree of survey coverage after the elephant seal count for each island was completed. A "total" rating was assigned when all sites of the rookery were photographed or visually inspected. A "near-total" rating was assigned when small portions of the rookery were not photographed (the number of seals missed was estimated to be equal to or less than 1% of the total counted). A "partial" rating was assigned when >1% of the total counted were assumed not to have been photographed. Total counts of seals for surveys with a partial rating are normally not provided. However, three partial surveys, two at San Miguel Island in 1985 and one at San Nicolas Island in 1992, were augmented with counts from photographs taken from high altitude (1985) or from the previous peak breeding-season survey (1992).

Figure 1

(A) Northern elephant seals, *Mirounga angustirostris*, at Point Bennett, San Miguel Island, California. The photograph was taken with a 126-mm-format camera with IMC from an altitude of 259 meters (850 feet). (B) Enlarged inset from (A). These photographs display the following: 1) gulls (probably western gulls, *Larus occidentalis*) among the elephant seals; 2) decomposed carcasses of pups; 3) pups; 4) adult males; 5) subadult males within the harem; 6) adult females with a pup; 7) adult females that appear parturient; 8) California sea lions, *Zalophus californianus;* and 9) tracks on the sand made by elephant seals.

Precision

Independent counts were made of elephant seals in photographs taken at San Miguel Island, the largest northern elephant seal rookery (Stewart et al., 1994), to examine the precision of the counts obtained from aerial photographs. Three counts were made for each of the two 1988 surveys and four counts were made for each of the two 1989 surveys. Two persons conducted the counts in 1988 and three persons in 1989 (for each year, one person made two counts for each survey, and the other person(s) made one count). The coefficient of variation (CV) of replicate counts was used to compare precision in the counts of all age and sex class categories of seals. Precision was rated excellent, good, acceptable, or unacceptable according to CV's obtained by ground counts at Piedras Blancas (described below). The following ratings, and criteria for defining each rating, are given as follows: 1) excellent when the CV was less than one-half the smallest CV obtained by ground counts; 2) good when the CV was between the smallest CV of ground counts and half that value; 3) acceptable when the CV equaled those obtained by ground counts; and 4) unacceptable when the CV exceeded the largest CV obtained by ground counts.

The counts of elephant seals by people on the ground were compared with counts made from 126-mm-format aerial photographs to ascertain the pre-

cision of each method. Three independent trials were made during two days at the rookery located at Piedras Blancas, California (a 1-1/4 hour interval separated trial 2 and trial 3 on the second day). Three distinct groups of elephant seals were photographed from the air while they were counted on the ground by three persons (each person made two counts of each group). The seals in the photographs were also counted by three persons (each person made two counts of each group). Total counts of all seals were made to eliminate problems associated with classifying a seal to an age and sex class category. The ground count was made from an unobstructed view atop cliffs or sand dunes that were approximately 10–15 meters above the seals.

The Wilcoxon paired-sample test was used to compare CV's obtained from ground counts with photo counts at Piedras Blancas to determine whether the precision of the two methods were equal. The counts were then $\log_{10}$-transformed to meet requirements of homoscedasticity. Analysis of variance (ANOVA) was used to determine whether ground counts and photo counts were equal; the factors tested were method (ground vs. photo), person, group (of seals), trial, and their interactions. An ANOVA was also performed on ground counts and another on photo counts; the factors tested for each test were person, group (of seals), trial, and their interactions.

A comparison of elephant seal counts made at Santa Barbara Island was conducted in 1995 to examine aerial photographic counts, small-vessel and ground counts, and estimates of births for this island. Elephant seals were counted from two aerial photographic surveys (Table 1) and from a small-vessel and ground survey conducted two days after the second aerial survey.

Estimate of births

The number of northern elephant seal births was estimated by summing the counts of pups that were alive or of unknown status and the counts of decomposed pup carcasses. When more than one survey was made each year, the greater count of each category (from either survey) was used. Estimates of births for San Miguel, San Nicolas, and Santa Rosa Islands made by Stewart (1992) were compared with those from this study. Long-term changes in birth rates were examined for San Miguel Island for 1985 through 1991 (data for the other islands were insufficient for this comparison) with log-linear regression analysis (Eberhardt and Simmons, 1992).

Estimates of births at Santa Barbara Island were made from the number of pups counted. The number of adult females counted during the peak breeding-season survey was also compared with the number of pups counted during the three surveys because Stewart (1989) used the count of adult females during peak-breeding season to estimate births for this rookery.

Results

Total or near total survey coverage was achieved for most surveys (90%, Table 1). No counts are available for San Miguel Island in 1987 or for the peak breeding-season survey at San Miguel Island in 1992 owing to missed photographic coverage.

Counts of northern elephant seals at Piedras Blancas, California, from vertical 126-mm-format photographs were more precise than counts made by people at ground-level (Table 2). The CV's of photo counts (between 0.002 and 0.009) and ground counts (between 0.054 and 0.231) were significantly different ($P<0.008$).

The counts obtained from 126-mm-format photographs at Piedras Blancas were significantly different from counts obtained by people on the ground ($P\leq0.001$, Table 3). There was a significant difference between persons for the counts obtained on the ground ($P<0.001$) but not between persons counting the seals from aerial photographs ($P=0.065$). Each method detected a significant difference between the size of the three groups of seals and between the three trials ($P\leq0.002$).

The lowest CV obtained by counting northern elephant seals at Piedras Blancas was 0.054 and the highest CV was 0.231 (Table 2). By our definition, excellent precision would be a CV of <0.027, good precision would be between 0.027 and 0.054, acceptable precision would be between >0.054 and 0.231, and unacceptable precision would be >0.231. Thus, the counts of elephant seals from aerial photographs taken at Piedras Blancas had excellent precision. The replicate counts from the photographic surveys of San Miguel Island in 1988 and 1989 also had excellent precision for counts of pups that were alive or of unknown status, total number of pups, adult females, subadult and adult males, and for total counts of all northern elephant seals (Table 4). The precision for counts of decomposed carcasses of pups was good or acceptable.

Estimates of northern elephant seal births from large-format aerial photographic surveys differed from estimates made from ground surveys at San Miguel and San Nicolas Islands by –8.4% to +11.2% and from small-format aerial photographic surveys at Santa Rosa Island by –14.8% to +17.8% (Table 5). Estimates from aerial photographic surveys were higher than estimates from ground surveys for six of ten comparisons, but the differences were not statistically significant ($P>0.05$). At Santa Barbara Island, the number of pups counted from large-format aerial

Table 2

Ground and aerial photographic counts of three groups of northern elephant seals, *Mirounga angustirostris*, at Piedras Blancas, California. The coefficient of variation (CV) is given for each set of counts. The ground counts and photo counts were made by different persons. Three trials were conducted during a two-day period (trials 2 and 3 occurred on the second day).

		Group 1		Group 2		Group 3	
Trial	Counter	Ground	Photo	Ground	Photo	Ground	Photo
1	A	271	310	712	753	762	852
	A	294	302	726	755	749	856
	B	292	305	645	750	681	857
	B	303	305	686	756	711	858
	C	321	305	812	756	857	862
	C	339	308	844	754	820	857
	CV	0.079	0.009	0.103	0.003	0.086	0.004
2	A	239	297	616	634	878	934
	A	245	297	649	642	818	919
	B	262	297	538	634	741	936
	B	248	294	576	646	776	933
	C	380	299	699	636	963	946
	C	376	296	660	637	879	934
	CV	0.231	0.006	0.094	0.008	0.096	0.009
3	A	303	320	625	665	852	969
	A	299	323	615	668	865	967
	B	300	319	552	661	795	952
	B	313	320	544	665	798	953
	C	338	321	648	667	986	964
	C	332	323	683	668	959	974
	CV	0.054	0.005	0.089	0.004	0.092	0.009

photographs differed from that of the small-vessel and ground survey by –36%, and the number of adult females counted during peak breeding season differed from the number of pups counted 18 days later by small-vessel and ground survey by +157% (Table 5).

Analysis of the trend in pup production over time for San Miguel Island, based on counts obtained from aerial photographic surveys or from ground surveys, showed that 1) a log-linear relationship between count and year (Fig. 2) fits counts from photographs better (R^2=0.979) than counts from the ground (R^2=0.788); 2) the standard errors of the constant and the slope from each regression indicated that the counts from photographs were less variable; 3) each had a significant slope and intercept (P<0.03); and 4) there was no significant difference between the slopes (P=0.66) or the elevations of the regressions (P=0.32).

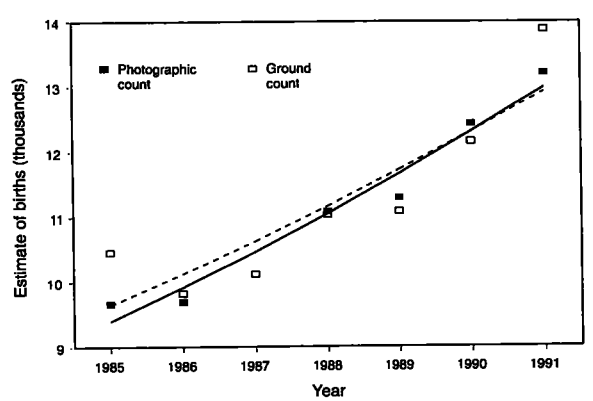

Figure 2

Comparison of northern elephant seal, *Mirounga angustirostris*, birth estimates from 1985 to 1991 for San Miguel Island, California, based on large-format aerial color photographs with estimates based on ground surveys (Stewart, 1992). The solid line represents the regression line for photographic counts (R^2=0.979) and the dashed line represents the regression for ground counts (R^2=0.788).

Discussion

Large-format color transparency photographs were useful for obtaining accurate and precise counts of northern elephant seal pups and adults. The preci-

Table 3

Results of three separate analysis-of-variance (ANOVA) tests with $\log_{10}$-transformed counts of northern elephant seals, *Mirounga angustirostris*, from Piedras Blancas, California. The first ANOVA is for ground and photo counts (emphasis on differences between methods), the second ANOVA is for ground counts, and the third ANOVA is for photo counts (the latter two emphasize differences between persons). Method refers to counts made at ground level and counts made from 126-mm-format aerial color photographs. Only first-order interactions are presented.

Category	Sum of squares	df	Mean square	*F*-value	*P*-value
Ground and photo counts					
Method	0.018	1	0.018	174.929	<0.001
Person	0.037	2	0.019	179.633	<0.001
Group	4.053	2	2.027	19480.595	<0.001
Trial	0.008	2	0.004	38.954	<0.001
Method * person	0.034	2	0.017	161.846	<0.001
Method * group	0.006	2	0.003	30.720	<0.001
Method * trial	0.000	2	0.000	1.388	0.258
Error	0.006	54	0.000		
Ground counts					
Person	0.071	2	0.035	177.694	<0.001
Group	1.890	2	0.945	4731.476	<0.001
Trial	0.004	2	0.002	9.286	0.001
Person * group	0.010	4	0.002	12.270	<0.001
Person * trial	0.004	4	0.001	5.588	0.002
Error	0.005	27	0.000		
Photo counts					
Person	0.000	2	0.000	3.021	0.065
Group	2.169	2	1.085	130915.433	<0.001
Trial	0.005	2	0.002	282.652	<0.001
Person * group	0.000	4	0.000	0.734	0.577
Person * trial	0.000	4	0.000	1.348	0.278
Error	0.000	27	0.000		

sion and accuracy of the counts, respectively, were demonstrated by the small CV's between multiple counts of seals at a large rookery (Table 4) and between counts made from photographs and those by persons on the ground (Fig. 1; Tables 2 and 3).

This study was the first to use a large-format camera with fine-grain, color transparency film and a camera equipped with IMC. Image interpretation is improved because colors that print as the same shade of gray in a black-and-white photograph can be differentiated in a color photograph. Large-format cameras have better resolution than medium-format (70-mm) or small-format (35-mm) cameras (Glegg and Scherz, 1975) that are commonly used for aerial photographic surveys of pinnipeds (e.g. Stewart, 1989; Hanan et al.[3]). The IMC mechanism improves the resolution in photographs taken with a large-format camera (compared with one not equipped with IMC) by eliminating the forward motion of the aircraft when the photograph is taken. The result is that color photographs taken with a large-format camera equipped with IMC record more detail in the photograph and, thus, make it possible to interpret what is on the ground precisely and accurately.

Elephant seal births are used as a relative index to measure population growth and to estimate population size (Laws, 1994; Stewart et al., 1994). It is not possible to determine the absolute number of births for large rookeries because pup mortality prior to the census can only be estimated. Stewart et al. (1994) describes various methods to estimate northern elephant seal births. Where comparisons in estimates are possible with the various methods described by Stewart et al. (1994), large within-year discrepancies exist (Table 5). These differences can be attributed to several factors: 1) the large variance associated with ground counts of pups and with phenological studies; 2) differences between the dates each census was conducted (storms are a known

[3] Hanan, D. A., E. S. Konno, and M. J. Beeson. 1991. Harbor seal, *Phoca vitulina richardsi*, census in California, May–June 1990. Southwest Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, La Jolla, CA. Admin. Rep. LJ-91-05, 68 p.

Table 4

Replicate independent counts of northern elephant seals, *Mirounga angustirostris,* found in 126-mm-format aerial color photographs taken at San Miguel Island, California, made by three persons. The mean and coefficients of variation (CV) of the counts are also shown.

		Pups				Sub-adults and adults			
Date of survey	Counter	Alive and unknown	Unnown carcasses	Total	Juveniles	♀[1]	♂	Unknown sex	Grand total
1 Feb 1988	A	10,146	168	10,314	4	10,266	1,705	0	22,289
	A	10,207	180	10,387	15	10,173	1,731	0	22,306
	B	10,053	118	10,171	5	10,220	1,684	15	22,112
	Mean	10,135	155	10,291	8	10,220	1,707	5	22,236
	CV	0.008	0.212	0.011	0.760	0.005	0.014	1.732	0.005
15 Feb 1988	A	10,901	182	11,083	0	4,842	1,493	3	17,421
	A	10,851	154	11,005	0	4,832	1,526	1	17,364
	B	10,595	161	10,756	4	4,778	1,527	14	17,093
	Mean	10,782	166	10,948	1	4,817	1,515	6	17,293
	CV	0.015	0.088	0.016	1.732	0.007	0.013	1.167	0.010
28 Jan 1989	A	10,114	147	10,261	20	10,461	1,663	7	22,412
	A	10,183	129	10,312	9	10,461	1,740	2	22,524
	B	10,048	186	10,234	2	10,398	1,719	5	22,363
	C	10,217	181	10,398	23	10,518	1,748	3	22,691
	Mean	10,140	161	10,301	14	10,459	1,717	4	22,497
	CV	0.007	0.170	0.007	0.722	0.005	0.022	0.522	0.006
16 Feb 1989	A	11,117	175	11,292	3	3,772	1,648	0	16,715
	A	11,266	145	11,411	3	3,697	1,685	4	16,800
	B	11,237	171	11,408	2	3,685	1,657	3	16,756
	C	11,142	156	11,298	4	3,692	1,675	0	16,669
	Mean	11,191	162	11,352	3	3,712	1,666	2	16,735
	CV	0.006	0.086	0.006	0.272	0.011	0.010	1.178	0.003

[1] The count of adult females may contain an extremely small percentage (estimated to be ≤1%) of males that are of similar size as adult females.

cause of pup mortality [Le Boeuf and Reiter, 1991; Stewart and Yochem, 1991]); 3) differences in estimates of precensus pup mortality; and 4) the inferior resolution of small-format (35-mm) photographs (Glegg and Scherz, 1975) when they are used in aerial surveys to estimate total number of births. While differences exist between estimates of the number of births, at this time there is no significant difference in the long-term trend between estimates derived from ground counts or from counts made from large-format aerial color photographs.

A problem with ground surveys is that counts of pups are repeated when they differ by 5% to 10% (Stewart, 1989; Stewart et al., 1994). Large-format aerial color photography makes it possible to obtain accurate and precise counts of northern elephant seals without additional survey effort. In addition, the aircraft did not appear to disturb elephant seals and other sympatric species of pinnipeds (no animals abandoned the haulout area).

The topography at San Miguel Island, San Nicolas Island, and the western end of Santa Rosa Island is ideal for conducting vertical aerial photographic censuses of northern elephant seals because the coastlines of these islands lack tall vertical cliffs. High vertical cliffs that are adjacent to beaches obscure elephant seals by their overhangs and by the shadows that they create. The topography at Santa Barbara Island is not ideal for aerial photographic censusing because cliffs that range up to 122 meters in height obscure elephant seals at the haulouts below them. Counts obtained from aerial photographs at Santa Barbara Island may result in an underestimate of the number of pups present (Table 5).

Counts of northern elephant seals obtained from ground and small-vessel surveys require calibration against counts obtained from vertical aerial color photographs taken with a large-format, IMC-equipped camera. These calibrations are needed for each rookery to evaluate the effects of rookery size

Table 5

Estimates for births of northern elephant seals, *Mirounga angustirostris*, at San Miguel, San Nicolas, Santa Rosa, and Santa Barbara Islands, California, obtained from large-format aerial photographic surveys in comparison with ground surveys or small-format aerial photographic surveys from data presented in Stewart (1992).

	Estimate of births			
Year	Large-format aerial photographic survey (LF)	Ground survey (G)[1]	Small-format aerial photographic survey (SF)[1]	Percent difference (PD)[2]
San Miguel Island				
1985	9,665	10,459		–7.6
1986	9,693	9,824		–1.3
1988	11,083	11,035		+0.4
1989	11,292	11,079		+1.9
1990	12,424	12,152		+2.2
1991	13,209	13,884		–4.9
1992	13,343			
1993	13,900			
1994	14,838			
1995	13,462			
San Nicolas Island				
1988	3,154	3,366		–6.3
1989	4,751	4,466		+6.0
1990	4,147	4,101		+0.5
1991	4,614	4,082		+13.0
1992	5,560			
1993	5,234			
1994	5,790			
1995	6,575			
San Rosa Island				
1990	23		27	–14.8
1991	86		73	+17.8
1992	67			
1993	123			
1994	315			
1995	186			
Santa Barbara Island				
1993	53 (109)[3]			
1994	47			
1995	28 (113)[3]	44[4]		–36 (+157)

[1] From Stewart (1992).
[2] $PD = [(LF - G)/G] \times 100$ or $[(LF-SF)/SF] \times 100$.
[3] The number of adult females counted is enclosed within parentheses; Stewart (1989) used the number of adult females to estimate births.
[4] This study.

and topography on the counts obtained by ground and small-vessel surveys.

Northern elephant seal rookeries at San Miguel and San Nicolas Islands cover many miles of coastline. Observers counting northern elephant seals on the ground at these rookeries require an entire day or several days to complete a census at just one island (Stewart et al., 1994). They have the advantage of being able to spend more time to perform the count, repeat it if necessary, or to determine the sex and age class of a seal correctly, but they can cause a great deal of disturbance to elephant seals and pinnipeds sympatric with them (DeMaster et al.[4]) and their counts lack precision and accuracy. Aerial photo-

[4] DeMaster, D. P., R. L. DeLong, B. S. Steward, P. K. Yochem, and G. A. Antonelis. 1984. A guide to censusing pinnipeds in the Channel Islands National Marine Sanctuary and Channel Islands National Park. Southwest Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, P.O. Box 271, La Jolla, CA. Admin. Rep. LJ-84-44, 22 p.

graphic censuses, on the other hand, provide a nearly instantaneous look at a population that is spread over a wide coastal area with little, if any, disturbance to these pinnipeds and produce counts that are very precise and accurate.

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Field validation of annular growth rings in the American eel, *Anguilla rostrata*, using tetracycline-marked otoliths

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The American eel, *Anguilla rostrata*, is a catadromous species which enters freshwater or estuarine habitats as a glass eel after metamorphosing from the planktonic leptocephalus larval stage. The glass eel phase is followed by the yellow phase, which is the primary feeding and growth stage. The yellow phase is maintained until a critical length is obtained, at which time the eel undergoes another metamorphosis to the silver stage and begins a return migration to the Sargasso Sea (Frost, 1945; Helfman et al., 1987). The age at which the eel reaches the size necessary for the silver metamorphosis is an important factor in understanding the growth of the eel in specific habitats.

Age determination of anguillid eels is restricted to otolith analysis (Tesch, 1977). Numerous otolith examination techniques exist (summarized by Panfili et al., 1990). The common problems with present methods are the subjective nature of interpreting annuli and the difficulty in distinguishing false rings (Deelder, 1976, 1981; Michaud et al., 1988). These problems can be reduced by validating the periodicity of otolith ring formation. Once the presence of true annuli is established, false (supernumerary) rings can be more easily discerned.

Several annulus validation methods have been reported. These have used eels of known age (*Anguilla rostrata*: Liew, 1974), tagged eels in the field (*A. anguilla*: Berg, 1985), and tetracycline- or calcein-treated eels in captive ponds (*A. anguilla*: Panfili et al., 1991; Mounaix et al., 1992; Dekker[1]). Chisnall and Kalish (1993) used tetracycline-treated otoliths to confirm the periodicity of ring formation in wild populations of *Anguilla dieffenbachii* and *A. australis*. No validation study has been done for any wild population of American eels. This study validates annular ring formation and describes supernumerary zones for tetracycline-injected American eels from a Rhode Island river.

Materials and methods

Eels were collected from the Annaquatucket River, North Kingstown, RI (lat. 41°30'N , long. 71° 22'W), a tributary of Narragansett Bay. Collections were made from seven locations along a 5.5-km section of the river (Fig. 1).

Yellow-phase American eels, *Anguilla rostrata*, were collected in August 1990 and September 1990. Eels were collected with a Smith-Root model 12 Electrofisher. Captured eels were anesthetized in MS-222, measured (total length, TL), and individually marked with liquid nitrogen-cooled brands. Four hundred eels less than 30 cm TL were given an intraperitoneal injection of 75 mg tetracycline/kg body weight (after Dekker[1]). Eels larger than 30 cm were not injected owing to the high probability of migration out of the river in the fall. Most eels (more than 95%) undergo the silver-phase metamorphosis and begin their seaward migration out of the Annaquatucket River at total lengths between 30 and 40 cm (Oliveira, unpubl. data). Upon recovering from anesthesia, all eels were released at the location from which they were captured.

All stations were resampled bimonthly from August 1990 to September 1992. Marked, tetracycline-injected eels recaptured from April through September (1991 and 1992) were kept for otolith examination. Some marked eels recaptured prior to the 1992 interval were anesthetized, identified, and measured prior to being released again; nine of these eels were eventually recaptured and kept for otolith examination.

Both sagittal otoliths were removed from each eel, cleaned of extraneous tissue, and stored dry in glass vials. Otoliths were prepared for examination according to Secor et al. (1992) with the following modifications. One of each pair was embedded in epoxy, and a 0.18 mm section that transected the nucleus was cut with an Isomet low-speed saw. The sections were mounted on glass slides with Crystal Bond 509 thermoplastic adhesive and polished with 5-μm and 3-μm metallurgical lapping film. Polished sections were viewed under

[1] Dekker, W. 1986. Age reading of eels using tetracycline marked otoliths. ICES Council Meeting 1986; Copenhagen, Denmark, 14 p.

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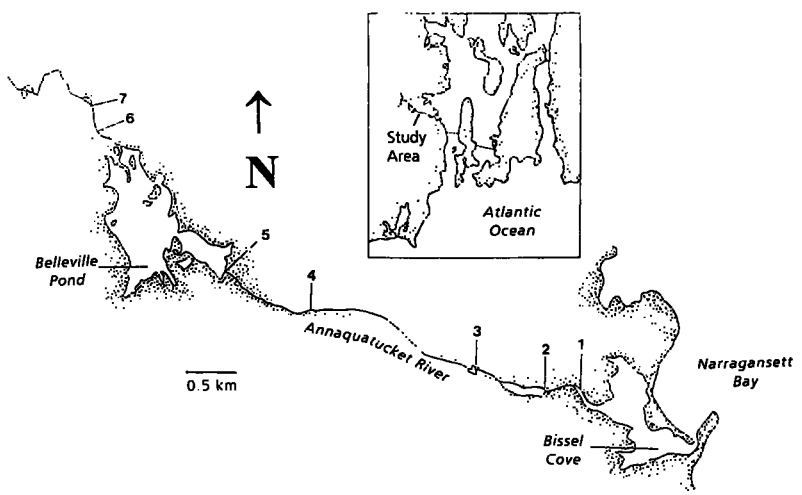

Figure 1

Map of collection sites in the Annaquatucket River, a tributary of the Narragansett Bay, Rhode Island. The inset shows the location of the river to the Bay as well as the Atlantic Ocean. Yellow-phase American eels, *Anguilla rostrata*, were electrofished from stations 1–7 in August and September 1990.

fluorescent light with a compound microscope at 40× magnification. When a fluorescent ring was visible, a preliminary count of the number of rings after the tetracycline mark was made. The sections were then etched for one minute with a 5% ethylenediaminetetraacetic acid (EDTA) solution and stained for two minutes with 0.01% toluidine blue. This procedure enhanced all otolith rings and enabled the differentiation of supernumerary zones. A 3-minute treatment with both EDTA and toluidine blue produced greater resolution of rings but decreased the intensity of the fluorescent mark. The otoliths were also observed under both transmitted light and reflected UV light so that the tetracycline mark and ring formations were visible simultaneously. All opaque ring formations (complete and incomplete) described were observed with transmitted light.

Results

Nine tetracycline-injected eels were recaptured after the first winter and 11 after the second winter at liberty. Examination under UV-light revealed a fluorescent mark on all otoliths. All otoliths showed a distinctive, complete opaque ring aligned with the external edge of the tetracycline mark (Fig. 2). This ring (false complete) was distinguishable from other complete rings because of its association with the tetracycline mark and its atypical spacing compared with other complete rings (Fig. 2). The association of these rings and the tetracycline marks was the same for all eels, whether tagged in early August or late September; therefore no seasonal effect was apparent.

Eels were recaptured from all locations except station 5: 3 from station 1, 3 from station 2, 1 from station 3, 4 from station 4, 2 from station 6, and 7 from station 7. Nine eels were recaptured more than once (4 twice, 3 three times, and 2 four times), but only one false complete ring was observed on each otolith. These nine eels were all recaptured twice prior to the first winter.

After the fluorescent mark and its associated false ring, one complete ring (an opaque zone which completely encircled the otolith, as seen with transmitted light) for each winter was visible on all otoliths (Fig. 2). Otoliths from all locations had a similar tetracycline mark and false ring arrangement as well as only one new ring for each winter.

Many otoliths had numerous incomplete rings made of narrow opaque zones which did not extend completely around the otolith. These incomplete rings were located throughout the translucent zone bounded by complete rings (Fig. 2).

Discussion

All otoliths showed a single complete ring (annulus) for each winter after the tetracycline mark. Two complete rings beyond the tetracycline mark were

Figure 2

Transverse section from a tetracycline-marked sagittal otolith taken from an American eel, *Anguilla rostrata*, at liberty for two winters after marking. The section was etched with 5% EDTA and stained with 0.01% toluidine blue. Photographed with both transmitted light and reflected UV light. A = tetracycline mark; B = false complete ring; and C = complete ring (annulus). The first complete ring after the tetracycline mark was not fully enhanced owing to the dissolution of the tetracycline mark with extensive EDTA treatment.

present only in otoliths from eels recaptured after the second winter at liberty, indicating that normal complete ring formation takes place during winter months. For this population of *Anguilla rostrata*, it may be concluded that complete rings are produced annually. This is in agreement with Liew (1974) and with reports for *A. anguilla* (Frost, 1945; Berg, 1985; Panfili et al., 1991; Mounaix, 1992).

Two forms of false annuli were present: complete and incomplete. The false rings most similar to true annuli (false complete) were found only adjacent to the fluorescent mark and resulted from one or a combination of several stressful events: anesthetizing, tagging, and tetracycline injection. Tagging has been reported to cause growth discontinuities in the otoliths of *Anguilla anguilla* (Berg, 1985). In the present study, eels recaptured more than once, but receiving no further branding or injection, did not produce additional false complete rings. The lack of additional false complete rings after the tetracycline mark in these eels suggests that the stimulus for their production was absent. Natural stimuli necessary for formation of false complete rings appear to be missing. Therefore, ages of eels reported for this river are not overestimated by misconstrued false complete rings.

Incomplete rings may result from environmental stresses associated with a freshwater habitat (Mounaix, 1992). Deelder (1981) and Liew (1974) suggested that temperature extremes were a source of supernumerary zone formation. The Annaquatucket River is a shallow freshwater system subject to extreme temperature fluctuations in the summer months (Oliveira, unpubl. data). The presence of incomplete rings throughout the interval between annuli indicates that incomplete rings form throughout the year. The similarity in ring formation among otoliths collected from different locations indicates that the factors influencing ring formation are homogeneous in the Annaquatucket River.

The validation of the formation of true annuli and the clarification of false rings in this study facilitate the use of otoliths for ageing Annaquatucket River eels. Extension of these conclusions to eels from other locations requires further study.

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Timing of hyaline-zone formation as related to sex, location, and year of capture in otoliths of the widow rockfish, *Sebastes entomelas*

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Widow rockfish, *Sebastes entomelas*, are an important component of the west coast commercial groundfish fishery. Annual landings between 1983 and 1992 were 9,700 metric tons (Pacific Fishery Management Council[1]). In addition to widow rockfish, many other rockfish species are important targets of commercial and sport fisheries. Most stock assessments of rockfish are based on ageing methods (Pacific Fishery Management Council[1]). In most cases, rockfish are aged by the broken-and-burnt otolith method (Chilton and Beamish, 1982).

Age validation of several rockfish species has been conducted by marginal increment analysis. The following species have been validated: yellowtail rockfish, *S. flavidus* (Kimura et al., 1979); shortbelly rockfish, *S. jordani* (Pearson et al., 1991); chilipepper rockfish, *S. goodei* (Mellow[2]); and widow rockfish (Lenarz, 1987). In all four studies, the hyaline zone formed between December and April.

Marginal increment analysis relies on the assumption that if a hyaline zone is laid down once a year, there should be a clear pattern of periodic growth on the edge during the year. Marginal increment analysis is appropriate only if all fish in the population lay down the hyaline zone at the same time. An annulus would then consist of a single hyaline zone and an opaque zone. Conventionally, hyaline zones are counted for age determination purposes.

The hyaline zone is believed to form during periods of slow growth (Blacker, 1974; Schramm, 1989). Specifically, hyaline-zone formation has been attributed to reproduction (Hostetter and Munroe, 1993), water temperature (Thomas, 1983; Schramm, 1989), lack of food (Schramm, 1989), and environmental perturbation (Beckman et al., 1991). Schramm (1989), in a laboratory experiment with bluegill, *Lepomis macrochirus*, found that low temperature produced a hyaline zone. He was also able to induce the formation of hyaline zones by varying photoperiod and restricting food intake, but reported that the hyaline zones formed by these environmental agents were much fainter than those resulting from temperature.

If the hyaline zone is formed exclusively by one factor (i.e. reproduction), and if the factor occurs exactly once a year, at the same time each year, every year, and at the same time in all areas where fish are collected, then samples can be combined from multiple years and different areas. However, Thomas (1984) found that hyaline-zone formation in West African pilchard, *Sardinops ocellata*, otoliths varied between years, and false marks (checks) were laid down with some degree of periodicity. Given the large number of factors known to produce hyaline zones, it seems likely that timing of hyaline-zone formation is variable.

Rockfish are ovoviviparous; parturition occurs about one month after fertilization (Moser, 1967), and thus males expend energy on reproduction at a different time than do females. If spawning is important in the formation of the hyaline zone for rockfish, then it is possible that males do not lay down the hyaline-zone at the same time as females. Failure to account for differences among sexes in the timing of hyaline-zone formation could result in errors in age determination.

The purpose of this study was to examine the otoliths of an important rockfish species and to determine whether there were sexual, geographical, or annual variations in the time of hyaline-zone formation. Possible causes of variations in the time of hyaline formation are also discussed.

Methods

Sagittal otoliths of widow rockfish were obtained from California and Washington commercial groundfish port sampling programs for the years 1983–87. This interval was selected because in 1983 an El Niño event occurred (Glynn, 1988) and a sequential series of years with adequate sample sizes was desired. Otoliths were collected from widow rockfish caught in northern Califor-

[1] Pacific Fishery Management Council. 1993. Status of the Pacific Coast groundfish fishery through 1993 and recommended acceptable biological catches for 1994. Report of the Pacific Fisheries Management Council, Portland, OR, 467 p.

[2] Mellow, J. 1993. Bodega Bay Field Office, California Department of Fish and Game, 1785 Highway 1, Bodega Bay, CA 94923. Personal commun.

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Fishery Bulletin 94:190–197 (1996).

nia (lat. 40° to 42°N) and throughout the coast of Washington (lat. 46° to 49°N).

Otoliths were examined only from fish less than 45 cm fork length because it is seldom possible to determine reliably the edge type of older, larger fish. On the basis of age-length relationships developed by Pearson and Hightower (1991), these fish ranged between four and twelve years. The dates of capture were not provided to the age reader; however, the reader did know the source (state) from which the otoliths were collected. The otoliths were broken and burnt according to the methods described by Chilton and Beamish (1982) and examined with reflected light with a dissecting microscope (20–30×). Edge types were classified as hyaline, narrow opaque (opaque area less than 1/2 of the previous opaque zone), and wide opaque (opaque area greater than 1/2 of the previous opaque zone). In about 1% of the fish (older fish), the edge could not be clearly identified owing to the narrowness of the rings. In this situation the otolith was omitted from the analysis. An attempt was made to obtain edge types of otoliths from 100 fish per month, per year, per state, but this was not possible in many cases (Table 1). A total of approximately 10,230 otoliths were initially examined, and edge types were ultimately determined for 6,384 fish.

The purpose of this study was to examine the timing of hyaline-zone formation. More than 95% of all otoliths had formed new opaque zones by July, and because sample sizes were small and patchy for August through December, these samples were not tested.

As some edge types were rare in certain months, edge types were omitted from some of the monthly analyses for both states as follows. When fewer than three otoliths had a given edge type, and when the edge type was uncharacteristic for that month, the otoliths were removed from the analysis. In January and February, narrow opaque edges were omitted; in April and May, wide opaque edges were omitted; and in July, hyaline edge types were omitted.

To determine whether significant differences in edge type existed between sexes, locations, and years, multiway contingency tables were examined by chi-square analysis with the CATMOD procedure, which has the log-linear option, in the SAS statistical analy-

Table 1

Numbers of widow rockfish, *Sebastes entomelas*, otoliths with identifiable edge types from Washington and California in 1983–87, by month. October, November, and December were omitted from the marginal increment study owing to small sample sizes.

State	Month	1983	1984	1985	1986	1987	Total
California	Jan	10	54	116	92	69	341
	Feb	75	17	111	101	63	367
	Mar	37	126	115	71	98	447
	Apr	45	54	107	66	102	374
	May	39	53	80	88	111	371
	Jun	24	89	56	70	52	291
	Jul	41	50	50	59	93	293
	Aug	39	66	54	18	137	314
	Sep	35	30	52	53	63	233
	Oct	15	14	57	18	82	186
	Nov	10	1	13	6	1	31
	Dec	2	1	1	1	1	6
	Total	372	555	812	643	872	3,254
Washington	Jan	97	98	88	100	39	422
	Feb	40	30	0	97	64	232
	Mar	99	67	93	100	50	409
	Apr	83	42	99	99	90	413
	May	34	81	0	68	48	232
	Jun	96	95	0	73	0	266
	Jul	67	59	77	69	25	297
	Aug	99	0	93	0	43	237
	Sep	0	28	0	0	95	126
	Oct	1	91	1	20	79	192
	Nov	1	14	57	67	1	140
	Dec	1	26	1	100	36	164
	Total	619	632	513	795	571	3,130

sis program (SAS Institute Inc., 1987). The log-linear option was used because edge types would not be normally distributed within the month. The analyses were used to test for interactions between edge type and each factor (sex, year, and location). In addition, two-way interactions were tested for the relationship of edge type to sex by year, sex by state, and year by state. Since there were no samples from Washington in February 1985, May and June of 1985, and June of 1987 (Table 1), the analyses of state, year by state, and state by sex, were not done for these months. Each test was conducted separately by month because edge type was known to vary between months (Lenarz, 1987) and because the purpose of this study was to examine differences among sexes, years, and areas.

The times of formation of the hyaline zones are discussed in light of sea-surface temperature data from northern California and southern Washington. Mean monthly sea-surface temperatures were obtained from National Weather Service marine buoys located off Point Arena (northern California) and the Columbia Basin (where many of the Washington fish were caught).

Results

There was a significant difference in edge type between the sexes for the month of March (Table 2). Examination of the data indicates this difference was due to a difference in the percentage of opaque zone types present. Males had a slightly smaller fraction of narrow opaque zones than did females (5.7% vs. 6.3%), and a slightly larger percentage of wide opaque zones (8.4% vs. 6.9%). There were no significant differences between the sexes for any other month.

There were significant differences in the timing of hyaline-zone formation between the states for all months that could be tested (Table 2). Both hyaline and opaque zones form earlier in Washington than in California (Fig. 1). By July, about 50% of all otoliths from Washington have a wide opaque zone whereas only about 20% of the otoliths from California have a wide opaque zone.

There were significant differences in edge types among years for all months (Table 2). Hyaline zones formed earlier in 1985 and 1987, at an intermediate time in 1986, and later in 1983 and 1984 (Fig. 2, A and B).

There were significant differences in edge type for all months for which the year-state interaction could be tested (Table 2). This indicates that the states do not vary to the same extent. Yearly differences are much more pronounced in California than they are in Washington (Fig. 2, A and B). In all cases, the annual variations are in the same direction; however, the changes are smaller in Washington (Table 2).

Table 2

Chi-square values and probabilities of significance for variables associated with differences in edge type on widow rockfish, *Sebastes entomelas*, otoliths collected from California and Washington. Years used were 1983–87. * = significant difference ($P<0.05$).

Month	Variable	df	χ^2	P
January	Year	4	22.79	0.0001*
n=760	State	1	66.26	0.0001*
	Sex	1	3.28	0.0699
	Year × State	4	86.77	0.0001*
	Year × Sex	4	3.38	0.4964
	State × Sex	1	0.43	0.5138
February	Year	4	163.49	0.0001*
n=592	Sex	1	1.73	0.1887
	Year × Sex	3	12.50	0.0059*
March	Year	8	43.12	0.0001*
n=856	State	2	14.05	0.0009*
	Sex	2	20.95	0.0001*
	Year × State	3	42.64	0.0001*
	Year × Sex	8	23.56	0.0027*
	State × Sex	2	20.63	0.0001*
April	Year	4	94.10	0.0001*
n=731	State	1	126.52	0.0001*
	Sex	1	0.23	0.6307
	Year × State	4	44.12	0.0001*
	Year × Sex	8	23.56	0.0027*
	State × Sex	1	1.15	0.2836
May	Year	4	113.53	0.0001*
n=583	Sex	1	2.88	0.0898
	Year × Sex	3	9.53	0.0230*
June	Year	8	300.22	0.0001*
n=555	Sex	2	2.29	0.3177
	Year × Sex	4	4.43	0.3509
July	Year	4	129.40	0.0001*
n=575	State	1	73.72	0.0001*
	Sex	1	0.09	0.7704
	Year × State	4	69.78	0.0001*
	Year × Sex	4	6.49	0.1654
	State × Sex	1	.92	0.3376

There were significant differences in edge types in February, March, and April for the year-sex interaction. There were no differences for this interaction for January, May, or June. These differences may be attributed in part to the strong effect of yearly variability. Examination of the frequency distributions also suggests that a somewhat higher fraction of females have hyaline zones in February, March, and April in 1983, whereas the fraction tends to be equal in other years.

There was a significant difference in edge types in March for the state-sex interaction (Table 2). There

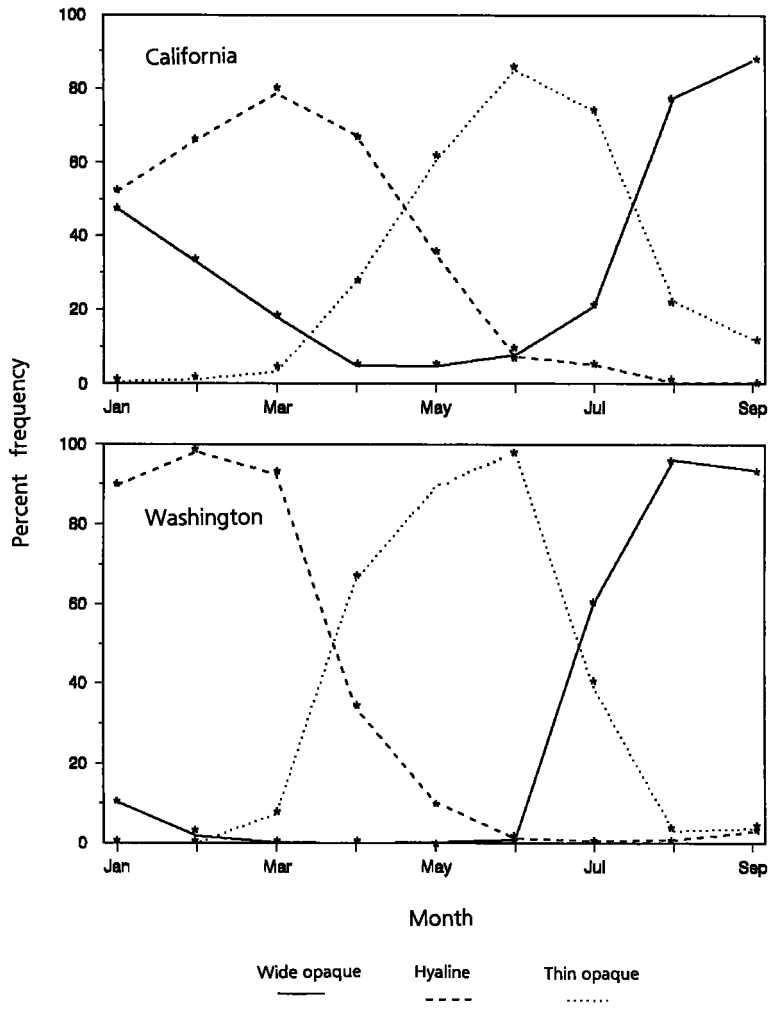

Figure 1

Marginal increment comparison for widow rockfish, *Sebastes entomelas*, between Washington and California for the years 1983–87 combined (unweighted means) and sexes combined. Large opaque is defined as an opaque edge >1/2 the size of the previous opaque zone; small opaque is defined as an opaque edge <1/2 the previous opaque zone.

were no differences in edge types for the months of January, April, or July. This difference appears to be due to the tendency of females in California to have a smaller portion of their population with hyaline edges and more of both late opaque and early opague edges in March. Males tended to be similar among states.

Discussion

Significant differences in the time of hyaline-zone formation exist among years and states and may have important ramifications for age determination. It is important to consider whether differences in the seasonal expression of the hyaline zone might cause errors in age determination and, if so, what type of errors might occur.

By convention all fish are considered to be born on 1 January (Chilton and Beamish, 1982) to assure proper year-class identification. In addition, if the edge appears hyaline before January, it is not counted, and if it is opaque after December, a hyaline edge is assumed to be present and therefore counted.

The results of this study indicate that the hyaline zone forms earlier in otoliths from fish in Washing-

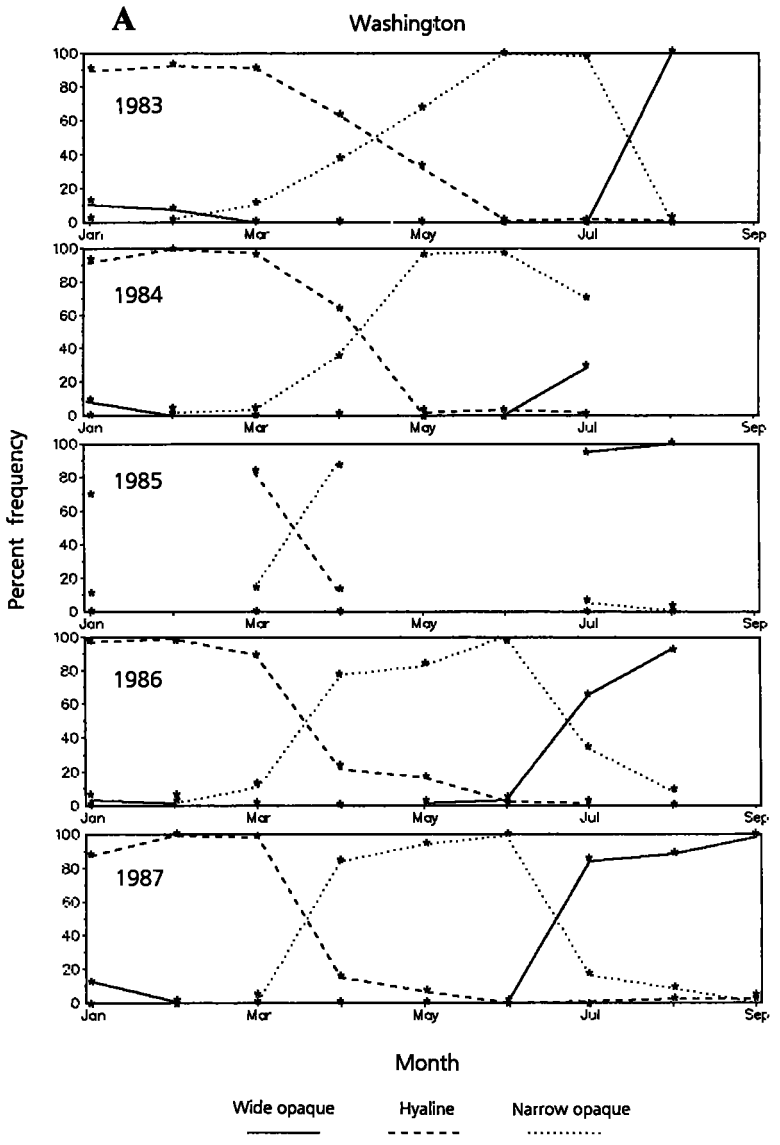

Figure 2

Marginal increment comparison for widow rockfish, *Sebastes entomelas*, between states and years 1983–87. Refer to Table 1 for sample sizes.

ton than in those from fish in California. In addition, there are annual differences in the timing of hyaline-edge formation. Problems in age determination may arise when the forming annulus is small relative to preceding annuli. In this case, a fish collected in March might be mistakenly aged as one-year younger. This would occur because the reader might consider the completed opaque zone to be new growth for the current year. This problem is more likely to occur in young fish where the relative size of the annuli is comparatively large.

The later time of hyaline-zone formation in 1983 (Fig. 2) suggests a possible explanation for the observation that the opaque zone formed that year was smaller than those formed in preceding and subsequent years (Woodbury[3]). As the opaque zone formed later in 1983, particularly in California (Fig. 2), there was less time for the opaque zone to form, and therefore a smaller opaque zone was visible for that year.

[3] Woodbury, D. P. 1994. National Marine Fisheries Service, 3150 Paradise Drive, Tiburon, CA 94920. Unpubl. data.

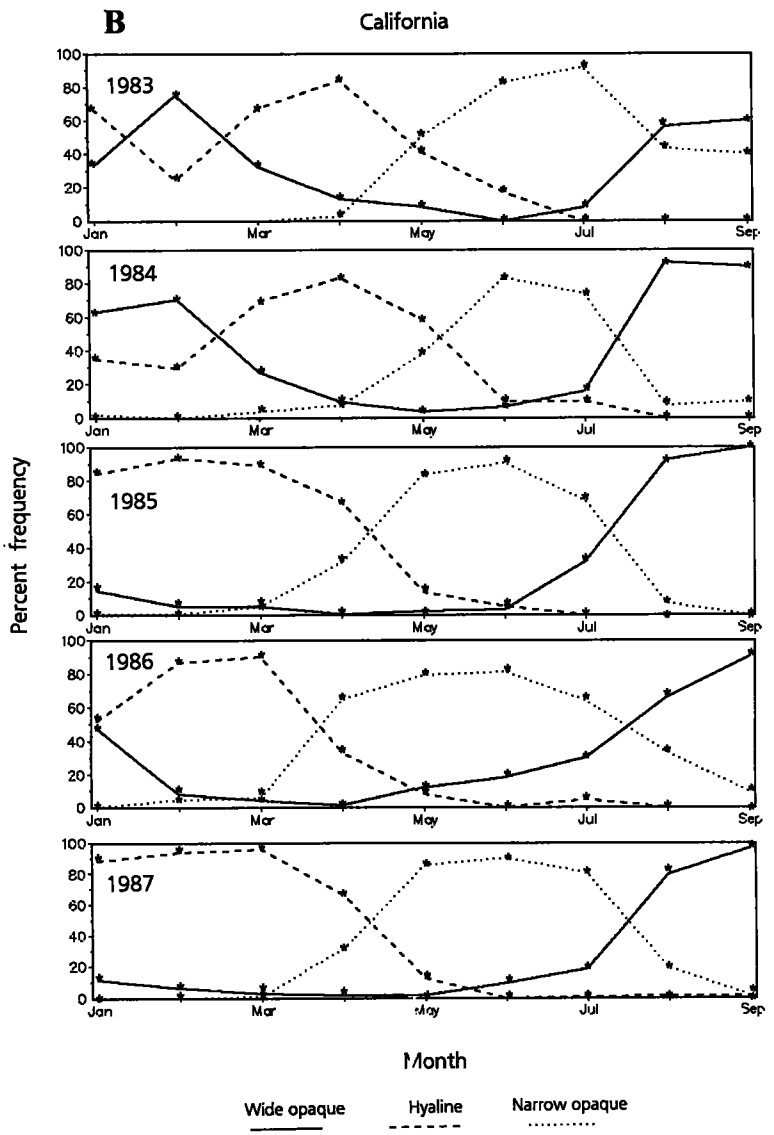

Figure 2 (continued)

The late onset of opaque-zone development may be related to ocean temperature.

The 1983 El Niño event began early in the year (Fig. 3). During the spring of 1983, sea-surface temperature was the warmest of all spring temperatures from 1983 through 1987. In addition, the minimum temperature off California occurred later in 1983 than in other years. These environmental changes coincide with the late formation of the hyaline zone in 1983.

The temperature-hyaline zone formation relationship is supported by the fact that the timing of the spring sea-surface temperature minimum in Washington is more constant than in California (Fig. 3). This is similar to the pattern observed in hyaline-zone formation in otoliths between the two states. Finally, the temperature declines earlier in Washington than it does in California, which is consistent with the earlier onset of hyaline-zone formation in otoliths from fish in Washington. Although the link between temperature and hyaline-zone formation is not conclusive, it is suggestive. It is possible that some factor, related to temperature, is responsible for formation of the annulus (e.g. food availability or nutrient content of prey).

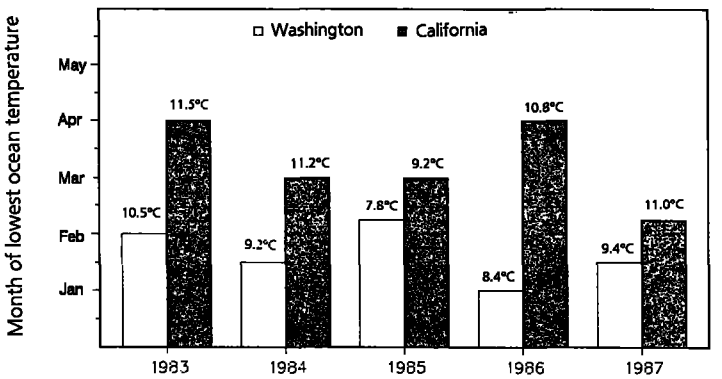

Figure 3

Month of minimum sea-surface temperatures in Washington and California from 1983–85. Source: Pacific Fisheries Environmental Group, National Marine Fisheries Service, P.O. Box 831, Monterey, California 93942, unpubl. data, January 1984.

Reproduction is unlikely to play a significant role in the time of hyaline-zone formation. The only difference among the sexes in timing of hyaline-zone formation occurred in March. In that month it appeared that females were more likely to have either wide or narrow opaque zones. It should be noted, however, that 81% of the females had hyaline zones (88% of males had hyaline zones). Males expend energy on spermatogenesis from October through January, whereas females expend most of their energy on reproduction later, with parturition in February (Wyllie Echeverria, 1987).

In some studies, maturity has been shown to be related to the time of annulus formation (Chugonova, 1931; Konstantinova, 1958). Although maturity was not recorded, about half of the fish from both areas in this study should have been sexually mature on the basis of maturity-at-length relationships (Barss and Wyllie Echeverria, 1987). If immature fish had failed to lay down a hyaline zone, the differences should have been evident in Figure 2; that is to say, a large fraction of the fish would show no hyaline-zone at any time of the year. If the timing of hyaline-zone formation had been markedly different between mature and immature fish, this would have been reflected as a second mode in the month of hyaline-zone formation.

Several different methods of marginal increment analysis have been used to validate ages. Beckman et al. (1991) used four edge types in a classification designed to characterize more precisely when the hyaline zone is formed. Many researchers have measured the width of the edge (Nelson and Manooch, 1982; Barger, 1985; Maceina et al., 1987; Manooch and Drennon, 1987; Bullock et al., 1992; Hyndes et al., 1992; Hostetter and Munroe, 1993). The measurement approach has an advantage in that it should be possible to plot growth of the edge over time to verify that only a single hyaline mark is laid down each year. However, in some species, it can be difficult to determine a consistent location to measure on the otolith because of the inherent variability of their otoliths. In addition, a great deal of time is required to process the otoliths. The classification of edge types into three or more categories is one way to qualitatively judge the width of the edge (usually relative to the preceding opaque zone). This approach has an advantage over simply classifying the edges as either hyaline or opaque in that it indicates whether the opaque zone has just formed or whether a new hyaline zone may be ready to form.

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Abstract.—The reproduction of blue-eye trevalla, *Hyperoglyphe antarctica*, off Tasmania, southern Australia, is studied in detail through analysis of gonad maturation, spawning location and season, size at maturity, fecundity, and spawning frequency.

Results show that the fecundity of blue-eye trevalla is determinate, and it has a high annual fecundity which increases exponentially with the length of females (to a maximum of about 11 million oocytes). Females are partial spawners and possibly spawn all their oocytes in 3 or 4 large batches, the size of batches increasing with the length of females. Both sexes reach sexual maturity at large sizes, 71.3 and 61.6 cm fork length for females and males, respectively. One major spawning ground was identified off Tasmania where blue-eye trevalla aggregate from October to May. Smaller fish join the aggregation first, at early stages of gonad maturation, whereas larger fish appear to join the aggregation later, just prior to spawning. Spawning takes place at the end of summer–autumn (early March to early May).

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Biology and dynamics of the reproduction of blue-eye trevalla, *Hyperoglyphe antarctica* (Centrolophidae), off Tasmania, southern Australia

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Blue-eye trevalla, *Hyperoglyphe antarctica* (Centrolophidae) are widely distributed in the southern oceans, from New Zealand to southern Australia, South Africa, and the southern Indian Ocean (Haedrich, 1967; McDowall, 1982). In Australia, they are found from central New South Wales to southern western Australia (Fig. 1) and on offshore seamounts. The fishery has developed off southeast Australia, particularly off Tasmania (Fig. 1). Fishing is traditionally done with drop-lines on hard sea bottom associated with the continental shelf break, at depths between 300 and 500 m. Commercial landings are relatively small (about 800 metric tons per year), but blue-eye trevalla is an excellent table fish and fresh fish fetch high prices on the domestic market.

In the late 1980's, a conflict arose between traditional line fishermen and trawl fishermen who intended to develop mid-water trawling techniques to target blue-eye trevalla. At that time, there was limited information on the biology and size of the resource, and it was feared that mid-water trawling would increase fishing effort to unsustainable levels. As a result, a research program was implemented in 1991 to study the biology of blue-eye trevalla off Tasmania. Anecdotal information on the breeding season of this species was available from Jones[1] in South Australia and from Horn and Massey (1989) in New Zealand; no fecundity study had been undertaken. In this paper the reproductive biology (gonad maturation, size at maturity, spawning frequency, and fecundity) and the composition and dynamics of the main spawning aggregation are studied in detail, and a discussion is provided on some of the implications for the fishery.

Materials and methods

Sampling

Blue-eye trevalla were collected on board commercial vessels during drop-line fishing operations, between November 1991 and July 1993. Drop-lines are polypropylene lines that are anchored with a weight to the sea bottom at depths between 300 and 500 m and that are supported vertically by boys. Ten to 15 lines are used during fishing, each carrying about 100 hooks. At least one sample was obtained each

[1] Jones, G. K. 1988. The biological status of the deepsea trevalla (*Hyperoglyphe antarctica*) offshore line fishery in South Australian waters. Department of Fisheries, South Australia, discussion paper, April 1988, 15 p.

month from most fishing grounds around Tasmania (Fig. 1). A sample represented the total catch made during one fishing trip (of 1–3 day duration) on the same ground. Fish were examined individually as they were hauled on deck, and the entire catch (or the majority of it) was processed during each fishing trip (representing between 50 and 500 fish). Fish were measured (fork length [FL]) to the nearest cm below the true length, sexed, and staged macroscopically by using the maturity stages described in Table 1 (adapted from Hunter and Macewicz, 1985, a and b; Schaefer, 1987; West, 1990). To calculate the gonadosomatic index (GSI), ovaries and testes were collected to be weighed in the laboratory to the nearest 0.1 g. The GSI was calculated as the proportion of gonad weight divided by body weight with the following length-weight relationship: Log (*gutted weight*) = 3.081 × Log (*fork length*) –4.385, where weight is in g and length in cm (Baelde, unpubl. data). For later histological examination and measurement of whole oocytes, ovaries at various stages of maturity were preserved in Davidson's solution immediately after the catch. Nearly all mature ovaries (stages 4 to 6, Table 1) were preserved.

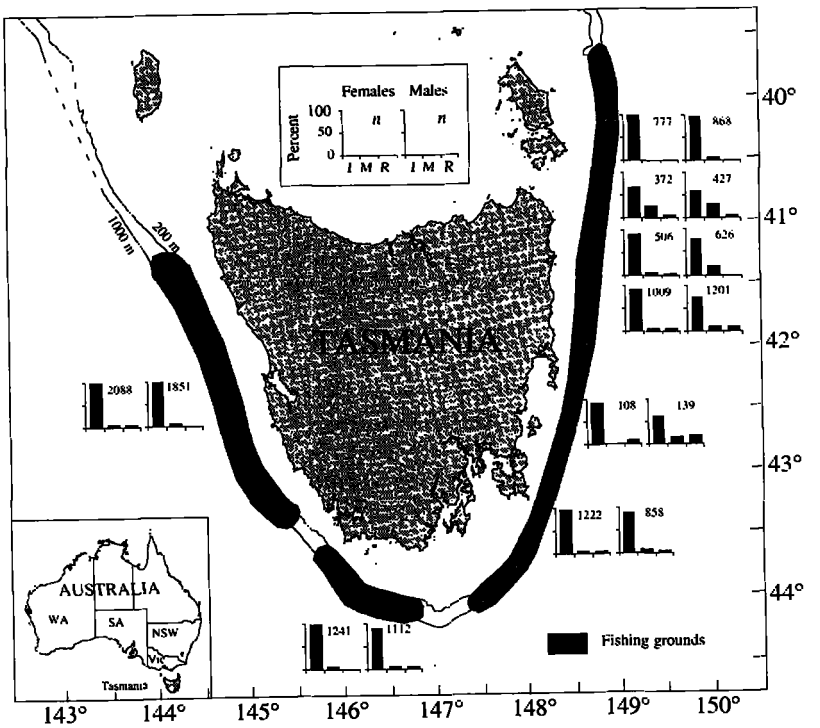

Figure 1

Proportions (as a percentage) by sex of immature (I), mature (M), and resting (R) blue-eye trevalla, *Hyperoglyphe antarctica*, in samples collected from major fishing grounds around Tasmania. I = stages 1 to 3 for females, 1 to 2 for males; M = stages 4 to 6 for females, 3 and 4 for males; and R = stages 7 and 8 for females, stage 5 for males. Depth contours in meters. WA = Western Australia, SA = South Australia, Vic = Victoria, and NSW = New South Wales. Numbers in graphs are the number of fish sampled.

Histological staging of ovaries

A total of 447 ovaries were examined histologically to check macroscopic staging and to note the presence of atretic oocytes and postovulatory follicles (see description in Table 1; Fig. 2; Fig. 3, A and B). Ovary sections were stained in haematoxylin and eosin and ovaries were staged on the basis of the most advanced type of oocytes present, regardless of their abundance (West, 1990).

Size at maturity

The average size at maturity ($FL_{0.5}$) was the size at which 50% of the fish caught during the breeding season were mature (i.e. stages 4 to 6 for females, and stages 3 and 4 for males). For each sex, the proportion (p) of mature individuals, by 1-cm fork length intervals, was fitted to the logistic function

$$p = e^{(a+bFL)} / \left(1+e^{(a+bFL)}\right)$$

by using generalized linear models (Genstat 5 Reference Manual). The average size at maturity was also estimated for length and maturity data collected off the east coast of Tasmania during the 1950's (Cowper and Downie[2]).

Spawning frequency and fecundity

Hunter et al. (1992) have identified three main factors that can affect fecundity estimates: 1) the rate of atresia in reducing the number of oocytes spawned; 2) the occurrence of previous spawnings (as shown by the presence of postovulatory follicles); and 3) the accurate identification of which oocytes to include in estimating fecundity. These three factors were examined as shown below.

Rate of atresia The proportion of atretic oocytes was determined in ovaries at various stages of maturity

[2] Cowper, T. R., and R. J. Downie. 1995. CSIRO, Division of Fisheries and Oceanography, Cronulla, New South Wales, Australia. Unpubl. data.

Table 1

Female and male blue-eye trevalla, *Hyperoglyphe antarctica*, maturity stages based on macroscopic and histological examination. Adapted from Hunter and Macewicz (1985, a and b); Schaefer (1987); West (1990); Hunter et al. (1992); Davis and West (1993).

Females			
Stage	Macroscopic description	Histological description	Oocyte development
1 Immature	Small thread-like ovaries, pink and translucent;	Chromatin nucleolar stage: very small oocytes, nucleus surrounded by a thin layer of dark-blue-stained cytoplasm;	
2 Early developing	Oocytes not visible, ovaries pink and translucent; *First-time developing females:* ovaries up to 10 cm long, 1 cm across, ovary wall thin and transparent; *Redeveloping females:* ovaries up to 20 cm long, 5 cm across, flaccid, ovary wall thick, whitish, and opaque;	Perinucleolar stage: oocyte size increases slightly as dark-blue-stained cytoplasm thickens, nucleoli appear at the periphery of nucleus;	Cytoplasm homogeneous, brownish and transparent, comparatively large dark nucleus;
3 Developing	Small oocytes becoming visible, still translucent, ovaries occupy less than 20% of body cavity;	Cortical alveoli stage: appearance of cortical alveoli in pale-blue-stained cytoplasm, pink-stained zona radiata distinguishable, oil vesicles appearing, lampbrush chromosomes often visible in the nucleus;	Oocytes more or less spherical, cytoplasm thickened, darker, granular, but still translucent, nucleus still visible;
4 Late developing (yolked)	Small opaque oocytes clearly visible, marked increase in ovary size (20% to 100% of body cavity) and change from pink to yellow-orange color, ovary wall thin and transparent;	Yolk stage: marked increase in oocyte size, cytoplasm filled with pink-stained yolk granules, cortical alveoli and oil vesicles increase in size and number; degenerating postovulatory follicles visible if spawning has started;	Oocytes dark, completely opaque, size increasing with development, nucleus occluded; degenerating postovulatory follicles visible if spawning has started;
5 Ripe	Ovary size as in previous stage, large transparent (hydrating) oocytes visible among smaller opaque oocytes;	Nuclear migration stage: migration of nucleus to periphery of oocyte, fusion of yolk granules into yolk plates; fusion of oil vesicles into the oil droplet; degenerating postovulatory follicles visible if spawning has started;	Occurrence of partly translucent oocytes (hydrating), yolk plates visible;degenerating postovulatory follicles visible if spawning has started;
6 Running-ripe	Ovary size as in previous stage, hydrated oocytes larger, easily expressed from ovaries;	Hydration stage: further increase in size of oocytes, all yolk granules fused into a few plates;	Occurrence of very large, almost totally translucent oocytes, oil droplet visible;
7 Spent	Ovaries flaccid, occupy about 20% of body cavity, greyish ovary wall thickened and wrinkled, some residual oocytes visible within translucent material;	Postovulatory follicles clearly visible, no yolked oocytes left except for a few undergoing atresia; structure of ovaries generally loose, hydrated oocytes may be present in lumen;	Postovulatory follicles visible, remaining yolked oocytes at early stage of atresia;

continued

Table 1 (continued)

Females (continued)

Stage	Macroscopic description	Histological description	Ooycte development
8 **Resting**	Aspect of ovaries as in previous stage, not accurately distinguishable.	Oocytes at stages 2 and 3 predominate, no trace of postovulatory follicles left, advanced atresia of remaining yolked oocytes, hydrated oocytes sometimes still present in lumen.	Very small oocytes (stages 2 and 3) predominate, advanced atresia of remaining yolked oocytes.

Males

Stage	Macroscopic description
1 **Immature**	Testes very small, flat, and threadlike;
2 **Early developing**	Testes increase in size, rounder in shape;
3 **Developing**	Size of testes increases further, lobed in formation and marked groove in the middle of each testis visible, creamy or white milt sometimes present;
4 **Late developing to running-ripe**	Testes very large and multilobed, white or pinkish, sometimes bloodshot, free-flowing milt;
5 **Spent and resting**	Testes much smaller, very bloodshot, milt sometimes present, become thinner, brownish and rubbery as they regress to resting stage.

by using samples preserved in Davidson's solution. Only early stages of atresia (stages alpha and beta as described by Hunter and Macewicz, 1985b) were considered (Fig. 3, B, C, and D); oocytes at later stages of atresia are too difficult to identify with commonly used histological techniques.

Occurrence of postovulatory follicles The presence of postovulatory follicles in ovaries was used to identify females that had begun to spawn. In addition, examination of morphological changes in postovulatory follicles after ovulation (as described by Hunter and Macewicz, 1985b; Schaefer, 1987; Macewicz and Hunter, 1993) provided information on spawning frequency. Postovulatory follicles were classified into two types according to the degree of resorption visible in histological sections. Type-1 postovulatory follicles (Fig. 3A) were more recent, presenting an involuted zona radiata with numerous folds and an open cavity, as well as granulosa cells aligned within the zona radiata; type-2 postovulatory follicles were small, had fewer involutions, and showed a much more reduced follicular cavity; at that stage the zona radiata has thickened markedly and the granulosa cells are disorganized. When present in ovaries, 50 postovulatory follicles were randomly measured (along the perimeter) with NIH image analysis software.

Staging and measurement of whole oocytes Staging and measurement of whole oocytes was used to assess whether the fecundity of blue-eye trevalla is determinate or indeterminate, that is, whether yolk formation is completed before spawning starts or continues after (Hunter et al., 1985). This information is needed to know whether the annual fecundity of blue-eye trevalla can be estimated from a standing stock of yolked oocytes (i.e. vitellogenic) present in ovaries. Subsamples of ovaries preserved in Davidson's solution were mixed in small jars with water and 3-mm glass beads and shaken manually to dissociate the oocytes. All ovaries used had been previously staged histologically, and histological sections were used to stage corresponding whole oocytes under a microscope (see description in Table 1 and Fig 3, C and D, adapted from West, 1990; Hunter et al., 1992; Davis and West, 1993). Fifty oocytes were measured (along the maximum diameter) for 135 females at various stages of maturity. Figure 3D also shows whole, preserved postovulatory follicles of type 1 (type 2 were too small to be properly dissected and photographed).

Fecundity estimation Only ovaries that showed no sign of previous spawnings (absence of postovulatory follicles), no sign of major atresia, and in which oocytes were fully yolked (as indicated by their diam-

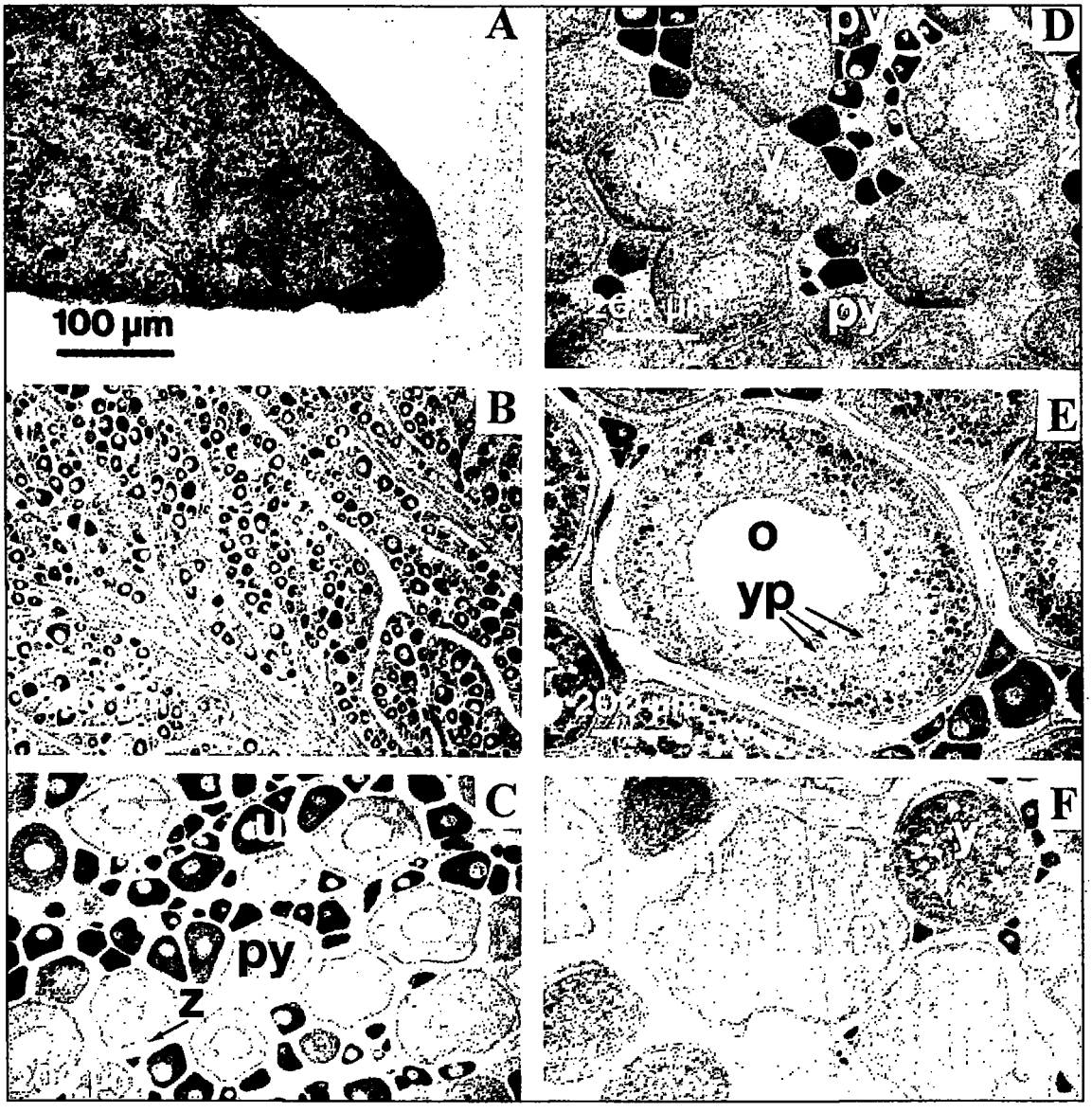

Figure 2

Histological sections showing ovary maturation stages of blue-eye trevalla, *Hyperoglyphe antarctica*. (**A–F**) represent stages 1–6 successively. (D) shows an "early stage 4" characterized by the nonuniform size of yolked oocytes. h = hydrating oocyte (irregular shape due to loss of fluid during histological processing); n = nucleus; o = oil droplet; py = partially yolked oocyte; u = unyolked oocyte; y = yolked oocyte; ym = yolk mass (fusion of yolk plates); yp = yolk plate; z = zona radiata.

eter, see below) were used to estimate the annual fecundity of blue-eye trevalla. Before estimating fecundity, a check was made that the oocytes were uniformly distributed within the ovaries. From five fish, the number of oocytes per gram was compared between subsamples taken across the ovaries (near the periphery and near the center) and along the ovaries (within the anterior, median, and posterior regions). ANOVA showed no differences between subsamples across the ovaries (F=0.68, df=1,4, P=0.42), or between subsamples along the ovaries (F=0.74, df=2,8, P=0.49). Oocytes were then routinely dissociated and counted from three weighed subsamples taken randomly within the ovaries.

Batch fecundity was estimated for eight ripe females by estimating the number of hydrated oocytes;

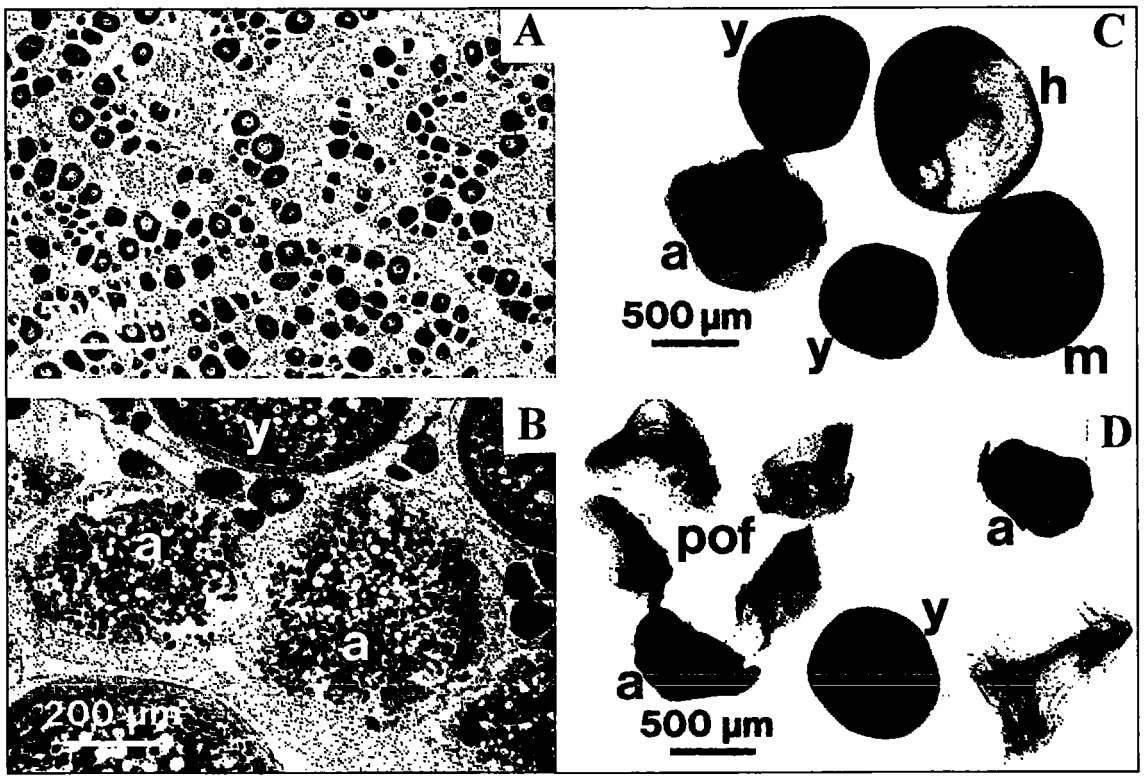

Figure 3

Histological sections of the ovary of blue-eye trevalla, *Hyperoglyphe antartica*. (**A**) Histological section of ovary at stage 7 showing type-1 postovulatory follicles. (**B**) Histological section showing two yolked oocytes at early alpha-stage atresia (a) and a healthy yolked oocyte (y). (**C**) and (**D**) show whole preserved oocytes. (C) shows an oocyte at alpha-stage of atresia (a), stage-4 yolked oocytes (y), a stage-5 oocyte (m) (yolked plates only faintly visible in this photo), and a hydrating oocyte (h) with oil droplet. (D) shows postovulatory follicles (pof) of type 1 and yolked oocytes at an early stage of atresia (a).

only ovaries in which hydrated oocytes formed a well-defined mode were used. Also, the number of yolked oocytes remaining in partially spent ovaries was determined for 24 females.

Results

Gonad maturation

Ovaries at stages 1 and 2 could not be distinguished accurately by macroscopic examination and were grouped together in the analyses, as were stages 7 and 8. GSI values varied greatly within maturity stages (Table 2) and could not be used alone to assess the development of ovaries. Macroscopic staging of the testes was more difficult than that for the ovaries (Table 1). The main criterion used to assess male maturity development, based on the presence or absence of milt, was not consistent. As already observed by Horn and Massey (1989) in New Zealand, milt was sometimes present in small, developing testes but absent in large testes.

Histological examination of stage-4 ovaries led to the distinction, within this stage, of ovaries at an early stage of yolk formation. These ovaries were characterized by a great variation in the size of oocytes (Fig. 2D) compared with the uniform size of fully yolked oocytes. They will be referred to as "early stage 4" in the text. Partially spent ovaries (i.e. stage-4 or stage-5 ovaries containing postovulatory follicles and which were not identifiable macroscopically) will be referred to as stages 4* and 5*.

Spawning location and season

Mature fish of both sexes (stages 4–6 for females and stages 3–4 for males) were caught mostly off the northeast coast of Tasmania, at about 41°S (Fig. 1), but a few were occasionally caught in other areas.

Table 2

Range and median value of female gonadosomatic index (GSI) by stage of maturity for blue-eye trevalla, *Hyperoglyphe antarctica*. * indicates partially spent ovaries (presence of postovulatory follicles). Standard deviations are in parentheses. *n* = sample size.

	Gonadosomatic index		
Stage	Range	Mean	*n*
1+2	0.2–1.1	0.4 (0.2)	58
3	0.3–2.0	0.8 (0.3)	203
Early 4	1.6–12.0	5.2 (2.5)	19
4	3.3–19.5	10.2 (3.1)	92
4*	3.3–15.9	9.5 (3.8)	18
5	8.9–19.4	13.9 (4.7)	5
5*	5.1–14.8	10.0 (3.5)	6
6	20.6	—	1
7	1.6–3.8	2.5 (0.6)	8
8	0.7–2.5	1.5 (0.4)	66
Atretic	0.7–8.1	1.8 (1.6)	21

Table 3

Average size at maturity ($FL_{0.5}$) by sex, and 95% confidence limits for blue-eye trevalla, *Hyperoglyphe antarctica*. Data were fitted to the logistic equation shown in text. Results are shown for data collected during the current study and for data collected in the mid 1950's before the fishery developed (from Cowper and Downie's unpubl. data). CL = confidence limits.

	n	*a*	*b*	$FL_{0.5}$	95% CL
Current data					
Females	1803	–29.86	0.419	71.3	70.7–71.9
Males	1613	–21.06	0.342	61.6	61.2–62.1
Cowper and Downie's data					
Females	813	–23.79	0.341	69.8	69.2–70.3
Males	498	–24.05	0.397	60.6	59.6–61.4

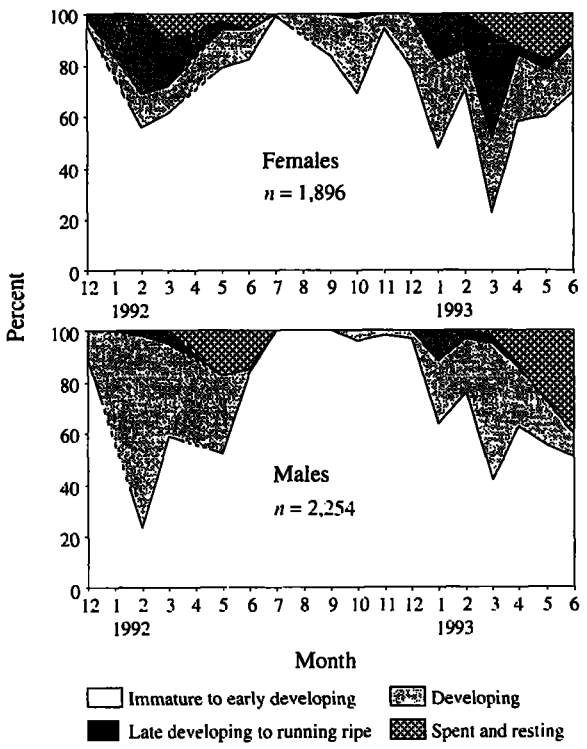

Figure 4

Monthly proportions (as a percentage) of maturity stages by sex for blue-eye trevalla, *Hyperoglyphe antarctica*. *n* = sample size.

Off northeast Tasmania, and over the 20-month sampling period, mature fish were caught in small numbers between October and December; then their abundance increased markedly between January and March (Fig. 4). Stage-4 females caught from October to December 1992 were at early stage of yolk formation (early stage 4) with a low GSI ranging from 1.6 to 2.3. GSI values then increased to a mean of 5.6 (with a standard deviation [SD] of ±2.3) in January, 8.0 (±2.9) in February, and 9.4 (±2.7) in March, 1993. In both 1992 and 1993, ripe (stage-5) and partially spent (stage-4* and stage-5*) females were caught from early March to early May; females in postspawning condition (stages 7 and 8) were caught from mid-March, their maximum abundance occurring in May and June (66.3% of the total 445 postspawning females examined). Thus, maturation of ovaries spanned several months, from October to February, and actual spawning apparently took place from early March to early May.

Size at maturity

The smallest mature female observed during the present study was 59 cm FL, and the smallest mature male was 52 cm FL. The estimated average sizes at maturity were 71.3 and 61.6 cm FL for females and males, respectively (Table 3; Fig. 5). These sizes were very similar to those estimated from data collected in the mid 1950's (Table 3).

Rate of atresia

The rate of atresia for both unyolked and yolked oocytes was generally low (atretic oocytes represented between 1 and 10% of all oocytes when present). However, a few ovaries presented a high level of atresia (about 90%) of their yolked oocytes. These atretic

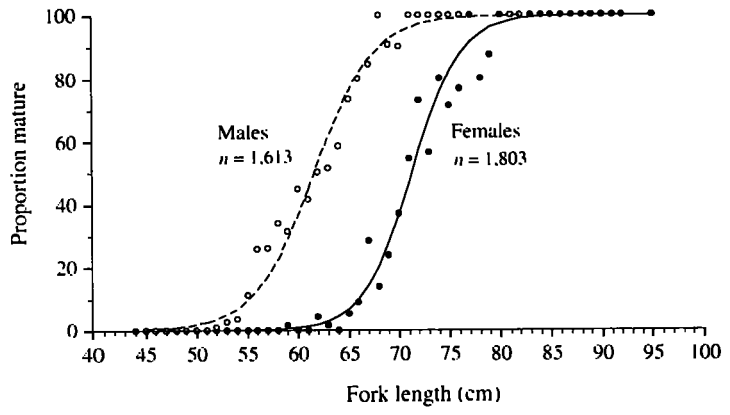

Figure 5

Relative abundance of mature individuals of blue-eye trevalla, *Hyperoglyphe antarctica* (stages 4–6 for females, stages 3–4 for males) by 1-cm size intervals. Data were fitted to the logistic equation shown in text. Black dots represent females; white dots represent males; and n = sample size.

ovaries were of two types. The first type consisted of small ovaries with abundant white oocytes visible macroscopically within a translucent, pinkish mass of unyolked oocytes. Histological examination later revealed that the white oocytes were oocytes at an early stage of yolk formation and were undergoing atresia. This type of ovary was observed in May and June 1992 and 1993, and represented 64% of all yolked ovaries examined during these periods. It was always observed in preadult females at size below the average size at maturity (mean FL=63.6 cm [±3.2 cm SD]).

Only two females presented the second type of atretic ovaries; they had large ovaries (GSI of 6.9 and 8.1) and nearly all fully yolked oocytes were at an early stage of atresia. These atretic oocytes could not be detected macroscopically, but they were recognizable microscopically in preserved samples (Fig. 3, C and D). The two females were caught during the spawning period in March 1993; they represented only 1.2% of all mature ovaries examined histologically.

Occurrence of postovulatory follicles

Postovulatory follicles were found in 16.8% of all mature ovaries examined (n=167). They were never found in ovaries at early stage of yolk formation. Both type-1 and type-2 postovulatory follicles were usually present in stage 4*, whereas only type-2 postovulatory follicles were found in hydrating ovaries (stage 5*) (Fig. 6).

Measurement of whole oocytes

As maturation progressed, a clear gap appeared between unyolked and yolked oocytes (Fig. 7, A–D), showing that the fecundity of blue-eye trevalla is determinate. The recruitment of oocytes from the reserve of unyolked oocytes was completed when the average diameter of yolked oocytes reached about 650 μm (Fig. 7E). Unyolked oocytes present in these ovaries were at stage 2 and had a diameter of less than 100 μm (the gap in size between unyolked and yolked oocytes was clear and unyolked oocytes were no longer measured in most advanced ovaries). The diameter of yolked oocytes then increased slightly to about 700 μm (Fig. 7G) before migration of the nucleus and hydration began (Fig. 7. H–I). After a batch was spawned, formation of a new batch began from the remaining pool of yolked oocytes, showing migration of nucleus and hydration (Fig. 7, J–K). The mean oocyte diameter of stage-4 ovaries used to construct graphs E to G ranged from 500 to 770 μm (having an overall mean of 640 [±60 SD] μm, n=81). Hydrating oocytes observed during the present study were about 1.3 mm (Fig. 7I).

Fecundity

Because fecundity was found to be determinate, annual fecundity was estimated from the standing stock

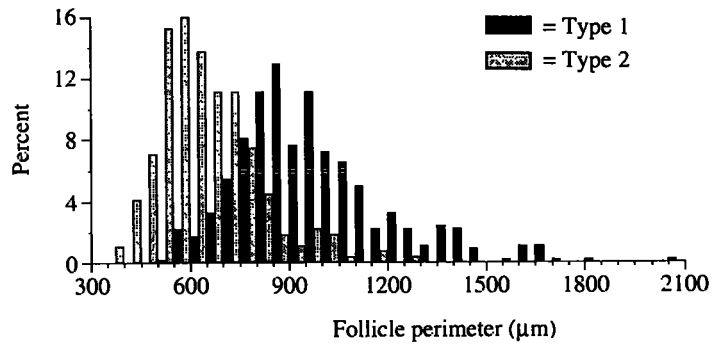

Figure 6

Frequency distributions of the perimeter (micrometers) of type-1 and type-2 postovulatory follicles (pooling of measurements from 16 ovaries) for blue-eye trevalla, *Hyperoglyphe antarctica*.

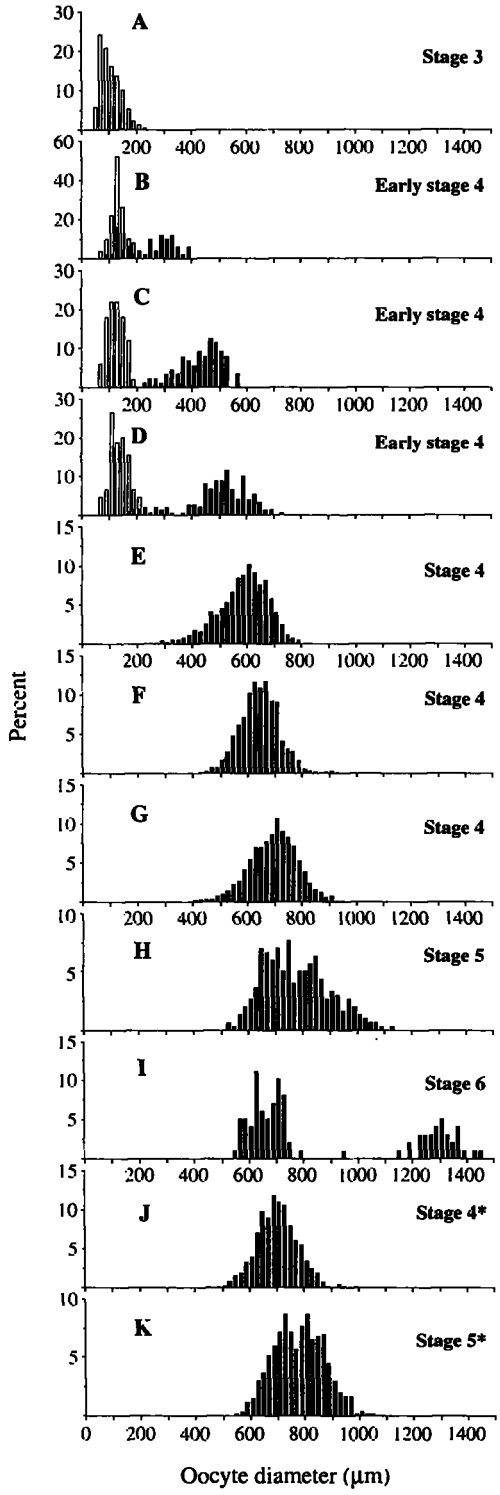

Figure 7

Frequency distribution of oocyte diameter by stage of maturity (measurements from several ovaries pooled in each graph) for blue-eye trevalla, *Hyperoglyphe antarctica*. White and black bars represent independent measurements of unyolked and yolked oocytes, respectively (unyolked oocytes were not measured in stage-4 ovaries from graph E). * = partially spent ovaries.

of yolked oocytes in stage-4 and stage-5 ovaries (Fig. 7, E–H). The fecundity (F) ranged from 1.3 to 11.0 million oocytes per fish, and although varying considerably at given length (Fig. 8), it showed a significant exponential increase with the length (FL) of females, following the equation

$$F = 4.2 \times 10^{-8} \times FL^{4.22},$$

where F is in millions and FL in cm. The linear regression between log-transformed data was statistically significant: F=110.6, df=82; P<0.001, R^2=0.57. Multiple regression analysis showed that the variation in average diameter of yolked oocytes between mature females (as illustrated in Fig. 7, E–H) did not affect fecundity estimates (Table 4). The average relative fecundity was 480 oocytes (±125 SD) per g (gutted weight) and did not show clear trends with the size of fish.

Batch fecundity estimated for ripe females ranged from 0.5 to 2.4 million oocytes (n=8) and also increased with length (Fig. 9). The number of yolked oocytes left in partially spent ovaries ranged from 0.6 to 7.9 million (Fig. 8), with a median value at 2.4 million (n=24).

Spawning aggregation

The bulk of the commercial catch for blue-eye trevalla consisted of small (<55 cm FL), immature fish year

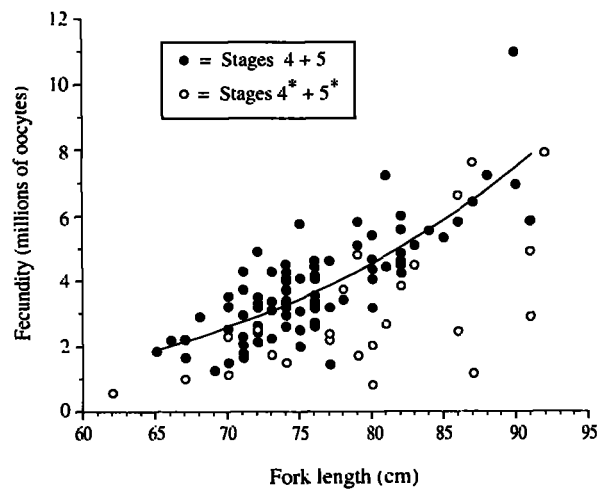

Figure 8

Annual fecundity estimates (black dots) and power relationship between annual fecundity and size of females (line drawn from equation $F = 4.2 \times 10^{-8} \times FL^{4.22}$) for blue-eye trevalla, *Hyperoglyphe antarctica*. Fecundity estimated for partially spent ovaries is also shown (white dots) but was not included in the regression analysis.

Table 4

Multiple regression between log-transformed annual fecundity, fork length (FL, cm), and mean oocyte diameter (micrometers) for blue-eye trevalla, *Hyperoglyphe antarctica*. Sample size = 84, SE = Sampling error.

Source	Partial coefficient	SE	t	P (2-tail)
Constant	–3.942	2.263	–1.742	0.086
Log (*FL*)	4.059	0.437	9.291	0.000
Log (oocyte diameter)	0.228	0.302	0.757	0.451

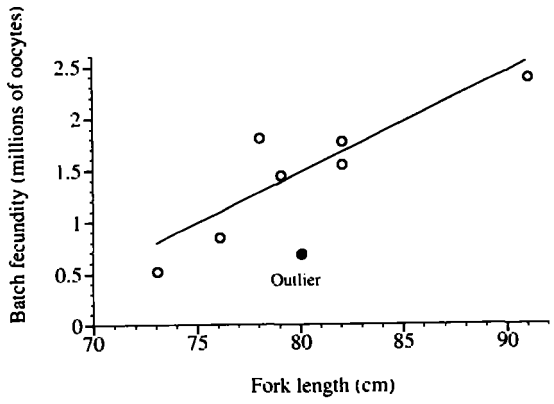

Figure 9

Linear relationship between batch fecundity and size of females for blue-eye trevalla, *Hyperoglyphe antarctica*. Line drawn from the equation *Batch Fec.*= 0.097 × *FL* – 6.28 (F=20.2, df=5, P<0.001, R^2=0.80. R^2 increased from 0.65 to 0.80 when the outlier was excluded from the regression).

round, and the proportion of larger fish increased during the breeding season (Fig. 10). The proportion of these large fish (both sexes) increased in catches from 31.1% during the "nonspawning period" (May to December) to 61.3% during the "spawning period" (January to April).

Examination of size composition and sexual maturity data for females >55 cm FL allowed broad distinction of three groups of fish in commercial catches during the breeding season (Fig. 10): 1) preadult females at size below the average size at maturity (i.e. <69 cm FL), most in the developing stage of maturity, but only a few of which would spawn during the current spawning period; 2) females just reaching size at maturity (i.e. between 69 and 75 cm FL), ranging from developing to ripe stages of maturity, about half of which would spawn for the first time during the current spawning period; and 3) large females (i.e. >75 cm FL), most in the fully developed stage of maturity and likely to spawn. Preadult females were caught all around Tasmania from November to May; first-time spawners were caught mainly off the northeast coast of Tasmania and were more abundant between January and April; largest females were also caught primarily off the northeast coast of Tasmania but only during a brief period, from early March to early May, and quickly disappeared from catches afterward (very few were caught in postspawning condition).

For males, several groups could also be distinguished (Fig. 10), although not as clearly as those for females, because of their generally more compact length-frequency distributions.

Preadult females (<69 cm FL) represented as much as 45.6% of all three groups defined above. Similarly, 31.5% of males >55 cm FL had not reached the average size of sexual maturity. In addition, first-time spawners (i.e. mature females at ≤75 cm FL and mature males at ≤65 cm FL) represented as much as 56.7 and 75.9% of all mature females and males, respectively.

Discussion

Ovary maturation, spawning frequency, and fecundity

Maturation of ovaries appears to be group-synchronous for blue-eye trevalla, spanning from spring to summer (October–February) and followed by a brief spawning period in late summer–autumn (early March–early May). As observed for other fish species (Hunter and Macewicz, 1985b), the occurrence of atretic ovaries marks the end of spawning. The timing of spawning coincides well with the discovery, in June 1991 and May 1993, of a few juvenile blue-eye trevalla among floating seaweed off the Tasmanian east coast (Last et al., 1993). These juveniles ranged in size from about 30 to 60 mm standard length and were estimated to be about 2.5 to 3 months old on the basis of daily ring counts of otoliths (Proctor[3]).

Blue-eye trevalla reach sexual maturity at a large size, and according to yet unvalidated age data,[4] females are about 11–12 years old and males about 8–9 years old at sexual maturity. The bulk of immature fish in commercial catches are about 3 to 4 years old. Analysis of data collected in the 1950's showed

[3] Proctor., C. 1994. CSIRO, Division of Fisheries, Hobart, Tasmania. Personal commun.

[4] Morison, S. 1995. Victorian Fisheries Research Institute, Department of Conservation and Natural Resources, P.O. Box 114, Queenscliff 3225, Australia. Unpubl. data.

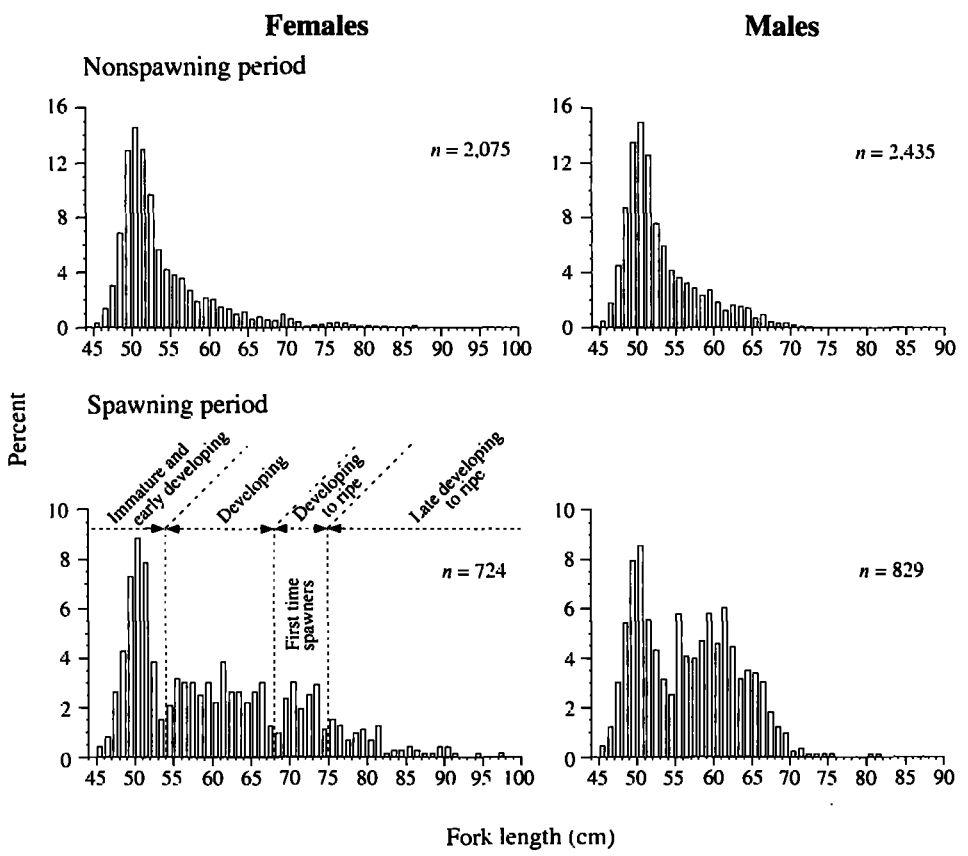

Figure 10

Comparison by sex of frequency distributions between "nonspawning" (May to December) and "spawning" (January to April) periods (years combined) for blue-eye trevalla, *Hyperoglyphe antarctica*. For females, most common maturity status is indicated for different size groups (see text). *n* = sample size.

that there had been no changes in the size at maturity of blue-eye trevalla since the fishery began.

The fecundity of blue-eye trevalla is clearly determinate; several batches of ripe oocytes are formed successively from a standing stock of yolked oocytes. Comparison of annual and batch fecundities suggests that females spawn all their oocytes in 3 or 4 large batches. Several studies (e.g. Macewicz and Hunter, 1993; Oda et al., 1993) have shown that postovulatory follicles usually persist in fish ovaries for short periods (days). The cooccurrence of postovulatory follicles and ripe oocytes in ovaries of blue-eye trevalla also suggests that hydration and ovulation of successive batches could take place within a short period. However, multiple samples taken at short intervals during spawning would be required to age postovulatory follicles accurately.

The average relative fecundity of blue-eye trevalla appears to be fairly high when compared with other middle slope species (e.g. hoki, *Macruronus novaezelandiae* off southern Australia [520 oocytes/g[5]] and sablefish, *Anoplopoma fimbria* off Oregon [110 oocytes/g [Macewicz and Hunter, 1994]). The rate of atresia in ovaries appears to be negligible, and, in the present study, it did not affect fecundity estimates (although this would not necessarily be true for all spawning seasons). The fact that female blue-eye trevalla are partial spawners constitutes more of a problem for estimating fecundity, even more so because spawning batches are large. Partially spent females cannot be identified macroscopically, and to avoid underestimating annual fecundity, it is necessary to check microscopically for the presence of postovulatory follicles in every female before estimating the number of oocytes.

[5] Bulman, C. CSIRO, Division of Fisheries, Hobart, Tasmania. Personal commun.

Composition and dynamics of the spawning aggregation

Blue-eye trevalla in spawning condition were mostly caught off the northeast coast of Tasmania, which may be a major spawning ground. However, the occasional occurrence of mature blue-eye trevalla on nearly all other Tasmanian fishing grounds, including an offshore seamount 120 miles south of Tasmania (data not included), and the presence of spawning aggregations off New South Wales (Rowling[6]) and South Australia (Jones[7]) indicate that spawning takes place on several grounds within southern Australia. The fact that no genetic difference was found between blue-eye trevalla collected off New South Wales, Tasmania, and South Australia (Bolch et al., 1993) further supports the view of a widely distributed spawning activity. Horn and Massey (1989) also believed that blue-eye trevalla spawned on many grounds in New Zealand.

During his work on hoki spawning aggregations, Langley (1993) identified several spawning groups arriving successively and then leaving the spawning ground. The situation is different for blue-eye trevalla, where the three groups of females identified in the summer aggregation seemed to correspond to progressive arrivals of different size (or age) groups and not to commuting spawning groups, spawning taking place at the end of summer. Older females join the aggregation just before spawning and leave shortly after; younger females (first-time spawners) aggregate earlier and stay on the grounds for some time after spawning.

The presence of preadults in the aggregation (i.e. at size below the average size at maturity and, thus, not all capable of spawning) suggests that this summer aggregation off northeast Tasmania is related to both feeding and spawning behaviors. Blue-eye trevalla feed mainly on the pelagic tunicate *Pyrosoma atlanticum* (Winstanley, 1978), and Cowper (1960) noted a maximum incidence of *Pyrosoma* in the stomachs of blue-eye trevalla during the summer. As observed for Atlantic cod, *Gadus morhua* (Swain, 1993), it is possible that blue-eye trevalla off northeast Tasmania migrate between deeper wintering grounds and shallower feeding and spawning summer grounds. The presence of preadult fish on other Tasmanian fishing grounds during spring and summer indicates that feeding aggregations are not restricted to the northeast coast of Tasmania. Winstanley (1979) also noted that blue-eye trevalla off Victoria probably move from deeper to shallower depths in spring.

The spawning population observed in commercial catches was young and the majority were first-time spawners. Larger fish used to be caught by drop-line in the early years of the fishery (Baelde, unpubl. data), and it is not known whether their low proportion in current catches reflects a lower vulnerability to line fishing (owing to age- or size-specific change in distribution and aggregating behavior), or reflects a significant decline in abundance owing to fishing. In addition, it is believed that there is one stock of blue-eye trevalla in southern Australia, and, as shown for other fish species with a wide geographic distribution (Schaefer, 1987; Bell et al., 1992; Rijnsdorp, 1993; Clark et al., 1994), size at maturity, spawning season, and fecundity could vary significantly between areas. Differences in the time of spawning and the size of spawners have already been observed between New South Wales and Tasmania.[6]

This study points out that a proper estimate of the spawning biomass of blue-eye trevalla stock off southern Australia would require fishery-independent surveys (i.e. identification of other spawning grounds and analysis of the age-specific movements of fish during spawning) to determine more accurately the structure and abundance of the spawning population.

Acknowledgments

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Growth of long-finned squid, *Loligo pealei*, in the northwest Atlantic

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Abstract.—The application of statolith ageing techniques to long-finned squid, *Loligo pealei*, suggests that this species has a life span of less than one year and grows more rapidly than previously thought. In this study we provide direct estimates of growth for long-finned squid in the northwest Atlantic based on a data set of 353 animals aged by counting putative daily statolith increments. We examine empirical patterns in length and weight at age and estimate parameters of a general growth model. The results indicate that growth rate increases rapidly as squid age and that growth in length and weight is exponential. Although there is substantial heterogeneity in *L. pealei* size at age, sexual dimorphism is evident: males grow more rapidly than do females and achieve larger sizes. Back-calculated hatching dates show that *L. pealei* spawning is not restricted to spring through late-autumn, as previously supposed, but occurs during winter months as well. Differences between growth rates of squid hatched during June–October and November–May are suggested and lend support to the hypothesis that growth can be influenced by seasonal environmental conditions. We discuss the practical implications of our findings for the assessment and management of the long-finned squid stock in the northwest Atlantic.

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The long-finned squid, *Loligo pealei* (also known as the longfin inshore squid (FAO, 1984), is a pelagic schooling loliginid distributed in continental shelf and slope waters from Newfoundland, Canada (Dawe et al., 1990), to the Gulf of Venezuela (Summers, 1983). A substantial commercial fishery exists in the northwest Atlantic where annual landings averaged 17,300 metric tons (t) during 1963–92, and totalled 22,300 t in 1993 for an ex-vessel value of approximately $30 million (NEFSC, 1995). Recent advances in the use of statolith increments to age squid directly and recent increases in fishing effort in the northwest Atlantic have led to a renewed interest in the life history of this species, and, in particular, its growth rate.

Several estimates of the growth rate of *L. pealei* have been made by comparing modes of length-frequency distributions (Verrill, 1881; Summers, 1968, 1971; Cohen, 1976; Mesnil, 1977; Whitaker, 1978; Lange, 1980; Lange and Sissenwine, 1980; Macy, 1980; Hixon et al., 1981). These studies generally have suggested that growth rate, measured by change in dorsal mantle length (ML), ranged from 10 to 24 mm per month, and that growth rate was dependent upon sex, hatching date, and season (Hixon et al., 1981). Sexual dimorphism was evident; males attained larger sizes than did females (Summers, 1971). Seasonal effects on growth were also suggested; higher growth rates occurred during summer months and lower rates during winter months (Mesnil, 1977). Latitudinal differences in age structure and mean size of *L. pealei* have also been proposed (Summers, 1971), namely that mean size has been suggested to be greater at higher latitudes. These studies, combined with the observed maximum size of approximately 46.5 cm mantle length (Summers, 1968), were consistent with a maximum life span of roughly three years in the northwest Atlantic, a value that was assumed for stock assessment (NEFSC, 1988).

The inferred growth rates of *L. pealei*, based on length-frequency analyses, should be viewed cautiously because they have not been supported by direct ageing data (Caddy, 1991). In general, growth rates of squid might be expected to vary with prey availability (O'Dor et al., 1980), temperature (Forsythe, 1993), and population density

(Dawe, 1988). Squid populations with protracted spawning seasons, such as that of *L. pealei* (Summers, 1971; Macy, 1980), can be composed of numerous broods or microcohorts that may experience different growth and survival rates (Caddy, 1991). As a result, length-frequency samples may consist of several microcohorts with differing growth rates. Migration of microcohorts with differing hatching dates and growth rates to and from an area (e.g. *Illex illecebrosus*, Dawe and Beck[1]; *Illex argentinus*, Arkhipkin, 1993a) may also substantially influence the size composition of a local population, and may bias growth estimates based on length-frequency data (Hatfield and Rodhouse, 1994). Further, postspawning mortality of squid may also influence local size composition if the sampled area is a spawning ground. For these reasons, analysis of length-frequency data may be inadequate in representing the potentially complicated pattern of individual growth within a squid population. Therefore, it is highly desirable to have a method to age individual squid directly.

Statolith ageing techniques (Jereb et al., 1991) have recently provided useful information on the age, growth, and population structure of several squid species (Rodhouse and Hatfield, 1990a; Jackson and Choat, 1992; Arkhipkin, 1993, a and b; Arkhipkin and Nekludova, 1993; Hatfield and Rodhouse, 1994). Ageing of squid, based on counts of fine increments presumed to have daily periodicity, was first developed for *Illex illecebrosus* (Lipinski, 1978) and *Loligo opalescens* (Spratt, 1979) in the late 1970's. Subsequently, studies of several species have indicated that increments within statolith microstructure are formed daily (Dawe et el., 1985; Hurley et al., 1985; Lipinski, 1986; Jackson, 1990, a and b; Jackson et al., 1993), although the mechanisms that regulate increment formation have not yet been determined (Jackson, 1994a).

The application of statolith ageing techniques to *L. pealei* suggests that this species has a life span of less than one year and grows more rapidly than previously thought (Macy, 1995; Macy[2]). In this study we provide estimates of growth rate for *L. pealei* in the northwest Atlantic based on a data set of 353 animals aged by counting putative daily increments on statoliths. We examine empirical patterns in length and weight at age and estimate parameters of a general growth model proposed by Schnute (1981) by squid sex and season of hatching. We discuss some practical implications of our findings for the assessment and management of the stock in the northwest Atlantic.

Materials and methods

Sampling

Data used in this growth study consisted of 353 squid collected during 1991–93. Squid samples were obtained from catches of a commercial fishing vessel[3] and from inshore research surveys in the northwest Atlantic (Table 1; Fig. 1). Samples were flash frozen and stored for subsequent analysis. Basic measurements of mantle length (ML) (to the nearest mm), wet weight (g), and morphometric characters needed to assess maturity stage according to the scheme of Macy (1982a) were taken. Statoliths were dissected from all animals and stored dry in plastic 96-well immunoassay microplates. Statoliths were randomly selected from representative size categories of squid on the basis of observed length-frequency distributions for male, female, and squid of indeterminate sex.

Statolith preparation

Statoliths were prepared by mounting them in a thermoplastic medium (Crystal Bond, Aremco Products; cf. Secor et al., 1991) and by grinding both anterior and posterior surfaces in a manner similar to that described by Jackson (1990a). Several steps were required to prepare a statolith for ageing (Fig. 2). First, a small piece of mounting medium was placed on a petrographic slide (26 × 46 mm) and melted with a hot-air gun. The statolith was then placed in the fluid medium with its concave anterior side down and allowed to cool (Fig. 2B). Material was ground from the exposed convex posterior surface (Fig. 2C) with a graded sequence (12 μm to 3 μm) of water-lubricated abrasive films (Imperial Brand lapping film, 3M Co.) to reveal the nucleus. Progress was monitored throughout the grinding procedure with a stereoscopic dissecting microscope. When the nucleus was clearly revealed, the exposed surface was polished with 0.3-μm aluminum oxide polish (Buehler micropolish) in water on a felt lapidary pad, rinsed with deionized water, and cleaned ultrasonically. After the posterior face was ground, the mounted

[1] Dawe, E. G., and P. C. Beck. 1992. Population structure, growth, and sexual maturation of short-finned squid at Newfoundland, Canada, based on statolith analysis. ICES Council Meeting, Shellfish Committee/K, 33 p.

[2] Macy, W. K., III. 1992. Preliminary age determination of the squid, *Loligo pealei*, using digital imaging. ICES, Shellfish Committee Council Meeting (mimeo), 9 p.

[3] FV *Huntress*, Deep Sea Fish Co., Point Judith, RI.

Table 1

Sample sizes of indeterminate-sex, female, and male long-finned squid, *Loligo pealei*, by collection date, location, source, and sampling gear. In the location field the map code refers to Figure 1. D.E.M. = Department of Environmental Management.

Collection dates	Location (map code)	Source	Sampling gear	Number of squid			
				Indeterminate-sex	Female	Male	Total
1991							
10 Apr	Block Island Sound (1)	Pt. Judith Fishermen's Coop.	Otter trawl[1]	—	7	7	14
10 May	Vineyard Sound (2)	Marine Biological Lab.	Otter trawl[2]	—	2	2	4
13–15 May	Block Island Sound (1)	Rhode Island D.E.M.	Otter trawl[3]	—	1	6	7
16–18 May	Narragansett Bay (1)	W.K. Macy	Dip net[4]	—	1	3	4
22 May	Block Island Sound (1)	Rhode Island D.E.M.	Otter trawl[3]	12	20	12	44
17–18 Jul	Narragansett Bay (1)	Rhode Island D.E.M.	Otter trawl[3]	31	8	6	45
31 Jul	Narragansett Bay (1)	W.K. Macy	Dip net[4]	—	1	2	3
15 Oct	Block Island Sound (1)	Rhode Island D.E.M.	Otter trawl[3]	28	25	27	80
1992							
1 Jan	Hudson Canyon (3)	F/V *Huntress*	Otter trawl[1]	—	—	1	1
9 Jan	Block Canyon (4)	F/V *Huntress*	Otter trawl[1]	—	—	5	5
31 Jan–2 Feb	Block Canyon (4)	F/V *Huntress*	Otter trawl[1]	—	—	2	2
17 Feb	Block Canyon (4)	F/V *Huntress*	Otter trawl[1]	—	—	1	1
11 Mar	Wilmington Canyon (5)	F/V *Huntress*	Otter trawl[1]	—	—	5	5
6–14 May	Narragansett Bay (1)	Univ. Rhode Island	Otter trawl[5]	—	27	23	50
7 Oct	Narragansett Bay (1)	Rhode Island D.E.M.	Otter trawl[3]	4	22	14	40
1993							
7 Feb	Hudson Canyon (3)	F/V *Huntress*	Otter trawl[1]	—	2	4	6
25 Feb–8 Mar	Hudson Canyon (3), Baltimore Canyon (6), and Lydonia Canyon (7)	F/V *Huntress*	Otter trawl[1]	1	22	19	40

[1] Mesh size not reported.
[2] 32-mm mesh.
[3] 6-mm mesh.
[4] Hand-held dip net with SCUBA gear.
[5] 19-mm mesh. Graduate School of Oceanography, Univ. Rhode Island, trawl survey described in Jeffries and Johnson (1974).

statolith was reheated to soften the medium and turned over with a pair of probes constructed of insect pins so that the anterior face could be ground (Fig. 2, C (2) and D). The statolith was oriented with the dorsal dome elevated and the anterior face was carefully ground. When the nucleus was clearly revealed, the anterior face was polished and cleaned.

Because the statolith of *L. pealei* grows outward from the oval-shaped nucleus in a curved manner (Fig. 2, A and B), a second grinding and polishing of the posterior surface (Fig. 2E) was generally needed to reveal the entire sequence of growth increments from the nucleus to the lateral dome (LD) margin. Because of this curvature, no single sectioning plane could have exposed all layers equally well. As a result, the use of the typical two-sided grinding method (Jackson, 1990a; Jereb et al., 1991) would have produced increments that were difficult to resolve. To circumvent this difficulty, the posterior surface was ground a second time (Fig. 2E) at a slightly different angle to approximate the curved statolith growth plane. For squid smaller than 2 cm ML, however, a single grinding of each surface was usually sufficient to reveal the statolith microstructure. After the second posterior grinding, the mounted statolith was reheated, and a thin film of fluid medium was smeared over the uppermost ground surface to improve transparency. As the medium cooled, the LD margin was elevated so that the last-ground plane was approximately parallel to the surface of the slide (Fig. 2F); this was done to improve the clarity of statolith microstructure under a 40× objective lens.

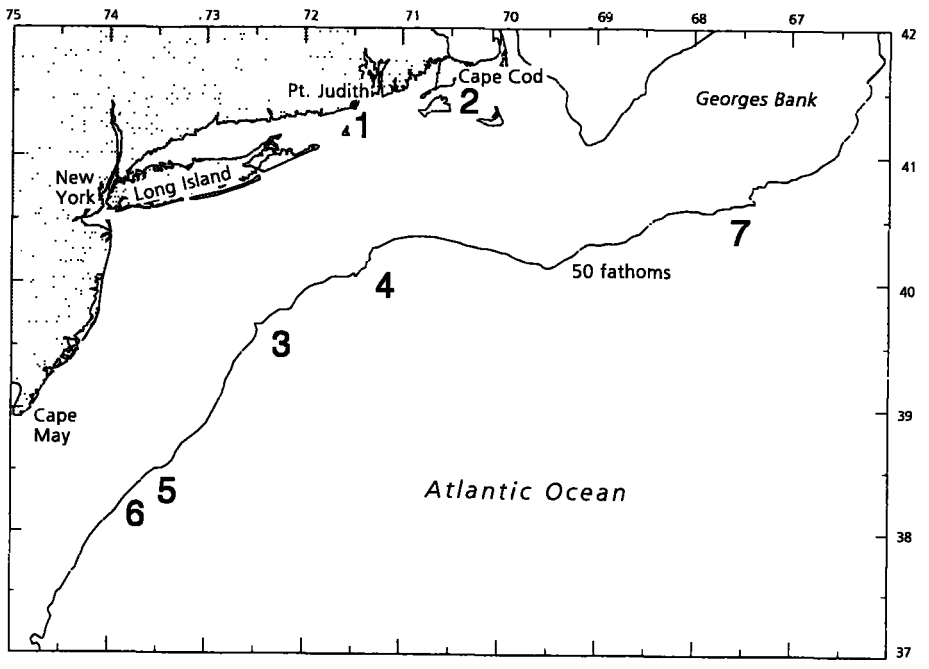

Figure 1

Collection sites for long-finned squid, *Loligo pealei*, samples off the northeast coast of the United States.

Statolith ageing

A video image processing system with high-resolution monochrome video camera (MTI-Dage 65, Newvicon) mounted on a compound microscope (Zeiss Universal) was used to count increments (Macy, 1995). Because of the low contrast seen in *L. pealei* statolith microstructure, image enhancement was employed to identify growth marks. Statolith increments were counted by using transmitted light with the microscope stage condenser (brightfield) set to the smallest aperture to obtain maximum depth of field. A rotatable polarizing filter was also placed above the field condenser to improve contrast between increments. Within a prepared *L. pealei* statolith, a series of paired bands that alternate from light to dark is observable in the LD, beginning at the nucleus and continuing to the LD margin. Two fractures that radiate outward from the nucleus are also apparent. These fractures are not the result of statolith preparation because they are also found in unprepared statoliths. In this study, the successive circumferential light bands in the statolith (appearing black in enhanced images) were counted and will be referred to hereafter as "growth increments."

Counting began with the first check or natal ring (Lipinski, 1986; Natsukari et al., 1988, Saleh-Eddine, 1991), which is a distinct oblong-shaped mark roughly the same size (100–120 μm) as the major axis length of a statolith from a *L. pealei* embryo. Although prehatching increments can sometimes be observed (Saleh-Eddine, 1991; Macy, 1995), their periodicity, if any, is unknown. Typically, counting proceeded along a series of transects extending outward from the first check across the LD to the edge. Up to six fields of view were used to enumerate the increments.

The consistency of increment counts between the reader of this study and another experienced reader was evaluated post hoc by using a sample of 76 *L. pealei* collected during 1994. Three statistical tests were applied to determine the consistency between age readings (cf. Campana et al., 1995): a linear regression analysis of paired counts; a paired *t*-test; and a paired Wilcoxon rank test. Results of the linear regression of one reader's counts on the other's indicated that the regression slope was not significantly different from 1 (b=1.046, σ_b=0.033, P=0.17) and that the regression intercept was not significantly different from 0(a=1.655, σ_a=4.697, P=0.73). This suggested that the readers' age determinations were consistent. Results of the paired *t*-test, however, indicated a significant mean paired difference of 7.6 days (σ=2.1, P<0.001). Similarly, results of the Wilcoxon signed rank test indicated a significant median paired difference (P<0.001) existed between

readers. The results of the statistical tests were equivocal but suggested that there was a potential bias between the readers' counts. However, the apparent bias was relatively small and did not suggest that there were substantial differences between the readers' recognition of increments.

An examination of *L. pealei* marked with oxytetracycline supported the hypothesis that statolith increments are formed daily (Macy, 1995). In particular, one marked squid that did grow appreciably during a 21-d period was found to have a total of 21 statolith increments (Macy, 1995). To date, the daily increment hypothesis has been verified by statolith marking for several squid species, including *Illex illecebrosus* (Dawe et al., 1985), *Alloteuthis subulata* (Lipinski, 1986), *Loligo opalescens* (Jackson, 1994b), *Sepioteuthis lessoniana* (Jackson, 1990a; Jackson et al., 1993), *Loliolus noctiluca* and *Loligo chinensis* (Jackson, 1990b), *Todarodes pacificus* (Nakamura and Sakurai, 1991), *Abralia trigonura* (Bigelow, 1992), *Ommastrephes bartramii* (Bigelow and Landgraf, 1993), *Onychoteuthis borealjaponica* (Bigelow, 1994), and validation is in progress for *Loligo plei*.[4] The daily increment hypothesis has also been verified by using laboratory-reared squid of known age for *Loligo opalescens* (Jackson, 1994b) and for *Sepioteuthis lessoniana* (Jackson et al., 1993), both loliginids, and is considered to be the best working hypothesis for statolith increment formation in *L. pealei* on the basis of limited marking data and by analogy with other loliginid species.

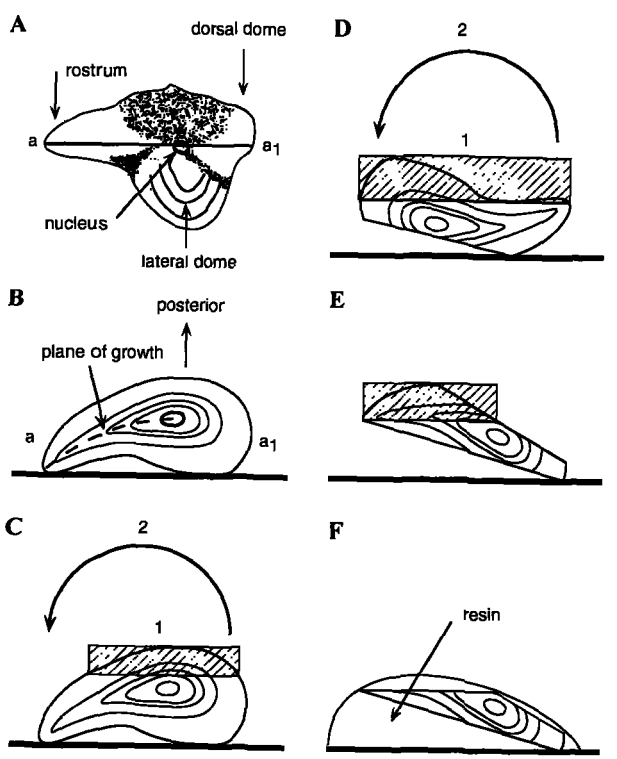

Figure 2

(**A**) Schematic view of posterior face of *Loligo pealei* statolith with a ventro–dorsal cross section indicated from points a to a_1. (**B**) Cross section [a, a_1] from (A) showing the curved plane where growth increments are counted. (**C**) After initial grinding removes the cross-hatched area to reveal the nucleus (1), the statolith is turned over (2). (**D**) After the anterior side of the statolith is oriented with the dorsal dome elevated and the cross-hatched material removed (1), the statolith is turned over again to show the posterior face (2). (**E**) The lateral dome is elevated while the resin cools and the cross-hatched material is removed. (**F**) The polished statolith is covered with molten resin and allowed to cool with the lateral dome elevated.

Month of hatching was backcalculated for all samples by subtracting the estimated age, based on statolith analysis, from the date of sample collection. Samples were categorized by sex (indeterminate, female, and male) and maturity stage (immature, maturing, and mature) to examine whether size at age was related to maturity stage. Samples were also categorized by month and year of hatching to examine monthly and seasonal patterns in size at age. Average monthly growth rates of individual squid were computed to examine individual variation in growth, where the growth rate in length was ML (mm) divided by age (months), and the growth rate in weight was total wet weight (g) divided by age. Summary statistics of the average monthly growth rate of individuals in ML and in weight were computed for squid categorized by sex, maturity stage, hatch month, and hatch year. Variances of growth rate in length and weight were log-transformed and tested for homogeneity by sex, maturity, hatch month, and hatch year by using Bartlett's test for homogeneity of variances (Sokal and Rohlf, 1981). Unplanned multiple comparison tests appropriate for equal variances and unequal samples sizes (Sokal and Rohlf, 1981) and for unequal variances and sample sizes (Games and Howell, 1976; Day and Quinn, 1989) were applied to test whether growth rate in length and weight differed by sex, maturity stage, hatch month, and hatch year.

Growth model

We applied the general growth model of Schnute (1981) to quantify the relationship between length

[4] Jackson, G. 1994. Department of Marine Biology, James Cook Univ., Townsville, Queensland 4811, Australia. Personal commun.

and weight at age for *L. pealei*. This flexible model includes asymptotic, linear, exponential, and other growth curves as particular cases. The complete set of size-at-age data consisted of the 353 squid that were aged. Size data for the ith individual were denoted as (t_i, y_i), where t_i was observed age in months, and y_i is either observed length in centimeters or weight in grams. Additionally, t_{max} and t_{min} denoted the maximum and minimum observed age in months for any subset of the size-at-age data. In the most general case, the Schnute model has four parameters: α, β, y_{min}, and y_{max}. The parameters α and β determine the shape of the growth curve, whereas the parameters y_{min} and y_{max} are the predicted sizes of the youngest and oldest individuals in the subset of weight-at-age data. That is, $y_{min} = Y(t_{min})$ and $y_{max} = Y(t_{max})$, where Y is the growth model.

There are four general forms for the Schnute growth model. The most general form (case I) gives size (Y) at age (t) as

$$Y(t) = \left\{ (y_{\min})^{\beta} + \left((y_{max})^{\beta} - (y_{min})^{\beta}\right) \frac{1-\exp[-\alpha(t-t_{min})]}{1-\exp[-\alpha(t_{max}-t_{min})]} \right\}^{\frac{1}{\beta}}. \quad (1)$$

In Equation 1, it is assumed that $\alpha \neq 0$ and $\beta \neq 0$ and that $y_{min} > 0$ and $y_{max} > 0$. A second form (case II) sets the β parameter to be 0 in the differential equation defining $Y(t)$. The resulting 3-parameter model is

$$Y(t) = y_{min} \exp\left[\ln\left(\frac{y_{max}}{y_{min}}\right) \frac{1-\exp[-\alpha(t-t_{min})]}{1-\exp[-\alpha(t_{max}-t_{min})]} \right], \quad (2)$$

where $\alpha \neq 0$ and $y_{min} > 0$, and $y_{max} > 0$. A third form (case III) sets the α parameter to be 0 in the differential equation defining $Y(t)$. This gives

$$Y(t) = \left\{ (y_{min})^{\beta} + \left((y_{max})^{\beta} - (y_{min})^{\beta}\right) \frac{t-t_{min}}{t_{max}-t_{min}} \right\}^{\frac{1}{\beta}}, \quad (3)$$

where $\beta \neq 0$ and $y_{min} > 0$, and $y_{max} > 0$. The fourth form (case IV) sets both α and β parameters to be 0. The resulting 2-parameter model is

$$Y(t) = y_{min} \exp\left[\ln\left(\frac{y_{max}}{y_{min}}\right) \frac{t-t_{min}}{t_{max}-t_{min}} \right], \quad (4)$$

where $y_{min} > 0$ and $y_{max} > 0$.

Two possible error structures were considered for estimating parameters of the Schnute model: additive and multiplicative. The additive error structure consisted of an additive normal term, where, for each data point,

$$y_i = Y(t_i) + \sigma\varepsilon_i, \quad (5)$$

whereas the multiplicative error structure consisted of a lognormally distributed term where, for each data point,

$$y_i = Y(t_i)\exp[\sigma\varepsilon_i]. \quad (6)$$

The random variables ε_i were independent and identically distributed standard normal random variables, and the variance term σ^2 was a positive constant. These two error structures differed in how individual size at age varied about the growth curve. Use of the additive error term implied that the model error in predicting individual size at age was invariant with respect to age. In contrast, the use of a multiplicative error term implied that the model error in predicting individual size at age was scaled with size so that more heterogeneity could be expected in size at age as age increased.

Least-squares estimates of growth parameters under the additive error structure were computed by minimizing the residual sum of squares, R_A, where

$$R_A(y_{min}, y_{max}, \alpha, \beta) = \sum_{i=1}^{n} [y_i - Y(t_i, y_{min}, y_{max}, \alpha, \beta)]^2, \quad (7)$$

Similarly, least-squares estimates of parameters under the multiplicative error structure were computed by minimizing the residual sum of squares R_M, where

$$R_M(y_{min}, y_{max}, \alpha, \beta) = \sum_{i=1}^{n} \left[\ln\left(\frac{y_i}{Y(t_i, y_{min}, y_{max}, \alpha, \beta)} \right) \right]^2. \quad (8)$$

We used SAS to compute least-squares estimates of parameters for the growth models (SAS Institute Inc., 1989). For the additive error structure, the nonlin-

ear regression model was given by Equation 5, whereas for the multiplicative error structure, the nonlinear regression model was

$$z_i = \ln(Y(t_i)) + \sigma\varepsilon_i, \quad (9)$$

where $z_i = \ln(y_i)$ was the log-transformed size of the ith squid in the data set.

We estimated parameters of the Schnute growth model for several subsets of the length-at-age and weight-at-age data to assess the adequacy of the additive and multiplicative error structures. The goodness of fit of the additive and the multiplicative error structures was compared by testing whether the residuals of estimated growth curves were normally or lognormally distributed with the Shapiro-Wilk test (Shapiro and Wilk, 1965). In particular, parameters for case I of the growth model were estimated for the set of pooled-sex samples (n=353) by using the additive and the multiplicative error structures. The set was then partitioned into immature squid of indeterminate sex (n=76), female (n=131), and male (n=146) samples, and parameters for case I were estimated. We also partitioned the set into samples with hatching dates from June to October (n=145) and from November to May (n=208), and parameters for case I were estimated. Last, female and male samples were partitioned into samples with hatching dates from June to October (n_F=61 and n_M=76) and from November to May (n_F=70 and n_M=70), and parameters of case I were estimated. Overall, growth curves for case I were estimated for each of 10 subsets of the length-at-age and weight-at-age data.

We then estimated parameters for cases II, III, and IV of the Schnute growth model for each of the 10 subsets of size-at-age data using the best error structure. For each subset of size-at-age data, the estimated growth curves were compared on the basis of two criteria. First, an estimated growth curve was rejected if at least one of its parameters was not significantly different from 0 at the 5% level of significance. Second, if more than one growth curve had significant parameters, an analysis of variance of the residual sum of squares (RSS) for full and reduced parameter cases was used to select the best fit on the basis of the variance ratio described by Schnute (1981; see also Bigelow 1994). A comparison between cases II and IV tested whether the hypothesis α=0 was acceptable, and a comparison between cases III and IV tested whether the hypothesis that β=0 was acceptable. Cases II and III were compared on the basis of the lowest RSS. For each of the 10 subsets of data, one growth curve was selected as the best relationship between length at age and weight at age.

Results

Month of hatching

Long-finned squid hatched during all months of the year (Table 2). The fact that some samples hatched during December–April indicated that *L. pealei* were successfully reproducing during the winter. Given this, our data show that *L. pealei* from the northwest Atlantic have the capacity to spawn throughout the year.

The frequency distribution of hatch month of *L. pealei* samples grouped by collection season (Fig. 3) indicated that several microcohorts were present within seasonal collections. For the winter collections (Fig. 3A), most squid were hatched during June–September. Considerable variability in squid size was apparent in the length-frequency distribution (ML ranged from 6.3 to 44.0 cm [μ=19.3, σ=11.1]). Most squid in the spring collections (Fig. 3B) were hatched during August–November. Again, considerable variability in squid size was apparent (ML ranged from 1.8 to 40.8 cm [μ=16.6, σ=9.0]). For the summer collections (Fig. 3C), most of the squid were hatched during December–March, with the exception of 17 juvenile squid of indeterminate sex from the 17 July 1991 Rhode Island Department of Environmental Management survey that hatched during May. In comparison to the winter and spring collections, there was less variability in squid size within the summer collections (ML ranged from 1.3 to 16.3 cm [μ=5.0, σ=3.5]). Most of the squid in the fall collections (Fig. 3D) were hatched during March–May and ML

Table 2

Summary of the number of *Loligo pealei* samples by back-calculated month and year of hatching.

Hatching month	Year 1990	1991	1992	Totals
January	—	11	—	11
February	—	10	—	10
March	—	28	17	45
April	—	39	16	55
May	—	39	8	47
June	—	12	4	16
July	4	6	19	29
August	7	7	18	32
September	7	17	6	30
October	18	20	—	38
November	25	6	—	31
December	9	—	—	9
Totals	70	195	88	353

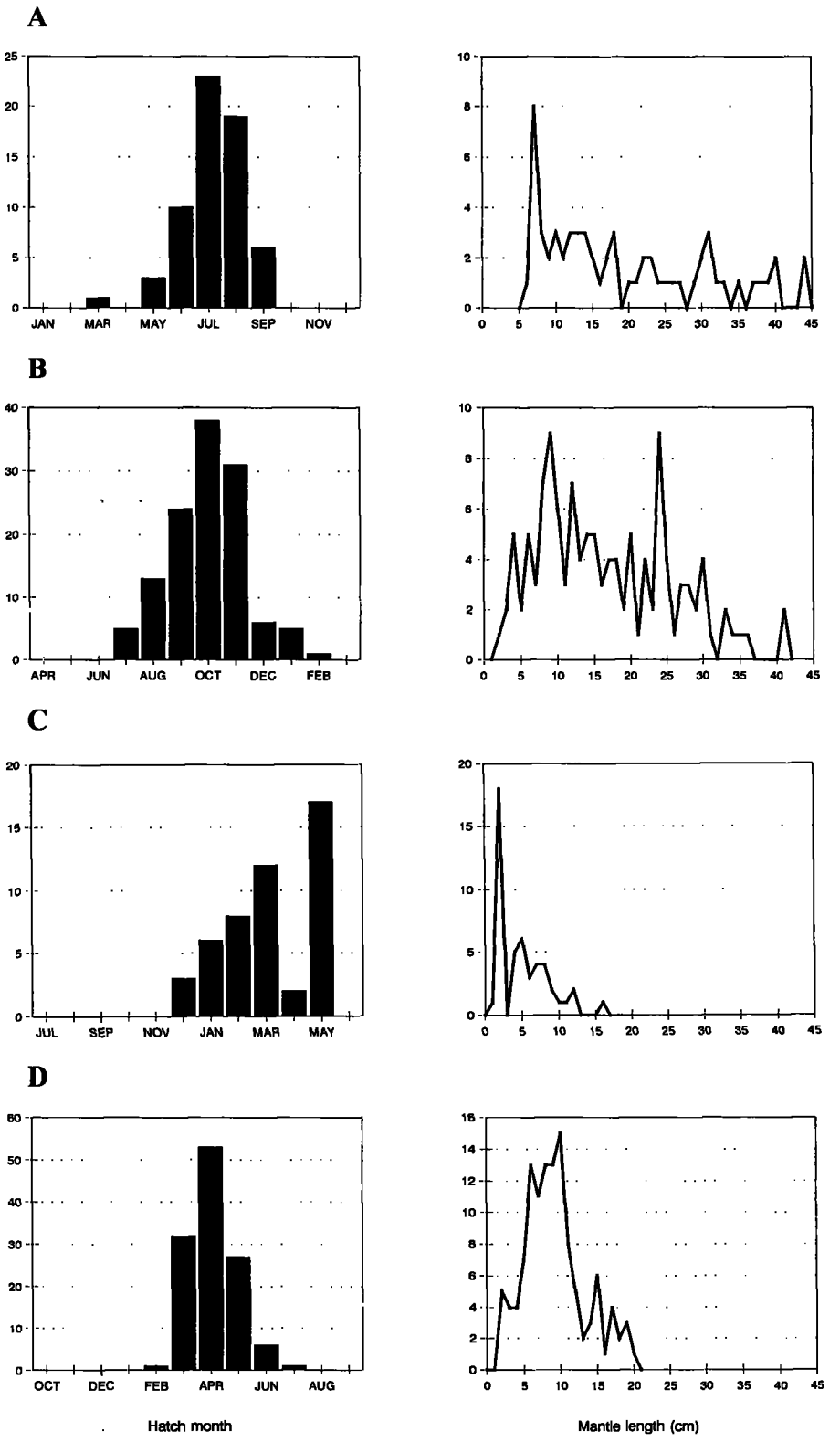

Figure 3

Frequency distributions of hatching month and mantle length of *Loligo pealei* collected during (**A**) winter, (**B**) spring, (**C**) summer, and (**D**) fall.

ranged from 1.8–20.0 cm (μ=9.1, σ=4.1). Squid size in the fall collections was more variable than in the summer collections and less variable than in the winter and spring collections.

Patterns in size at age

The average monthly growth rate in ML and weight suggested that individual growth of *L. pealei* was associated with maturity stage (Table 3) because higher growth rates were apparent for more advanced maturity stages. Relatively large coefficients of variation for the monthly growth rate indicated that the pattern of individual growth was highly variable, especially in terms of weight. Monthly growth rates of indeterminate-sex squid averaged 8.8 mm per month in ML (4.6–15.4 mm/month) and averaged 0.9 g per month in weight (0.1–3.0 g/month). Monthly growth rates of females averaged 18.2 mm per month in ML (8.8–36.6 mm/month) and averaged 9.5 g per month in weight (1.0–40.2 g/month). Monthly growth rates of males averaged 25.9 mm per month in ML (9.6–64.0 mm/month) and averaged 21.4 g per month in weight (1.5–98.2 g/month). The average growth rates in length of females and males were more than twice the average rates for indeterminate-sex squid. Similarly, the average growth rates in weight of females and males were more than 10 times the average rate for indeterminate-sex squid. For males, the average growth rates by length and by weight were 1.4 and 2.2 times greater than for females. Overall, these data indicated that individual growth was highly variable and was related to maturity stage and sex.

Average growth rates were tested for significant differences by sex and maturity stage by using unplanned multiple comparisons procedures. First, squid were categorized as indeterminate-sex, female, or male. With respect to maturity stage, squid were categorized as mature if they were maturing or mature; otherwise they were categorized as immature (Table 2). Bartlett's homogeneity of variance test was then applied to the sex and maturity stage groups. The natural logarithmic transformation was applied to the growth-rate data to stabilize variance prior to testing for differences. The null hypothesis of homogeneous variances for growth rate in length was rejected for the samples grouped by sex (X^2= 40.42>>$\chi^2_{0.05[2]}$=5.99) but was accepted for the samples grouped by maturity stage (X^2=0.40 < $\chi^2_{0.05[1]}$=3.84). The null hypothesis of homogeneous variances for growth rate in weight was rejected for the samples grouped by sex (X^2=9.35>>$\chi^2_{0.05[2]}$=5.99) and by maturity stage (X^2=26.46>>$\chi^2_{0.05[1]}$=3.84). Because variances were inherently heteroscedastic and sample sizes were unequal, the unplanned comparison test of Games and Howell (1976) (Day and Quinn, 1989) was applied to test for differences among group means of log-transformed length-at-age data categorized by sex. The group means of indeterminate-sex and female squid ($|Y_I-Y_F|$=0.71 > $MSD_{0.05[I,F]}$=0.14), indeterminate-sex and male squid ($|Y_I-Y_M|$=1.00 > $MSD_{0.05[I,M]}$=0.16), and female and male squid ($|Y_F-Y_M|$=0.30 > $MSD_{0.05[F,M]}$=0.16) were significantly different at the 5% level. For the length-at-age data categorized by maturity stage, the Tukey-Kramer comparison test (Sokal and Rohlf, 1981) was used because variances were homogeneous. The immature

Table 3

Average monthly growth rates and coefficients of variation (CV) in parentheses for long-finned squid, *Loligo pealei*, in length (millimeters per month) and weight (grams per month) and average age (months) by sex and maturity stage.

Sex category and maturity stage	mm per month Average (CV)	g per month Average (CV)	Age (months) Average (CV)	*n*
Indeterminate-sex				
Immature	8.8 (25%)	0.9 (87%)	4.4 (35%)	76
Female				
Immature	15.8 (29%)	5.8 (70%)	6.2 (14%)	88
Maturing	20.0 (24%)	11.3 (73%)	7.0 (16%)	20
Mature	26.1 (21%)	22.1 (44%)	7.5 (13%)	23
Male				
Immature	16.5 (30%)	6.6 (85%)	6.2 (10%)	60
Maturing	21.3 (24%)	12.2 (64%)	6.6 (16%)	15
Mature	34.9 (31%)	35.8 (65%)	7.4 (11%)	71

and mature groups means were significantly different at the 5% level ($|Y_I - Y_M| = 0.78 > MSD_{0.05[I,M]} = 0.08$). Because variances were heteroscedastic for the weight-at-age data grouped by sex and by maturity stage, the Games and Howell test was applied. The group means of indeterminates and females ($|Y_I - Y_F| = 2.47 > MSD_{0.05[I,F]} = 0.46$), indeterminates and males ($|Y_I - Y_M| = 3.08 > MSD_{0.05[I,M]} = 0.50$), and females and males ($|Y_F - Y_M| = 0.62 > MSD_{0.05[F,M]} = 0.40$) were significantly different at the 5% level. Similarly, the immature and mature group means were significantly different at the 5% level ($|Y_I - Y_M| = 2.13 > MSD_{0.05[I,M]} = 0.32$). Overall, the average growth rates in length and weight were found to be significantly different by sex and maturity stage.

The pattern of growth of *L. pealei* analyzed by month of hatching was also highly variable (Table 4). For indeterminate-sex squid, average growth in ML ranged from 5.9 (June-hatched) to 11.2 (September-hatched) mm/month, whereas average growth in weight ranged from 0.2 (July-hatched) to 1.9 (September-hatched) g/month. No seasonal pattern was apparent in the average growth rate for indeterminate-sex squid. However, few samples of indeterminate-sex squid hatched during July to December were available, and comparisons of growth rate by season of hatching were not possible. For females, average growth in ML ranged from 11.1 (December-hatched) to 22.5 (October-hatched) mm/month whereas average growth in weight ranged from 2.2 (December-hatched) to 19.5 (June-hatched) g/month. Average growth rates were generally higher for squid hatched from June to October when the average growth rate in weight exceeded 10 g/month. For males, average growth in ML ranged from 13.9 (December-hatched) to 40.9 (June-hatched) mm/month whereas growth in weight ranged from 3.4 (December-hatched) to 53.3 (June-hatched) g/month. Average growth rates of males were generally highest for squid hatched from June to October when the average growth rate in weight exceeded 20 g/month. Overall, these data suggested that the highest average growth rates were achieved by adult squid hatched from June to October.

The average growth rates by hatch month were also tested for significant differences by using unplanned multiple-comparisons procedures where the natural logarithmic transformation was applied to stabilize variance. The null hypothesis of homogeneous variances for the samples grouped by hatch month was rejected for growth in length ($X^2 = 44.41 >> \chi^2_{0.05[11]} = 19.67$) and in weight ($X^2 = 75.71 >> \chi^2_{0.05[11]} = 19.67$). A total of 16 pairs of group means for growth rate in length were significantly different at the 5% level (Table 5): July–January; July–February; July–March; July–April; July–May; July–November; July–December; September–April; September–May; September–December; October–January; October–March; October–April; October–May; October–November; and October–December. Overall, these tests indicated that there were significant differences between growth rates of squid hatched during November–May and July–October. Similarly, for growth rate in weight, a total of 16 pairs of group means for growth rate in length were significantly different at the 5% level (Table 6): July–January; July–February; July–March; July–April; July–May; July–November; July–December; August–May; September–April; September–May; September–December; October–March; October–April; October–May; October–November; and October–December. Overall, these tests indicated that there were significant differences between growth rates of squid hatched during November–May and July–October.

There was no consistent pattern in growth of *L. pealei* analyzed by year of hatching (Table 7). For indeterminate-sex squid, average growth in ML was lowest in 1990 (8.5 mm/month) and highest in 1992 (12.3 mm/month), whereas average growth in weight was lowest in 1991 (0.7 g/month) and highest in 1992 (2.2 g/month). For females, average growth in ML and weight was lowest in 1992 (16.3 mm/month and 7.2 g/month) and highest in 1990 (21.5 mm/month and 15.2 g/month). For males, average growth in ML and weight was lowest in 1992 (21.9 mm/month and 13.2 g/month) and highest in 1991 (27.8 mm/month and 25.0 g/month). Overall, these data suggested that growth rates varied by sex among years.

The average growth rates by hatch year were also tested for significant differences by using unplanned multiple-comparisons procedures where the natural logarithmic transformation was applied to stabilize variance. The null hypothesis of homogeneous variances for the samples grouped by hatch year was rejected for growth in length ($X^2 = 26.12 >> \chi^2_{0.05[2]} = 5.99$) and weight ($X^2 = 47.90 >> \chi^2_{0.05[2]} = 5.99$). The group means of 1990 and 1991 hatched squid were significantly different in length ($|Y_{1990} - Y_{1991}| = 0.28 > MSD_{0.05[1990,1991]} = 0.26$) and weight ($|Y_{1990} - Y_{1991}| = 0.93 > MSD_{0.05[1990,1991]} = 0.67$), but no general trend in growth by year was apparent.

Growth model

The additive and the multiplicative error structures were compared by testing whether the residuals of estimated case-I growth curves were normally or log-normally distributed. For 8 out of 10 subsets of length-at-age data, the hypothesis of an additive normal error structure was rejected at the 5% level. In contrast, the hypothesis of a multiplicative log-

Table 4

Average monthly growth rates and coefficients of variation (CV) for long-finned squid, *Loligo pealei*, in length (millimeters per month) and weight (grams per month) and average age (months) by sex and month of hatching.

Sex category and hatching months	mm per month Average (CV)	g per month Average (CV)	Age (months) Average (CV)	*n*
Indeterminate-sex				
January	8.3 (27%)	0.6 (58%)	4.2 (9%)	5
February	9.6 (16%)	1.1 (57%)	4.7 (11%)	7
March	10.6 (13%)	1.4 (29%)	5.1 (27%)	10
April	8.7 (24%)	1.1 (71%)	5.6 (22%)	15
May	8.8 (26%)	0.6 (141%)	3.0 (45%)	25
June	5.9 (18%)	0.3 (43%)	4.0 (6%)	6
July	6.1	0.2	3.4	1
September	11.2	1.9	6.2	1
November	8.7 (9%)	1.3 (29%)	6.1 (2%)	3
December	8.4 (23%)	0.9 (74%)	5.3 (3%)	3
Female				
January	13.2 (9%)	3.2 (27%)	6.0 (6%)	4
March	15.7 (25%)	5.6 (80%)	5.9 (21%)	16
April	17.2 (33%)	6.7 (68%)	5.8 (6%)	25
May	18.4 (30%)	8.0 (100%)	5.4 (19%)	12
June	19.5 (75%)	19.5 (128%)	7.7 (6%)	2
July	21.2 (21%)	15.9 (66%)	7.8 (8%)	9
August	17.9 (32%)	10.9 (78%)	7.4 (10%)	15
September	19.4 (32%)	11.4 (70%)	7.2 (12%)	17
October	22.5 (31%)	14.7 (74%)	6.9 (6%)	18
November	15.7 (43%)	6.3 (130%)	6.3 (3%)	12
December	11.1	2.2	6.7	1
Male				
January	19.6 (46%)	9.1 (100%)	6.0 (7%)	2
February	20.5 (22%)	8.2 (12%)	6.1 (22%)	3
March	20.8 (30%)	13.0 (74%)	6.8 (14%)	19
April	17.1 (28%)	6.9 (79%)	5.9 (5%)	15
May	21.9 (55%)	15.6 (141%)	5.7 (18%)	10
June	40.9 (19%)	53.3 (37%)	7.8 (11%)	8
July	35.5 (36%)	41.8 (66%)	7.6 (7%)	19
August	27.9 (53%)	25.4 (105%)	7.4 (12%)	17
September	33.1 (27%)	29.4 (47%)	7.5 (9%)	12
October	29.6 (36%)	21.1 (62%)	6.9 (5%)	20
November	17.4 (46%)	7.8 (157%)	6.1 (5%)	16
December	13.9 (16%)	3.4 (43%)	5.9 (12%)	5
Pooled-sex				
January	12.1 (45%)	3.1 (140%)	5.2 (19%)	11
February	12.8 (45%)	3.2 (108%)	5.1 (20%)	10
March	16.8 (37%)	7.8 (106%)	6.1 (21%)	45
April	14.9 (40%)	5.2 (93%)	5.8 (12%)	55
May	14.0 (61%)	5.6 (215%)	4.2 (42%)	47
June	25.1 (72%)	29.2 (101%)	6.4 (31%)	16
July	30.1 (44%)	32.3 (82%)	7.5 (13%)	29
August	23.2 (53%)	18.6 (115%)	7.4 (11%)	32
September	24.6 (41%)	18.3 (77%)	7.3 (11%)	30
October	26.2 (37%)	18.1 (68%)	6.9 (5%)	38
November	16.0 (47%)	6.6 (154%)	6.2 (4%)	31
December	11.8 (28%)	2.5 (66%)	5.8 (12%)	9

normal error structure could not be rejected for any subset of the length-at-age data. Similarly, for all 10 subsets of weight-at-age data, the hypothesis of an additive normal error structure was rejected at the 5% level, whereas the hypothesis of a multiplicative lognormal error structure could not be rejected for any subset. As a result, the multiplicative error structure was considered to be the best assumption for modelling variability in size at age.

Although the residuals from the curves estimated with the multiplicative error structure conformed to model assumptions, the parameters of these curves were imprecisely determined. In particular, the case-I curve was rejected for each subset of length-at-age and weight-at-age data because there was at least one parameter that was not significantly different from 0. Thus, the 4-parameter form of the Schnute model had more parameters than necessary to characterize *L. pealei* growth.

For the length-at-age growth curves, most of the case-II and case-III curves were rejected because their parameters were not significant. As a result, there were only 3 instances where comparison of RSS was used to select the best curve. The best curve for pooled-sex samples hatched during June–October was the case-II curve which was selected over the case-IV curve because the hypothesis $\alpha=0$ was rejected ($f=14.98 > 3.91=F_{0.05}(1,142)$). The best curve

Table 5

Results of Games and Howell test of differences between means of log-transformed growth rate in length by hatch month of long-finned squid, *Loligo pealei*. Absolute values of differences between means are given below the diagonal and corresponding values of the maximum significant difference at the 5% level are given above the diagonal. Significantly different means are indicated with an asterisk.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Jan	—	0.94	0.77	0.77	0.78	1.41	0.81	0.80	0.80	0.77	0.77	0.86
Feb	0.06	—	0.77	0.77	0.79	1.41	0.81	0.80	0.80	0.77	0.77	0.86
Mar	0.34	0.28	—	0.37	0.44	1.32	0.52	0.49	0.47	0.39	0.40	0.63
Apr	0.21	0.15	0.13	—	0.44	1.32	0.52	0.49	0.48	0.39	0.41	0.63
May	0.09	0.03	0.25	0.12	—	1.33	0.56	0.54	0.53	0.46	0.47	0.65
Jun	0.45	0.39	0.11	0.24	0.36	—	1.34	1.34	1.33	1.32	1.32	1.36
Jul	**0.89***	**0.83***	**0.55***	**0.68***	**0.80***	0.44	—	0.60	0.60	0.53	0.55	0.70
Aug	0.62	0.56	0.28	0.41	0.53	0.17	0.27	—	0.56	0.51	0.52	0.68
Sep	0.70	0.64	0.36	**0.49***	**0.61***	0.25	0.19	0.08	—	0.50	0.51	0.67
Oct	**0.79***	0.73	**0.45***	**0.58***	**0.70***	0.34	0.10	0.17	0.09	—	0.43	0.64
Nov	0.28	0.22	0.06	0.08	0.19	0.16	**0.60***	0.33	0.41	**0.50***	—	0.64
Dec	0.01	0.05	0.33	0.19	0.08	0.43	**0.87***	0.60	**0.68***	**0.77***	0.27	—

Table 6

Results of Games and Howell test of differences between means of log-transformed growth rate in weight by hatch month for long-finned squid, *Loligo pealei*. Absolute values of differences between means are given below the diagonal and corresponding values of the maximum significant difference at the 5% level are given above the diagonal. Significantly different means are indicated with an asterisk.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Jan	—	2.85	2.38	2.41	2.52	3.94	2.47	2.42	2.42	2.37	2.41	2.61
Feb	0.18	—	2.23	2.22	2.37	3.85	2.31	2.28	2.27	2.21	2.22	2.48
Mar	1.14	0.96	—	1.02	1.49	3.53	1.33	1.20	1.19	0.94	1.02	1.78
Apr	0.78	0.60	0.36	—	1.48	3.53	1.32	1.18	1.17	0.93	1.00	1.80
May	0.21	0.39	1.35	1.00	—	3.62	1.69	1.61	1.60	1.43	1.48	2.00
Jun	1.32	1.14	0.18	0.54	1.53	—	3.59	3.57	3.56	3.50	3.53	3.65
Jul	**2.61***	**2.43***	**1.47***	**1.83***	**2.83***	1.30	—	1.47	1.46	1.26	1.32	1.90
Aug	1.94	1.76	0.80	1.16	**2.16***	0.62	0.67	—	1.33	1.14	1.21	1.85
Sep	2.07	1.89	0.93	**1.29***	**2.29***	0.75	0.54	0.13	—	1.13	1.20	1.84
Oct	2.22	2.04	**1.08***	**1.44***	**2.44***	0.90	0.39	0.28	0.15	—	0.93	1.77
Nov	1.02	0.84	0.12	0.24	1.23	0.30	**1.59***	0.92	1.05	**1.20***	—	1.80
Dec	0.23	0.05	0.91	0.56	0.44	1.09	**2.39***	1.72	**1.85***	**1.99***	0.79	—

Table 7

Average monthly growth rates and coefficients of variation (CV) for long-finned squid, *Loligo pealei*, in length (millimeters per month), weight (grams per month), and average age (months) by sex and year of hatching.

Sex category and hatching year	mm per month Average (CV)	g per month Average (CV)	Age (months) Average (CV)	*n*
Indeterminate-sex				
1990	8.5 (16%)	1.1 (48%)	5.7 (8%)	6
1991	8.5 (23%)	0.7 (89%)	4.2 (37%)	65
1992	12.3 (17%)	2.2 (20%)	5.4 (17%)	5
Totals	8.8 (25%)	0.9 (87%)	4.4 (35%)	76
Female				
1990	21.5 (42%)	15.2 (87%)	6.7 (10%)	24
1991	18.4 (27%)	9.0 (72%)	6.5 (19%)	61
1992	16.3 (31%)	7.2 (95%)	6.5 (14%)	46
Totals	18.2 (34%)	9.5 (91%)	6.5 (16%)	131
Male				
1990	27.5 (47%)	22.7 (89%)	6.9 (13%)	40
1991	27.8 (46%)	25.0 (102%)	6.8 (16%)	69
1992	21.9 (40%)	13.2 (94%)	6.7 (12%)	37
Totals	25.9 (47%)	21.4 (102%)	6.8 (14%)	146
Pooled-sex				
1990	23.8 (52%)	18.3 (100%)	6.8 (13%)	70
1991	18.4 (62%)	11.9 (156%)	5.8 (30%)	195
1992	18.0 (39%)	9.4 (106%)	6.6 (14%)	88
Totals	19.4 (56%)	12.5 (136%)	6.2 (24%)	353

for female samples hatched during November–May was the case-IV curve which was selected over the case-II curve because the hypothesis $\alpha=0$ was accepted ($f=2.68 < 3.98=F_{0.05}(1,67)$). The best curve for male samples hatched during June–October was the case-II curve which was selected over the case-IV curve because the hypothesis $\alpha=0$ was rejected ($f=5.46 > 3.97=F_{0.05}(1,73)$). For each of the 7 other subsets of length-at-age data, case IV yielded the best growth curve (Table 8).

Case-IV curves were the best growth models for length at age of pooled-sex samples (Fig. 4A) and pooled-sex samples hatched during November–May (Fig. 5A). In general, the case-IV growth curves are power functions that represent unbounded accelerating growth with a theoretical minimum size. In particular, case-IV curves are what Schnute termed "T^{th} power" growth curves, where size (G) at age (T) is proportional to some positive constant $K>1$ raised to the Tth power. That is, $G \propto K^T = \exp[T \ln(K)]$, so that size increases exponentially as age increases. In contrast, the case-II curve was chosen for pooled-sex samples hatched during June–October (Fig. 5A). For these samples, growth in length appeared nearly linear over the range of data, although there was some indication of a slight decrease in growth rate past 250 days of age.

For the length-at-age data partitioned by sex, case-IV curves were also the best growth models, with one exception. Exponential growth in length was evident for indeterminate-sex (Fig. 6A), female (Fig. 7A), and male (Fig. 7A) samples. Similarly, growth in length was exponential for female samples hatched during June–October and during November–May (Fig. 8A) and for male samples hatched during November–May (Fig. 9A). In contrast, growth in length for males hatched during June–October was not exponential (Fig. 9A) and growth rate decreased between 200 and 250 days of age.

For the subsets of the weight-at-age growth data, most of the case-II and case-III curves were rejected because their parameters were not significant and there were only 4 instances where comparison of RSS was used to select the best curve. The best curve for pooled-sex samples was the case II curve which was selected over the case-IV curve because the hypothesis $\alpha=0$ was rejected ($f=4.30 > 3.87=F_{0.05}(1,350)$). The best curve for indeterminate-sex samples was the case-II curve which was selected over case-IV curve because the hypothesis $\alpha=0$ was rejected ($f=5.61 >$

Table 8

Summary of best growth curves for long-finned squid, *Loligo pealei*, length (cm) at age (months).

Data set	Sample size	Growth curve	r^2	α	β	t_{min}	y_{min}	t_{max}	y_{max}
Pooled-sex samples	353	IV	0.97	—	—	1.6427	1.3670	9.7249	47.1939
Indeterminate-sex samples	76	IV	0.97	—	—	1.6427	1.5267	6.8993	7.3841
Female samples	131	IV	0.98	—	—	4.0739	6.1918	9.2320	21.2922
Male samples	146	IV	0.98	—	—	4.4353	5.4317	9.7249	57.8786
Pooled-sex samples hatched Jun–Oct	145	II	0.98	0.2867	—	3.4497	1.4801	9.2320	30.6814
Pooled-sex samples hatched Nov–May	208	IV	0.97	—	—	1.6427	1.5796	9.7249	37.4441
Female samples hatched Jun–Oct	61	IV	0.99	—	—	5.4209	8.8066	9.2320	22.5526
Female samples hatched Nov–May	70	IV	0.98	—	—	4.0739	6.9978	8.6078	13.8768
Male samples hatched Jun–Oct	76	II	0.99	0.8284	—	5.6509	6.1309	9.1335	32.5621
Male samples hatched Nov–May	70	IV	0.98	—	—	4.4353	5.9896	9.7249	36.6641

$3.97=F_{0.05}(1,74)$). The best curve for pooled-sex samples hatched during June–October was the case-II curve which was selected over the case-IV curve because the hypothesis $\alpha=0$ was rejected ($f=18.64 > 3.91=F_{0.05}(1,142)$). The best curve for pooled-sex samples hatched during November–May was the case-III curve which was selected over case-IV curve because the hypothesis $\alpha=0$ was rejected ($f=6.82 > 3.89=F_{0.05}(1,205)$). For each of the 6 other subsets of length-at-age data, case IV yielded the best growth curve (Table 9).

For the weight-at-age data, case-II growth curves were chosen for pooled-sex samples (Fig. 4B) and pooled-sex samples hatched during June–October (Fig. 5B). Although these curves are sigmoidal and eventually approach an asymptote (cf. Schnute, 1981), it is important to note that the asymptotes are not approached within the range of data for the estimated curves and that growth is nearly exponential for the observed ages. In contrast, a case-III growth curve was chosen for pooled-sex samples hatched during November–May (Fig. 5B). This growth curve is not asymptotic and consists of an initial period of decelerated growth followed by a period of accelerated growth after a certain size is reached.

Case-IV growth curves were chosen for every data set where the weight-at-age data were partitioned by sex, with one exception. Growth in weight was exponential for female and male samples (Fig. 7B). Similarly, exponential growth was evident for female samples hatched during June–October and during November–May (Fig. 8B) and for male samples hatched during June–October and during November–May (Fig. 9B). In contrast, a case-II curve was chosen for indeterminate-sex squid (Fig. 6B), although growth rate was effectively exponential for the observed ages. In this case, the estimated curve would approach an asymptote outside the range of possible sizes for *L. pealei* that lack identifiable sexual characteristics.

For adult squid, the estimated growth curves indicated sexual dimorphism. Length-at-age curves for female (L_F) and male (L_M) samples were

$$L_F(d) = 2.3343e^{0.0079d}$$
$$L_M(d) = 0.7470e^{0.0147d}, \qquad (10)$$

where L is mantle length in centimeters and age (d) is measured in days (Fig. 7A). Similarly, weight-at-age curves for female (W_F) and male (W_M) samples were

$$W_F(d) = 1.1446e^{0.0182d}$$
$$W_M(d) = 0.1316e^{0.0311d}, \qquad (11)$$

Table 9

Summary of best growth curves for long-finned squid, *Loligo pealei*, weight (g) at age (months).

Data set	Sample size	Growth curve	r^2	α	β	t_{min}	y_{min}	t_{max}	y_{max}
Pooled-sex samples	353	II	0.94	0.0577	—	1.6427	0.1813	9.7249	783.6477
Indeterminate-sex samples	76	II	0.85	0.2058	—	1.6427	0.1985	6.8993	11.2208
Female samples	131	IV	0.96	—	—	4.0739	10.9940	9.2320	192.8125
Male samples	146	IV	0.97	—	—	4.4353	8.7765	9.7249	1314.8945
Pooled-sex samples hatched Jun–Oct	145	II	0.96	0.3038	—	3.4497	0.3545	9.2320	365.0887
Pooled-sex samples hatched Nov–May	208	III	0.92	—	0.1315	1.6427	0.1820	9.7249	323.5635
Female samples hatched Jun–Oct	61	IV	0.97	—	—	5.4209	23.7236	9.2320	222.6014
Female samples hatched Nov–May	70	IV	0.96	—	—	4.0739	14.1734	8.6078	78.0026
Male samples hatched Jun–Oct	76	IV	0.97	—	—	5.6509	39.6333	9.1335	681.9745
Male Samples hatched Nov–May	70	IV	0.97	—	—	4.4353	10.1822	9.7249	633.1753

where weight (W) is in grams and age (d) is measured in days (Fig. 7B). These curves gave instantaneous daily growth rates of 0.8% and 1.5% in length and of 1.8% and 3.1% in weight for females and males, respectively. Thus, female growth in length and weight was generally slower than that for males.

The estimated growth curves also indicated differences in growth rate between hatching seasons for both sexes. Length-at-age curves for female squid hatched during June–October ($L_{F,JO}$) and female squid hatched during November–May ($L_{F,NM}$) were (Fig. 8A):

$$L_{F,JO}(d) = 2.3116e^{0.0081d}$$
$$L_{F,NM}(d) = 3.7828e^{0.0050d}. \quad (12)$$

Weight-at-age curves for female squid hatched during June–October ($W_{F,JO}$) and female squid hatched during November–May ($W_{F,NM}$) were (Fig. 8B):

$$W_{F,JO}(d) = 0.9820e^{0.0193d}$$
$$W_{F,NM}(d) = 3.0617e^{0.0124d}. \quad (13)$$

These curves gave instantaneous daily growth rates of 0.8% and 0.5% in length and of 1.9% and 1.2% in weight for females hatched during June–October and during November–May, respectively. Thus, female growth rate in length and weight was generally more rapid for June–October hatched squid.

Differences in growth rate between hatching seasons were also evident for male squid. In particular, male growth in length (Fig. 9A) was more rapid at younger ages (≤225 d) for June–October hatched squid than for November–May hatched squid. In contrast, male growth in length was estimated to be more rapid at older ages (>225 d) for November–May hatched squid than for June–October hatched squid (Fig. 9A). However, this comparison should be viewed with caution because the sample size of older males hatched during November–May available for estimating the length-at-age curve was small. Weight-at-age curves (Fig. 9B) for male squid hatched during June–October ($W_{M,JO}$) and male squid hatched during November–May ($W_{M,NM}$) were

$$W_{M,JO}(d) = 0.3917e^{0.0268d}$$
$$W_{M,NM}(d) = 0.3190e^{0.0256d}. \quad (14)$$

These curves gave instantaneous daily growth rates of 2.7% and 2.6% of body weight for males hatched

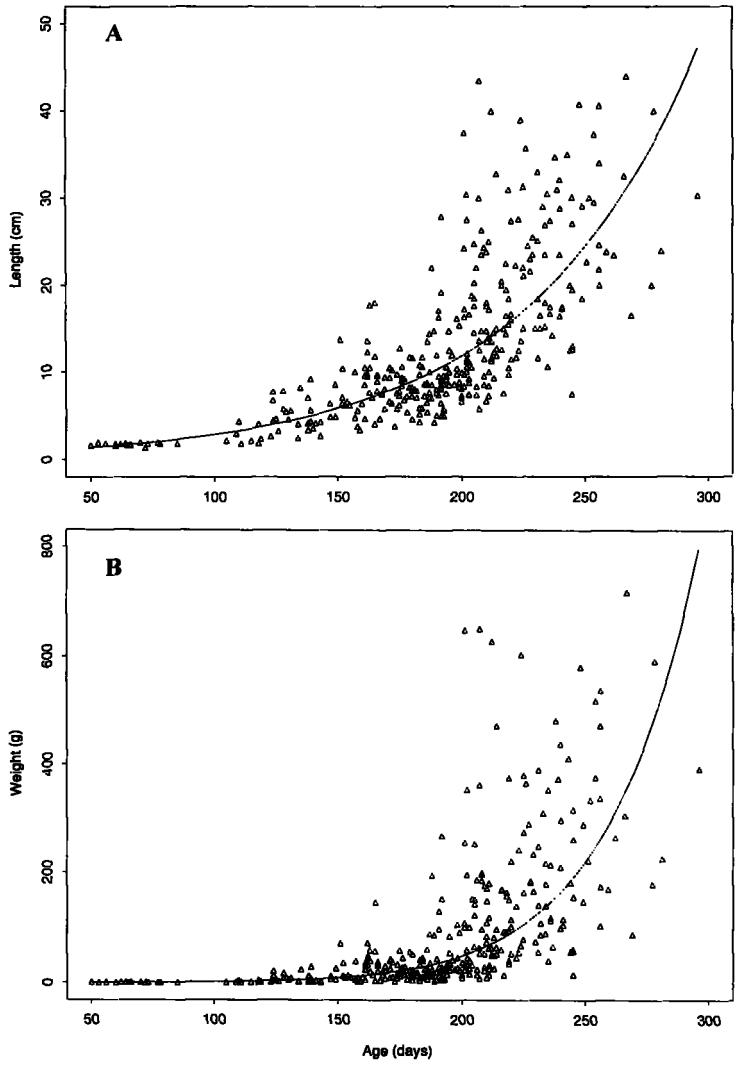

Figure 4

Growth curves for pooled-sex *Loligo pealei* in length (**A**) and in weight (**B**).

during June–October and during November–May, respectively. Overall, female growth in length and weight and male growth in weight were more rapid for June–October hatched squid. Male growth in length was also more rapid at younger ages for squid hatched during June–October than for squid hatched during November–May.

The selected growth curves indicated that *L. pealei* growth was dependent upon maturity stage, sex, and hatching season. Indeterminate-sex squid grew more slowly than adults whereas males grew more rapidly than females. Further, squid hatched during June–October grew more rapidly than squid hatched during November–May.

Discussion

Growth rates obtained in this study were generally higher than those reported in Hixon et al. (1981, Tables 1 and 2) but were lower than those in studies of cultured *L. pealei*. In particular, average monthly growth rates for males reported in this study (26 mm/month and 21 g/month) were lower than those reported by Hanlon et al. (1983) who found average growth rates of 44 mm/month and 37 g/month in a sample of 6 male *L. pealei* raised in a closed sea-water system. Additionally, Hanlon et al. (1987) reported an instantaneous daily growth rate of roughly 2% in ML for 10 *L. pealei* raised in a closed sea-water sys-

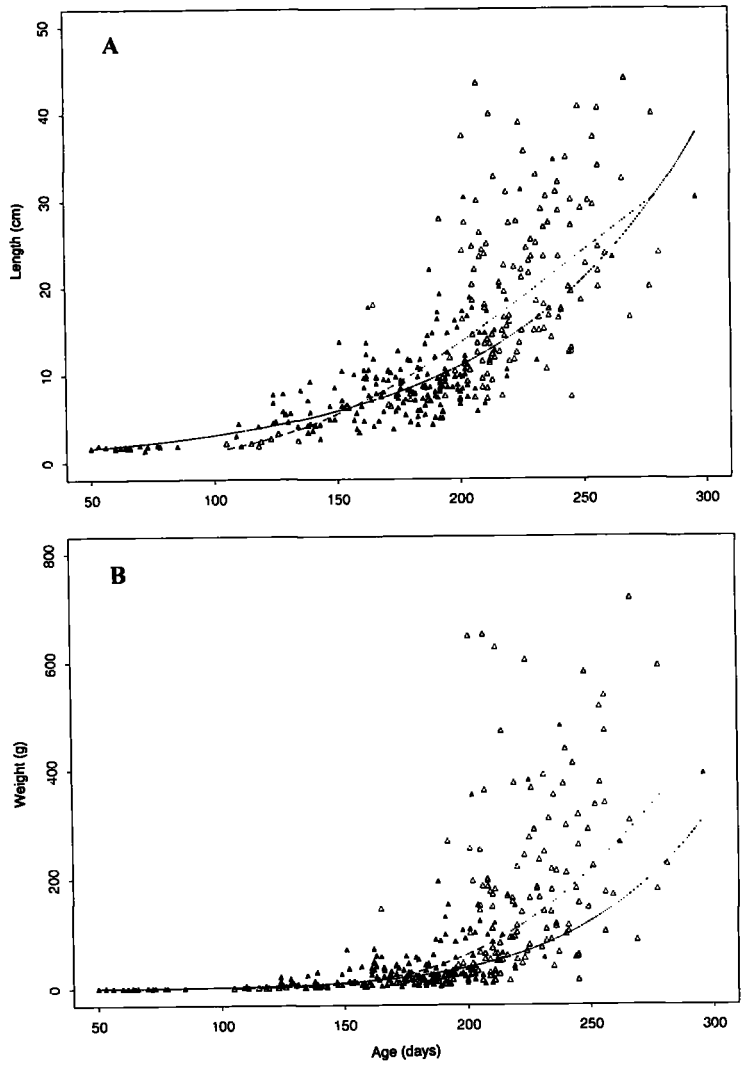

Figure 5

Growth curves for pooled-sex *Loligo pealei* hatched during June–October (dashed line and open triangles) and during November–May (solid line and solid triangles) in length (**A**) and in weight (**B**).

tem whereas the estimated growth curve for pooled-sex samples in this study indicated a growth rate of 1.4%. While the lower growth rates of wild squid were likely due to the better growth conditions experienced by the cultured squid, it should be noted that the largest squid in this study, a 44-cm male, was only 2.5 cm smaller than the largest reported *L. pealei*[5] (Summers, 1968). The fact that this 9-month-old male could have achieved the maximum reported size if it grew for one more month at average male growth rate suggested that it was unlikely that the lifespan of *L. pealei* exceeded 1 year.

Although a comprehensive growth model for squid has not yet been determined (Jackson, 1994a), we suggest that the Schnute model is a viable choice given its flexibility. In addition, we recommend the methods used to select the best form of the growth model because they provide an objective basis for evaluating alternative forms. Even though there was substantial heterogeneity in *L. pealei* size at age, the estimated growth curves for pooled sexes indicated that *L. pealei* growth in length and weight was effec-

[5] Based on a total of 55,616 length-frequency measurements, the maximum size of *L. pealei* taken in the domestic commercial fishery during 1972–91 was 45 cm (Northeast Fisheries Science Center, Woods Hole, MA, unpubl. data).

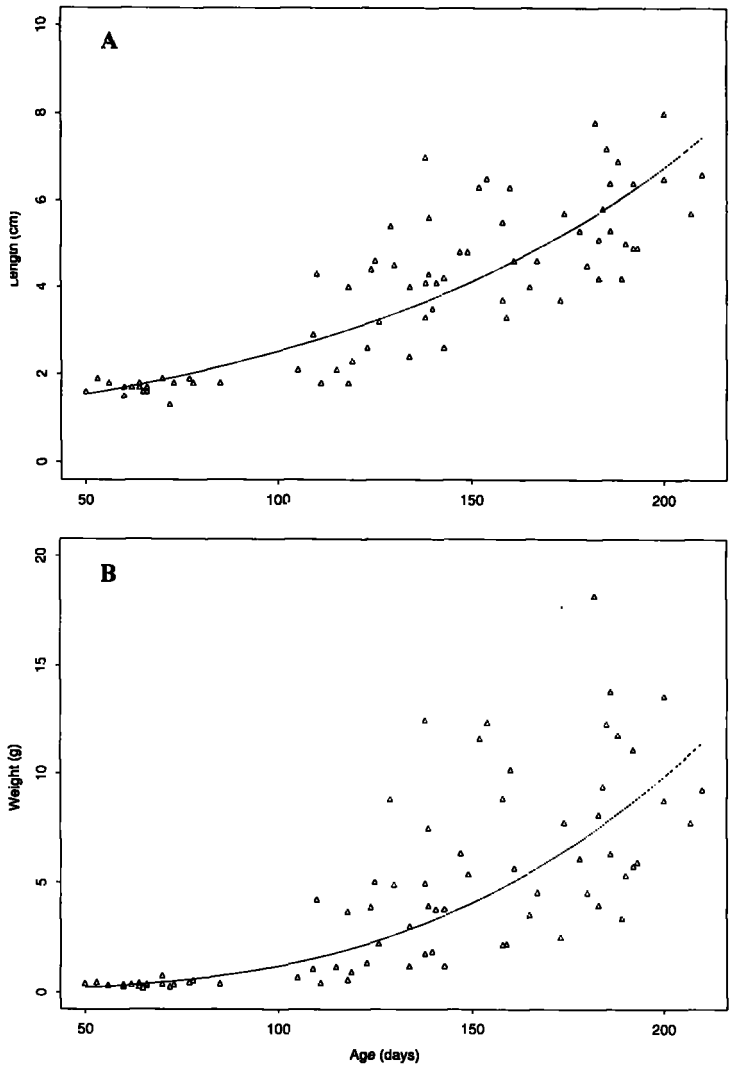

Figure 6

Growth curves of indeterminate-sex *Loligo pealei* in length (**A**) and in weight (**B**).

tively exponential, which is consistent with the findings of Forsythe and Van Heukelem (1987).

It is important to account for individual heterogeneity in size at age when determining a growth curve because the use of mean values for size classes can obscure the pattern of individual growth (Alford and Jackson, 1993). In this study, growth curves were estimated by using size-at-age data for individual squid. We found that the use of a multiplicative lognormal error term provided an adequate statistical framework for estimating growth curves despite substantial heterogeneity in squid size at age. In general, a growth curve with a multiplicative lognormal error term will be more appropriate than an additive normal error term when size-at-age distributions are skewed because prediction error scales with size at age under the lognormal assumption. Regardless, it is recommended that researchers use residual patterns to evaluate the adequacy of an assumed error structure for estimating a growth curve.

The fact that some *L. pealei* were hatched during December–April was unexpected because the protracted spawning season of *L. pealei* in the northwest Atlantic had previously been considered to extend from roughly April to November (Lange, 1982). McMahon and Summers (1971) found that embryonic development of *L. pealei* was related to water temperature. In their study, the average development time required before hatching was 26.7 days for wa-

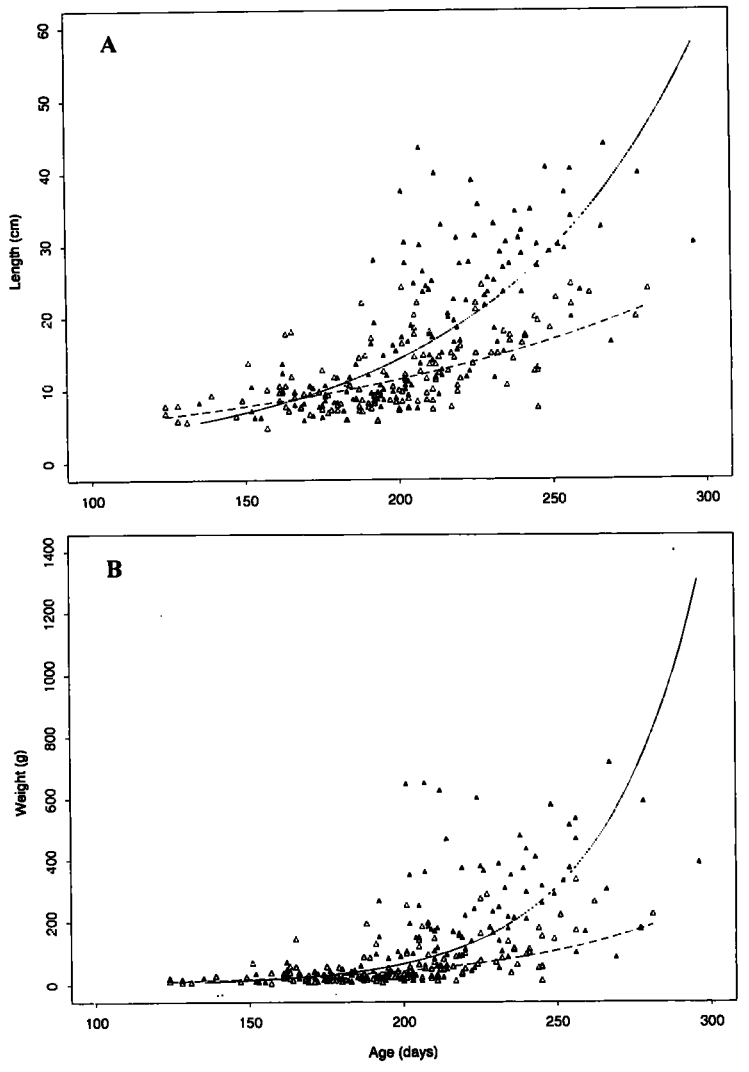

Figure 7

Growth curves for female (dashed line and open triangles) and male (solid line and solid triangles) *Loligo pealei* in length (**A**) and in weight (**B**).

ter temperatures of 12.0–18.0°C, 18.5 days for water temperatures of 15.5–21.3°C, and 10.7 days for water temperatures of 21.5–23.0°C. During winter, *L. pealei* move offshore to the edge of the continental shelf to avoid cooler inshore waters (Lange, 1982). Assuming that squid hatched during December–April encountered water temperatures of 9.0–13.0°C that are characteristic of the convergence zone at the edge of the continental shelf (Bowman, 1977), it would have taken about 1 month for them to develop to the hatching stage. Although our results indicated that winter spawning occurred, further research will be needed to evaluate the relative contribution of winter-hatched squid to the population's dynamics.

Our results lend support to the hypothesis that growth of *L. pealei* can be influenced by seasonal environmental variation and month of hatching. Empirical differences in growth rates between June–October and November–May hatched squid were apparent for both females and males. Further, significant differences in growth rate were detected between squid hatched during November–May and July–October. These differences were also evident in estimated growth curves. The notion that *L. pealei* growth can be influenced by hatching season and its associated temperature regime is consistent with the results of Rodhouse and Hatfield (1990b) who found an apparent effect of seasonal environmental varia-

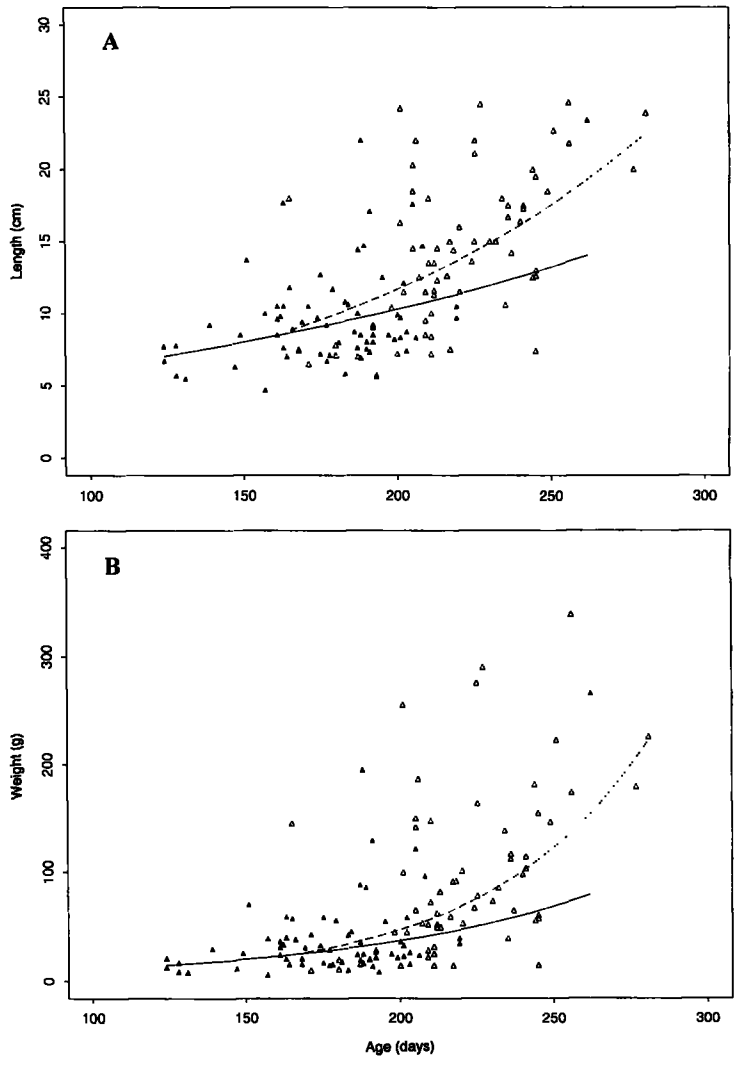

Figure 8

Growth curves for female *Loligo pealei* hatched during June–October (dashed line and open triangles) and during November–May (solid line and solid triangles) in length (**A**) and in weight (**B**).

tion on the growth rate of the Argentine short-finned squid, *Illex argentinus*. Using statolith ageing techniques, they found that older short-finned squid hatched during cooler months apparently grew more slowly than younger squid hatched during warmer months. They speculated that the faster growth of the younger cohort was due to the generally warmer temperatures experienced by hatchlings. Similarly, Forsythe (1993) conducted a simulation study to examine the potential effects of seasonal temperature regimes on the growth of juvenile cephalopods. He showed that small temperature changes could have a substantial effect on the growth of juvenile squid under certain conditions. Overall, further research to estimate directly the potential effect of temperature on the growth rate of *L. pealei* would help to quantify the potential yield from this resource on a seasonal basis.

The fact that the growth rate of *L. pealei* was found to be associated with maturity stage also has potential implications for the management of the resource. Empirical differences in growth rate by maturity stage were consistent for both females and males; on average, growth rates in length and weight were lowest for immature squid and highest for mature squid. Significant differences in growth rate by length

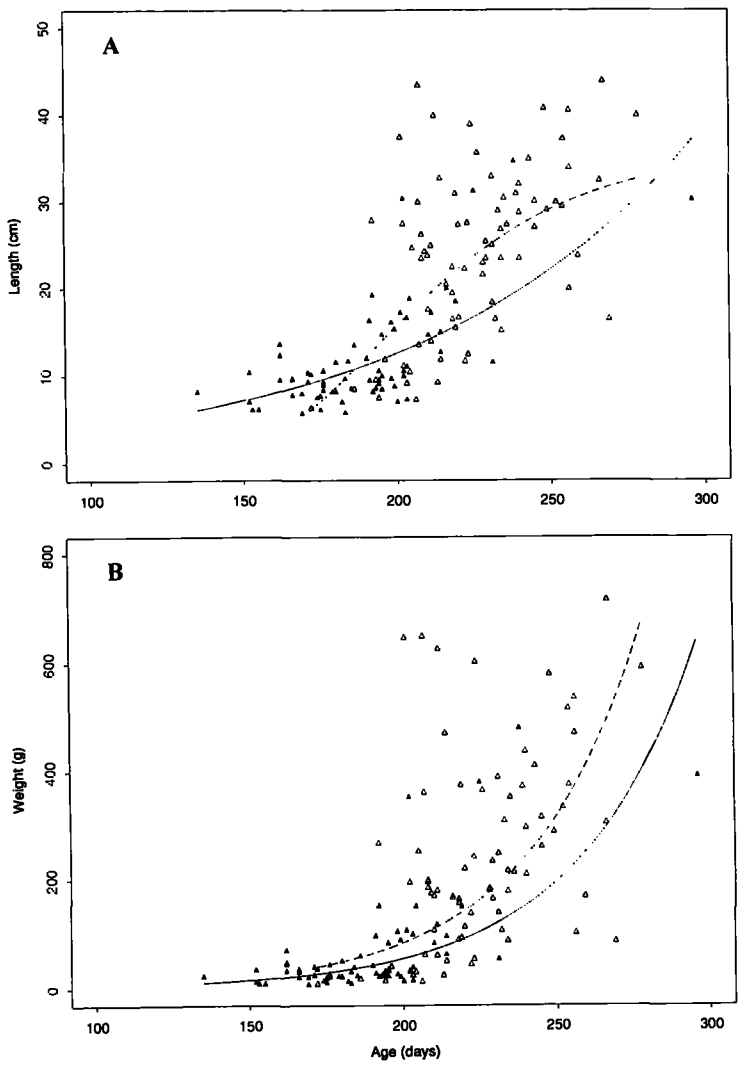

Figure 9

Growth curves for male *Loligo pealei* hatched during June–October (dashed line and open triangles) and during November–May (solid line and solid triangles) in length (**A**) and in weight (**B**).

and weight were also detected between immature and mature squid. In general, intensive harvest of slow-growing immature squid has the potential to reduce fishery production through a decrease in yield per recruit.

No clear effect of hatch year on growth rate was detected in this study. However, these data were not collected for the purpose of examining yearly differences in growth rates, and any annual effects were likely confounded by the effects of hatch month, sex, and maturity stage. Further research conducted with more extensive multi-year collections will likely be needed to ascertain the importance of annual effects on growth rate.

The estimated growth curves for indeterminate-sex squid indicated that their pattern of growth was exponential as suggested by Hanlon et al. (1987) who examined growth rates of juvenile *L. pealei* in closed-system aquaria. Growth of indeterminate-sex squid in weight was less rapid than that for adults and would be predicted to slow outside the range of observed ages, when these juveniles would develop identifiable sexual characteristics. In contrast, growth of indeterminate-sex squid in length was roughly 1.0% per day. In comparison, growth curves for females and males indicated exponential growth with instantaneous daily growth rates of 0.8% to 1.5%

in ML and 1.8% to 3.1% in weight. The exponential growth of *L. pealei* throughout their life cycle is consistent with the fact that squid have high gross-growth efficiency and are metabolic maximizers in comparison with teleosts (O'Dor and Webber, 1986).

The difference between growth rate in weight of indeterminate-sex squid and adults suggests that there may be a body size above which growth rate increases substantially. This critical size could be related to changes in diet because *L. pealei* undergo an ontogenetic shift in prey selection from crustaceans to fish and other squid as they grow (Vovk, 1972; Macy, 1982b; Vovk, 1985; Anderson and Griswold, 1988). Alternatively, this difference could be the result of a shift from somatic to gonadal growth as squid mature (Macy, 1995), although this seems less likely given the substantial variability in size at maturity of *L. pealei* (Macy, 1980). Regardless of the cause, understanding the implications of the rapid growth of adults and its relationship to maturity stage will be important for predicting how the population structure will respond to exploitation. Over the longterm, it is conceivable that intensive exploitation of an annual semelparous species, such as *L. pealei*, could lead to strong selective pressure for a smaller average size at maturity. Such a reduction in average size at maturity could diminish the reproductive potential of the population (cf. Murphy et al., 1994), and this could lower resilience to environmental fluctuations by reducing the genetic variation in the population.

The implications of these estimates of growth for *L. pealei* in the northwest Atlantic are substantial for the assessment and management of this resource. The short lifespan for this species, combined with the rapid growth of adults and the capacity to spawn year-round, implies that the stock will respond rapidly to environmental variation and fishing pressure. As a result, monitoring the stock for in-season management would likely require several assessments throughout the year.

New management measures are being developed for the long-finned squid stock to reflect the improved understanding of its growth and pattern of reproduction (MAFMC[6]). At present, management of the stock is based on a level of total allowable catch that cannot be exceeded (MAFMC[7]) and on an overfishing definition that has been characterized as "risky" (Rosenberg et al. 1994). A preliminary analysis of some of the weight-at-age data presented in this study indicated that the annual level of maximum sustainable yield, based upon average recruitment and an initial estimate of maximum yield per recruit, could be roughly 36,000 t (NEFSC[8]). This interim estimate was 18% lower than the estimate of 44,000 t, which was based on a presumed two-year lifespan (Sissenwine and Tibbetts, 1977) that has been used as the maximum optimum yield for the stock (MAFMC[7]). However, this estimate appears overly optimistic because landings above 36,000 t have occurred only once, in 1973, when 37,600 t were landed. Regardless, any revision of the annual level of sustainable yield for the stock will need to account for the seasonal patterns of growth and spawning, the potential discarding of juveniles, and variability in stock-recruitment dynamics. Further, it would be more appropriate to estimate sustainable yield and to develop an overfishing definition on a seasonal, rather than an annual, basis for this short-lived species. In contrast to the current quota-based harvesting strategy, a constant harvest-rate strategy that includes a proportional escapement target (Beddington et al., 1990) on a seasonal basis may be a useful management approach.

If the long-finned squid stock is managed on a seasonal basis, revised stock assessment procedures are likely to require rapid collection of catch and effort data and efficient data analysis during periods of peak fishing activity. Real-time assessment procedures have been used to monitor the short-finned squid stock in Falkland Islands waters during the fishing season to achieve proportional escapement goals (Rosenberg et al., 1990), and the use of a constant harvest-rate strategy is a potential option for management of the long-finned squid resource. Although a constant harvest-rate strategy can be overly restrictive in years of good recruitment and result in a loss of yield, it can also jeopardize the stock when recruitment is poor. Therefore, assessment procedures that permit in-season adjustment of the harvest rate would likely be necessary to maintain an adequate level of spawning biomass if management is conducted on a seasonal basis.

As with any renewable resource, long-term management of the long-finned squid stock will involve a balance of the risks and benefits of harvesting the resource. Because long-finned squid are semelparous and likely live for less than 1 year, the risk of re-

[6] Mid-Atlantic Fishery Management Council. 1995. Amendment 5 to the fishery management plan and the final environmental impact statement for the Atlantic mackerel, squid, and butterfish fisheries. MAFMC, Dover, DE.

[7] Mid-Atlantic Fishery Management Council. 1992. 1993–1994 allowable biological catch, optimum yield, domestic annual harvest, domestic annual processing, joint venture processing, and total allowable level of foreign fishing recommendations for Atlantic mackerel, *Loligo*, *Illex*, and butterfish. MAFMC, Dover, DE.

[8] Northeast Fisheries Science Center. 1994. Report of the 17th Northeast Regional Stock Assessment Workshop. NEFSC Ref. Doc. 94–06, Woods Hole, Massachusetts, 124 p.

cruitment overfishing is substantial for this stock. Further, because growth appears to be nearly exponential throughout its life cycle, the risk of growth overfishing is also considerable. On the other hand, harvesting impacts may be difficult to evaluate unless stock response to environmental variation, density-dependence in growth and survival, and community-level interactions with competitors and predators are better understood. Owing to its short lifespan, the immediate benefits of harvesting the long-finned squid resource are probably best measured by average seasonal yield and its variance, and an adaptive approach to management may be needed to ensure sufficient spawning escapement and to foster efficient utilization of this resource.

Acknowledgments

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Abstract.—This paper tested the null hypothesis that the statistical relationship between monthly sea turtle (species combined) stranding rates (strandings per 100 km of accessible shoreline) and monthly shrimp fishing intensities (days fished per 100 km^2) in the northwestern Gulf of Mexico was the same in 1990–93 as in 1986–89. The expectation was that regulations requiring use of turtle excluder devices (TED's) in shrimp trawls during 1990–93 would reduce the incidental catch of sea turtles and thereby diminish or eliminate the statistical relationship between stranding rates and fishing intensities. Significant positive correlations were detected between the log-transformed stranding rates and fishing intensities for shrimping landward of the 20-fathom (36.6-m) contour in 1990–93. The null hypothesis was not rejected; therefore TED regulations did not result in diminishing or eliminating the statistical relationship between sea turtle stranding rates and shrimp fishing intensities in the northwestern Gulf. Various hypotheses were suggested as possible explanations.

Relationship between sea turtle stranding rates and shrimp fishing intensities in the northwestern Gulf of Mexico: 1986–1989 versus 1990–1993

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Endangered Species Act amendments of 1988 mandated an independent review of scientific and technical information pertaining to conservation of sea turtles and the causes and significance of turtle mortality, including that caused by commercial trawling (National Research Council, 1990). Incidental capture of sea turtles in shrimp trawls was identified as the most important human-associated source of mortality in juvenile, subadult, and breeding sea turtles in coastal waters. It was concluded that shrimping could be compatible with sea turtle conservation if adequately controlled, especially through mandatory use of turtle excluder devices (TED's) at most places and times of year. Federal regulations requiring use of TED's by offshore (seaward of the COLREG's demarcation line [the boundary used by the U.S. Coast Guard to distinguish inshore from offshore waters]) shrimp trawlers longer than 25 ft were published in 1987 (Federal Register, vol. 52, no. 124, p. 24247–24262, 28 June 1987). These regulations did not require TED's in "try nets" (small trawls towed and retrieved intermittently during shrimping operations to sample abundance of shrimp), and TED's were used only sporadically in the northwestern

Gulf until 1990 (McDonald, 1990; Henwood et al., 1992; Crouse, 1993b; Weber et al.[1]; Crouse et al.[2]). Therefore, 1986–89 can be considered pre-TED years, for the most part. In contrast, 1990–93 were years during which TED regulations were in effect.

Caillouet et al. (1991) examined the statistical relationship between monthly sea turtle stranding rates (species combined) and monthly shrimp fishing intensities in the northwestern Gulf of Mexico during 1986–89. They detected significant statistical relationships between stranding rates and fishing intensities in some offshore depth intervals within 0 to 15 fathoms (fm) (27.4 m) in two geographic zones of the northwestern Gulf: the upper coast defined as shrimp statistical subareas 17–18, and the lower coast defined as subareas 19–21 (Fig. 1; see Kutkuhn, 1962).

In this paper, we used the approach of Caillouet et al. (1991) to determine whether or not the statistical relationships they detected between monthly sea turtle stranding rates and monthly shrimp fishing intensities during 1986–89 continued to exist after TED regulations had been promulgated. We tested the null hypothesis that the statistical relationship between monthly sea turtle stranding rates and fishing intensities in two geographic zones of the northwestern Gulf was the same in 1990–93 as in 1986–89. The expectation was that regulations requiring use of TED's in shrimp trawls during 1990–93 would reduce the incidental catch of sea turtles and thereby diminish or eliminate the statistical relationship between sea turtle stranding rates and fishing intensities.

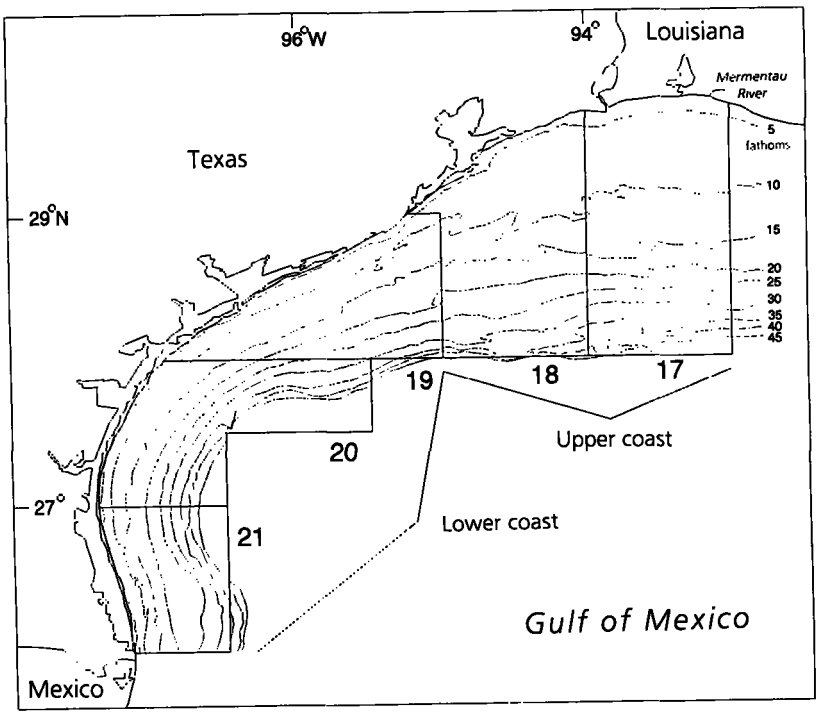

Figure 1

Boundaries of the upper coast (shrimp statistical subareas 17–18) and lower coast (subareas 19–21), and ten depth intervals of the northwestern Gulf of Mexico (see Kutkuhn, 1962; Patella, 1975).

Materials and methods

A data set (subareas 17–21) containing 2,445 sea turtle records was obtained from the Sea Turtle Stranding and Salvage Network (STSSN) headquarters, National Marine Fisheries Service (NMFS) Miami Laboratory, Miami, Florida. It contained records not only of sea turtle strandings but also of turtles caught or entangled in commercial and recreational fishing gears.

Stranded sea turtles, whether live or dead, exhibit no known external or internal signs of capture in shrimp trawls. To our knowledge, only mark-recapture studies have provided direct evidence that some tagged sea turtles captured incidentally in shrimp trawls have become stranded (e.g. Manzella et al., 1988; Fontaine et al., 1989). When examination of stranded sea turtles provides evidence of other causes of death, then capture in shrimp trawls may be ruled out; however, the remaining strandings still lack definite explanation. Strandings that had no explanation were the focus of our analyses.

Prior to our analyses, we deleted 890 records (419 from 1986 to 1989 and 471 from 1990 to 1993) based on codes in data fields named LAT, LONG, NOTE1, NOTE2,... NOTE6, HEADSTART, and TYPEREP (Table 1). The following categories of records were deleted:

[1] Weber, M., D. Crouse, R. Irvin, and S. Indicello. 1995. Delay and denial: a political history of sea turtles and shrimp fishing, 46 p. Center for Marine Conservation, 1725 DeSales St. NW. No. 500, Washington, D.C., 20036.

[2] Crouse, D. T., M. Donnelly, M. J. Bean, A. Clark, W. R. Irvin, and C. E. Williams. 1992. The TED experience: claims and reality, 17 p. A report by the Center for Marine Conservation, Environmental Defense Fund, and National Wildlife Federation. Center for Marine Conservation, 1725 DeSales St. NW, No. 500, Washington, D.C., 20036

Table 1

Frequencies of codes in data fields NOTE1–NOTE6, HEADSTART, TYPEREP, LONG and LAT of records deleted from the STSSN data for shrimp statistical subareas 17–21 and years 1986–93 prior to correlation analyses.[1]

Field	Code	Description	Frequency
NOTE1–NOTE6			
	01	Caught on hook and line	77
	02	Found in dredge hopper	0
	06	Power plant entrapment	3
	08	Cold stun related	69
	11	Entangled in fishing line	13
	13	Entangled in fishing net	4
	15	Found trapped in sunken wreckage	0
	18	Apparent propeller wounds, probably boat strike	53
	22	Caught in shrimp trawl	19
	24	Hook in mouth	17
	28	Entangled in debris, entangled on reef	0
	29	Rope tied to flipper(s) or neck, or both, or to body	13
	36	Emaciated	8
	40	NMFS Galveston Laboratory head-start	261
	41	Nature of wounds suggests entanglement in gill net, net of unknown type, trap line of unknown type, or line of unknown type	2
	43	Nature of wounds suggests bang stick	0
	44	Skull or head only	7
	45	Florida Department of Natural Resources head-start	2
	46	Butchered	6
	48	Entangled in a nonfishing gear medium	17
	51	Caught in a set net	0
	54	Blow to skull	1
	55	Live, adult turtle found flipped on beach	2
	56	Entangled in crab or lobster trap line	0
	58	Caught on trot line	1
	59	Caught in gill net	3
	60	Caught in fish trap	0
	61	Caught in fishing net of unknown type	0
	62	Miami Seaquarium head-start	0
	63	Caught in trawl not targeting shrimp	0
	64	Caught in cast net	0
	65	Catch method unknown	2
	68	Caught in drift net	0
	70	Posthatchling young of the year	165
	73	Nesting female, butchered apparently for eggs	0
	76	Stingray barb embedded in flesh or carapace	0
	80	Nature of wounds suggests crab or lobster trap line entanglement	0
	81	Living tag or apparent living tag noted	42
	82	Spear gun wounds	0
	83	Guts or part(s) only, probable butchering	0
	84	Apparent natural mortality in adult female on a nesting beach	0
	87	Guts or part(s) only, cause unknown	4
	88	Possible boat collision, but not from propeller	1
	90	Constriction wounds or marks on flippers or neck	6
	93	Caught in pound net	0
	95	Monofilament or steel line protruding from mouth or cloaca	1
	96	Probable dredge kill	1
	99	Additional tags applied this capture	0
	AE	Hook in flipper or other soft body part, but not in mouth	7
	AF	Monofilament line found in digestive tract upon necropsy or X-ray	2
	AG	Turtle has tag; number was not recorded	1
	AH	Caught in try net	1
	AI	Fishing hook(s) found in digestive tract upon necropsy or X-ray	9
	AJ	Binary coded internal tag verified	1
	AN	Caught in seine net	1
	AO	Caught in abandoned gear	1
	AP	Entangled in rope (not deliberately tied)	5
	AR	Apparent gaff or hook wounds	0
	AV	Caught on long-line	0
	AX	Found trapped in jetty rocks	2
	AZ	Hatchling found in stomach of predator	1
	BB	TED test turtle (captive-reared)	0
HEADSTART			
	H	Head-started Kemp's ridleys or greens	261
	T	Loggerheads captive-reared for TED certification trials	2
TYPEREP			
	I	Incidental catch or capture	109
LONG		East of longitude 93°07'30"W	8
LAT		South of latitude 26°00'00"N	17

[1] The frequencies in this table represent the number of records bearing a particular code, among the 890 records that were deleted. Therefore, the frequencies do not sum to the total records deleted. Zero frequency indicates that no records containing the code were found among the 2,445 records examined, but it was not known, a priori, that these codes were not represented in the data set.

- turtles that occurred south of subarea 21 (south of latitude 26°00'00"N), because they had been assigned erroneously to subarea 21 (Fig. 1);
- turtles that occurred along the coastline of subarea 17, east of longitude 93°07'30"W, which is near the mouth of the Mermentau River (Fig. 1), because access to it by the STSSN was limited by logistics (Caillouet et al., 1991);
- turtles reported as caught or entangled, either intentionally or incidentally, in commercial (including shrimp trawls) or recreational fishing gears;
- head-started turtles (identified by tags; see

Fontaine et al., 1993), because their temporal-spatial distribution was determined in part by when and where they were released (Manzella et al., 1988; Caillouet et al., 1995);

- small, pelagic-stage turtles, because they were not considered vulnerable to incidental capture in trawls;
- strandings for which likely or possible causes had been assigned.

In some cases, particular codes that defined records to be deleted did not occur among the 2,445 records examined (i.e. they had zero frequency, Table 1), but this was not known a priori. The 1,555 records (937 from 1986–89 and 618 from 1990–93) retained for analysis represented strandings of wild sea turtles for which no known or likely cause of mortality had been assigned. As a consequence of more stringent deletion criteria, our re-analyses for 1986–89 were based on 111 fewer sea turtle records than were the analyses of Caillouet et al. (1991).

For each year, monthly sea turtle strandings (species combined, including those identified to species as well as those not identified to species) were summed over subareas within the upper and lower coasts. This produced 96 observations of monthly sea turtle strandings (2 geographic zones × 4 years × 12 months). Each observation was standardized to S, the monthly number of strandings per 100 km of accessible shoreline bordering the Gulf, which was a measure of sea turtle stranding rate.

A set of offshore, monthly shrimp fishing effort (days fished) data for subareas 17–21 during 1986–93 was obtained from the NMFS Galveston Laboratory (Patella[3]). It was not possible to partition shrimp fishing effort within subarea 17 into portions east and west of longitude 93°07'30"W; therefore the eastern boundary of subarea 17 (Fig. 1) marked the eastern boundary of the upper coast in regard to fishing effort. The total fishing effort at depths seaward of 30 fm (54.9 m) represented less than 8% of the total fishing effort in 1986–89 and 1990–93 on the upper and lower coasts (Table 2), but we included depth intervals seaward of 30 fm for comparison with shallower intervals. For 1986–89 and 1990–93, monthly fishing effort was summed over subareas within the upper and lower coasts, by depth interval (0–5, 5–10, ... >45 fathoms; see Kutkuhn, 1962; Patella, 1975). This produced 960 observations of monthly fishing effort (2 geographic zones × 10 depth intervals × 4 years × 12 months). Each observation was standardized to E, the monthly fishing effort per 100 km^2, which was a measure of fishing intensity.

[3] Patella, F. 1994. Galveston Laboratory, Southeast Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, 4700 Ave. U, Galveston, TX 77551-5997. Personal commun.

Table 2

Percentage of shrimp fishing effort (days fished), total shrimp fishing effort, total catch (pounds of shrimp tails), and pounds caught per unit fishing effort on the upper and lower coasts of the northwestern Gulf of Mexico in 1986–89 and 1990–93, by depth interval.[1]

Depth interval		1986–89		1990–93	
(fm)	(m)	Upper Coast[2]	Lower Coast[3]	Upper Coast[2]	Lower Coast[3]
0–5	0.0–9.1	28.3	5.1	21.4	3.3
5–10	9.1–18.3	27.1	13.2	33.9	11.5
10–15	18.3–27.4	16.2	20.4	6.2	23.5
15–20	27.4–36.6	9.8	25.5	24.9	22.9
20–25	36.6–45.7	6.6	17.9	4.8	16.8
25–30	45.7–54.9	5.7	10.0	6.8	14.8
30–35	54.9–64.0	4.4	5.5	1.4	5.6
35–40	64.0–73.2	1.6	1.9	0.4	1.3
40–45	73.2–82.3	0.3	0.4	0.2	0.3
>45	>82.3	0.1	0.1	0.1	0.0
Total fishing effort		150,229	225,427	144,734	210,710
Total pounds caught		75,346,306	103,309,240	65,789,423	108,365,720
Pounds per unit fishing effort		502	458	455	514

[1] Based on data provided by Frank Patella (see Footnote 3 in the text).
[2] Shrimp statistical subareas 17 and 18 (Fig. 1; see Kutkuhn, 1962).
[3] Shrimp statistical subareas 19–21 (Fig. 1; see Kutkuhn, 1962).

Because some observations of S and E were equal to 0 and the data required logarithmic transformation to assure bivariate normality for correlation analyses, 1 was added to all observations of S and E. Tables 3 and 4 show that $\ln(S + 1)$ and $\ln(E + 1)$ had lower coefficients of skewness and kurtosis (both approaching zero) than did S and E, indicating that the log-transformed variables approached normality, whereas the nontransformed variables were not normally distributed.

Forty product-moment correlations (2 periods × 2 geographic zones × 10 depth intervals) between the paired variables $\ln(S + 1)$ and $\ln(E + 1)$ were calculated, each based on 48 observations (12 months × 4 yr) within a depth interval. These correlations were not statistically independent of each other, because each was based on one set of 48 observations of $\ln(S + 1)$ correlated with each of ten sets of 48 observations of $\ln(E + 1)$. Significant, positive correlations detected between $\ln(S + 1)$ and $\ln(E + 1)$ were tested for homogeneity by using chi-square. Finally, 140 product-moment correlations (2 periods × 2 geographic zones × 35 correlations) between pairs of $\ln(E + 1)$ for the ten depth intervals were calculated, each based on 48 observations. These correlations were statistically independent of each other.

Results

Ten significant positive correlations (i.e. correlation coefficients, r, greater than 0 at $P < 0.05$) were detected between the $\ln(S + 1)$ and $\ln(E + 1)$, half of them in 1986–89 (Fig. 2) and the other half in 1990–93 (Fig. 3). These ten correlations involved $\ln(E + 1)$ for some of the depth intervals between 0 and 20 fm

Table 3

Descriptive statistics for S, E, $\ln(S + 1)$, and $\ln(E + 1)$ for the upper and lower coasts of the northwestern Gulf of Mexico during 1986–89.

	S		E		$\ln(S + 1)$		$\ln(E + 1)$	
	Upper	Lower	Upper	Lower	Upper	Lower	Upper	Lower
n	48	48	480	480	48	48	480	480
Mean	3.98	2.72	9.02	12.51	1.09	1.10	1.57	2.01
Variance	40.62	8.87	340.25	283.53	0.91	0.39	1.32	1.39
Skewness coefficient	2.67	2.27	5.33	4.75	0.72	0.69	0.39	–0.27
Kurtosis coefficient	7.72	5.56	35.50	38.77	–0.27	0.31	–0.25	–0.77
Minimum	0.0	0.0	0.0	0.0	0.00	0.00	0.00	0.00
Maximum	30.7	14.4	170.0	197.4	3.46	2.74	5.14	5.29

Table 4

Descriptive statistics for S, E, $\ln(S + 1)$, and $\ln(E + 1)$ for the upper and lower coasts of the northwestern Gulf of Mexico during 1990–93.

	S		E		$\ln(S + 1)$		$\ln(E + 1)$	
	Upper	Lower	Upper	Lower	Upper	Lower	Upper	Lower
n	48	48	480	480	48	48	480	480
Mean	2.86	1.67	8.06	11.05	1.12	0.84	1.31	1.76
Variance	8.07	2.72	356.92	201.81	0.48	0.26	1.44	1.63
Skewness coefficient	1.47	1.92	5.24	1.76	0.20	0.69	0.81	0.05
Kurtosis coefficient	1.87	4.18	35.38	2.95	–0.80	0.02	–0.03	–1.24
Minimum	0.0	0.0	0.0	0.0	0.00	0.00	0.00	0.00
Maximum	11.3	8.1	195.4	77.0	2.51	2.21	5.28	4.36

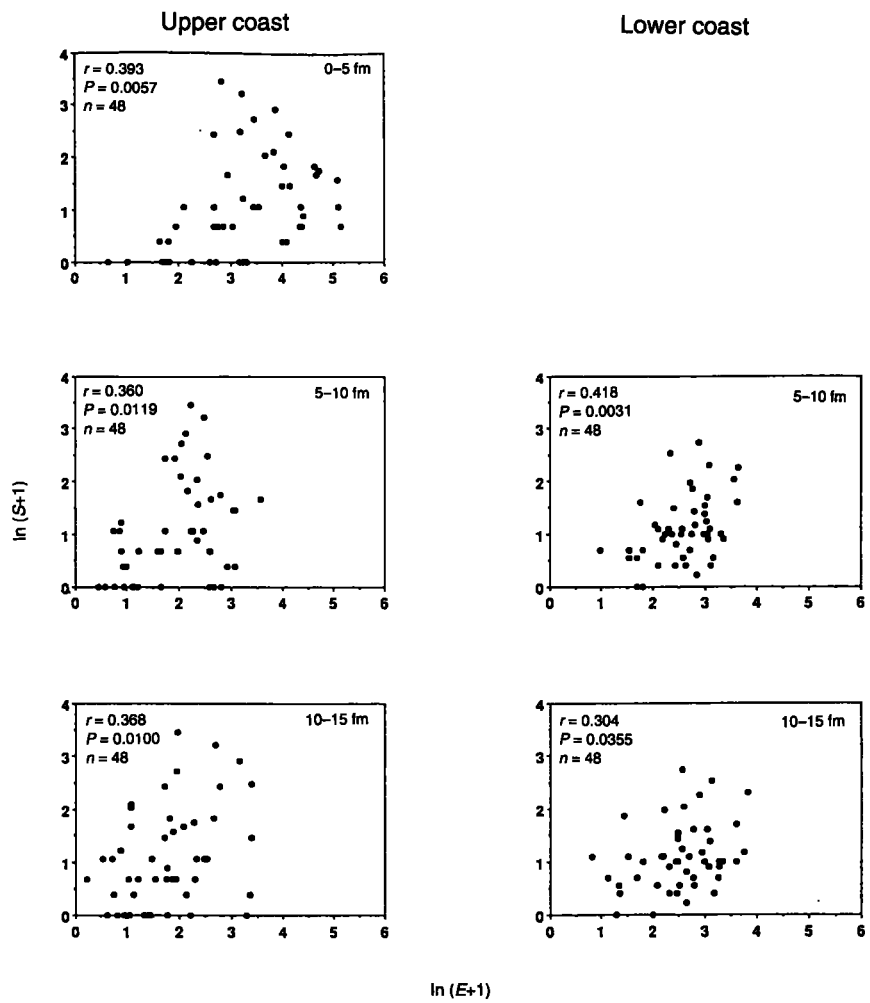

Figure 2

Scatter plots for significant (P<0.05), positive correlations between ln(S + 1) and ln(E + 1) on the upper coast (shrimp statistical subareas 17–18) and lower coast (subareas 19–21) of the northwestern Gulf of Mexico during 1986–89.

(36.6 m), suggesting that sea turtle stranding rates increased as fishing intensities increased in these depth intervals. The null hypothesis of homogeneity among the ten correlations was not rejected (χ^2=9.5, P >0.05), showing that the correlations did not differ significantly from one another. Thus, the null hypothesis that the statistical relationship between monthly sea turtle stranding rates and shrimp fishing intensities in the northwestern Gulf was the same in 1990–93 as in 1986–89 could not be rejected.

Four significant negative correlations between ln(S + 1) and ln(E + 1) were also detected for depth intervals seaward of 20 fm. Two occurred on the upper coast, one in 1986–89 for ln(E + 1) in >45 fm (r=–0.358, P=0.0125), and one in 1990–93 for ln(E + 1) in the 35–40 fm depth interval (r=–0.334, P=0.0203). Two occurred on the lower coast in 1986–89, one for ln(E + 1) in the 20–25 fm depth interval (r=–0.431, P=0.0022), and the other in the 25–30 fm depth interval (r=–0.308, P=0.0332).

A temporal-spatial pattern in monthly fishing intensities was evident from the correlations involving the ln(E + 1) of the ten depth intervals (Tables 5–8). Significant correlations between the ln(E + 1) of adjacent depth intervals tended to be positive, showing that monthly fishing intensities in such depth intervals increased or decreased in synchrony. Conversely, monthly fishing intensities in widely separated depth intervals varied in opposite directions, as indicated by significant negative correla-

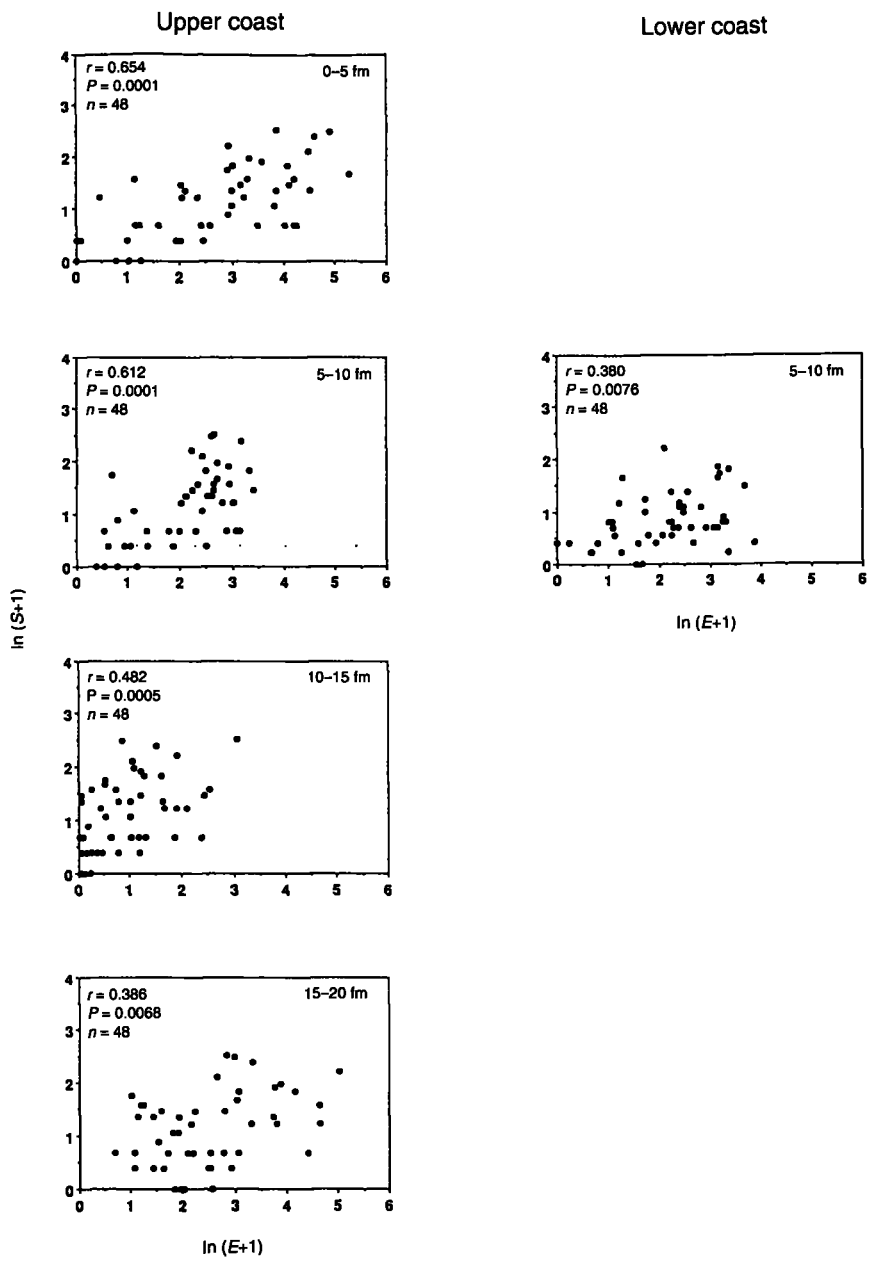

Figure 3

Scatter plots for significant ($P<0.05$), positive correlations between $\ln(S + 1)$ and $\ln(E + 1)$ on the upper coast (shrimp statistical subareas 17–18) and lower coast (subareas 19–21) of the northwestern Gulf of Mexico during 1990–93.

tions. Intermediate depth intervals represented a transition zone, as depicted by a general absence of significant correlations of $\ln(E + 1)$ between these depth intervals and either the shallower or deeper intervals.

In 1986–89 and 1990–93, loggerhead sea turtles, *Caretta caretta,* and Kemp's ridley sea turtles, *Lepidochelys kempii,* occurred most frequently in the strandings, followed by green sea turtles, *Chelonia mydas,* and leatherback sea turtles, *Dermochelys coriacea* (Tables 9 and 10). Strandings of hawksbill sea turtles, *Eretmochelys imbricata,* were equal in number to those of leatherback turtles in 1986–89 (Table 9), but fewer in number than leatherback turtles in 1990–93 (Table 10). Monthly strandings

summed over 1986–89 were highest in April and May (Table 9). Monthly strandings summed over 1990–93 were highest in April and July (Table 10). The total number of strandings decreased from 939 in 1986–89 to 618 in 1990–93.

Discussion

Even though TED regulations were in effect during 1990–93, significant statistical associations continued to exist between sea turtle stranding rates and fishing intensities in some offshore depth intervals within 0 to 20 fm. The 1990–93 period differed somewhat from the 1986–89 period with regard to which depth intervals had significant positive correlations. In 1986–89, significant positive correlations between $\ln(S + 1)$ and $\ln(E + 1)$ were detected on the upper coast only for the 0–5, 5–10, and 10–15 fm depth intervals. However, in 1990–93 on the upper coast, not only were there significant positive correlations for the 0–5, 5–10, and 10–15 fm depth intervals, but also for the 15–20 fm depth interval. On the lower coast, in 1986–89, significant positive correlations occurred between $\ln(S + 1)$ and $\ln(E + 1)$ for the 5–10 and 10–15 fm depth interval, but in 1990–93 only the 5–10 fm depth interval had a significant positive correlation. In addition, the significant positive correlations we detected for the period 1986–89 were somewhat lower (though not significantly) than the comparable ones detected by Caillouet et al. (1991), no doubt the result of excluding 111 more records from the data set, than they did, before conducting our analyses.

Table 5

Correlation coefficients, r, measuring the associations between the $\ln(E + 1)$ of ten depth intervals on the upper coast during 1986–89.

Depth interval	Depth interval (fm)								
	0–5	5–10	10–15	15–20	20–25	25–30	30–35	35–40	40–45
5–10	0.723*[1]								
10–15	0.497*	0.678*							
15–20	0.548*	0.508*	0.679*						
20–25	0.312*	0.237	0.447*	0.695*					
25–30	0.165	0.000	0.304*	0.319*	0.645*				
30–35	–0.142	–0.472*	–0.281	–0.217	–0.168	0.510*			
35–40	–0.447*	–0.505*	–0.300*	–0.276	–0.115	0.256	0.433*		
40–45	–0.372*	–0.459*	–0.213	–0.267	0.010	0.148	0.365*	0.491*	
>45	–0.492*	–0.549*	–0.290*	–0.160	–0.025	–0.162	0.154	0.340*	0.588*

[1] An asterisk indicates that the correlation coefficient, r, was significantly different from zero at $P < 0.05$.

Table 6

Correlation coefficients, r, measuring the associations between the $\ln(E + 1)$ of ten depth intervals on the lower coast during 1986–89.

Depth interval	Depth interval (fm)								
	0–5	5–10	10–15	15–20	20–25	25–30	30–35	35–40	40–45
5–10	0.151								
10–15	0.175	0.379*[1]							
15–20	0.375*	0.147	0.585*						
20–25	0.271	0.108	0.102	0.718*					
25–30	–0.050	0.281	–0.087	0.260	0.629*				
30–35	–0.176	0.116	–0.316*	–0.200	0.138	0.600*			
35–40	–0.143	–0.016	–0.272	–0.445*	–0.387*	0.100	0.447*		
40–45	–0.162	–0.121	–0.251	–0.373*	–0.460*	–0.112	0.317*	0.662*	
>45	0.031	0.040	–0.132	–0.278	–0.393*	–0.053	0.168	0.460*	0.580*

[1] An asterisk indicates that the correlation coefficient, r, was significantly different from zero at $P < 0.05$.

The statistical relationship between stranding rates and fishing intensities persisted despite our using more stringent criteria than did Caillouet et al. (1991) to exclude from the analyses strandings to which possible causes had been assigned. In the absence of significant heterogeneity among the significant positive correlation coefficients, the null hypothesis could not be rejected. Therefore, there was no significant change in the degree of statistical association between sea turtle stranding rates and fishing intensities for some offshore depth intervals within 0 to 20 fm, despite TED regulations, nor was there a significant difference in the degree of this association between the upper and lower coasts.

In 1990–93, as in 1986–89, there was a significant positive correlation between $\ln(S + 1)$ and $\ln(E + 1)$ within 0–5 fm on the upper coast, but not on the lower coast. Depth increases more rapidly with distance from shore on the lower than on the upper coast (Fig. 1). In addition, shrimp move to deeper waters as they migrate southward along the Texas coast each year, accompanied by a corresponding concentration of the shrimping fleet in areas of shrimp abundance. A smaller percentage of fishing effort occurred in the 0–5 fm depth interval on the lower coast than on the upper coast (Table 2).

The significant negative correlations detected between $\ln(S + 1)$ and $\ln(E + 1)$ for some depth intervals seaward of 20 fm probably resulted from a tendency for fishing effort to be concentrated seasonally within certain depth intervals. The pattern of correlations involving fishing intensities in various

Table 7

Correlation coefficients, r, measuring the associations between the $\ln(E + 1)$ of ten depth intervals on the upper coast during 1990–93.

Depth interval	Depth interval (fm)								
	0–5	5–10	10–15	15–20	20–25	25–30	30–35	35–40	40–45
5–10	0.594*[1]								
10–15	0.393*	0.453*							
15–20	0.299*	0.572*	0.528*						
20–25	0.095	0.165	0.153	0.295*					
25–30	–0.100	0.197	–0.048	0.038	0.629*				
30–35	–0.083	–0.135	–0.201	–0.086	0.289*	0.346*			
35–40	–0.416*	–0.314*	–0.390*	–0.255	0.005	0.209	0.109		
40–45	–0.232	–0.179	–0.433*	–0.136	–0.057	0.052	0.174	0.335*	
>45	–0.049	–0.092	0.225	0.001	0.109	0.238	0.117	0.011	–0.029

[1] An asterisk indicates that the correlation coefficient, r, was significantly different from zero at $P < 0.05$.

Table 8

Correlation coefficients, r, measuring the associations between the $\ln(E + 1)$ of ten depth intervals on the lower coast during 1990–93.

Depth interval	Depth interval (fm)								
	0–5	5–10	10–15	15–20	20–25	25–30	30–35	35–40	40–45
5–10	0.550*[1]								
10–15	0.520*	0.838*							
15–20	0.433*	0.636*	0.667*						
20–25	0.238	0.320*	0.439*	0.796*					
25–30	0.130	0.287*	0.347*	0.604*	0.791*				
30–35	–0.305*	–0.234	–0.096	–0.053	0.082	0.389*			
35–40	–0.330*	–0.129	–0.002	–0.202	–0.129	0.196	0.731*		
40–45	–0.256	–0.210	–0.096	–0.231	–0.269	0.026	0.515*	0.668*	
>45	0.117	0.114	0.085	0.145	0.142	0.229	0.266	0.282	0.165

[1] An asterisk indicates that the correlation coefficient, r, was significantly different from zero at $P < 0.05$.

Table 9

Numbers of sea turtle strandings in the northwestern Gulf of Mexico by species and month, summed over years 1986–89.[1]

Species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Loggerhead (*Caretta caretta*)	9	9	42	144	94	30	41	34	26	24	17	19	489
Kemp's ridley (*Lepidochelys kempii*)	0	6	32	81	47	37	23	44	23	21	15	10	339
Green (*Chelonia mydas*)	0	0	5	7	6	6	1	1	0	3	1	3	33
Leatherback (*Dermochelys coriacea*)	0	0	0	6	4	3	0	1	0	1	3	0	18
Hawksbill (*Eretmochelys imbricata*)	0	1	2	0	1	3	1	1	3	2	2	2	18
Undetermined	0	0	6	6	2	5	8	3	4	4	0	2	40
Total	9	16	87	244	154	84	74	84	56	55	38	36	937

[1] After some records were deleted (see Table 1).

Table 10

Numbers of sea turtle strandings in the northwestern Gulf of Mexico by species and month, summed over years 1990–93.[1]

Species	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Loggerhead (*Caretta caretta*)	8	11	27	50	16	8	48	30	22	15	16	31	282
Kemp's Ridley (*Lepidochelys kempii*)	5	2	18	38	20	17	44	34	38	22	22	11	271
Green (*Chelonia mydas*)	0	2	4	5	2	1	2	1	3	1	2	1	24
Leatherback (*Dermochelys coriacea*)	0	0	0	5	5	2	3	0	0	0	0	0	15
Hawksbill (*Eretmochelys imbricata*)	0	1	0	0	1	1	1	0	2	1	2	0	9
Undetermined	0	0	0	2	2	1	2	0	3	5	0	2	17
Total	13	16	49	100	46	30	100	65	68	44	42	45	618

[1] After some records were deleted (see Table 1).

depth intervals suggested that monthly fishing intensities in contiguous depth intervals increase or decrease in the same direction. This pattern also suggests that monthly fishing intensities are high in deeper waters when they are low in shallower waters, and vice versa, probably in association with the seasonal migrations of shrimp and the fishing fleet (Tables 5–8). Thus, when fishing intensities in depth intervals between 0 and 20 fm were positively associated with strandings, the fishing intensities seaward of 20 fm were low, producing inverse associations with stranding rates.

The pattern of correlations between the $\ln(E + 1)$ of the various depth intervals may have influenced the correlations between $\ln(S + 1)$ and $\ln(E + 1)$. Some of the significant positive correlations detected between $\ln(S + 1)$ and $\ln(E + 1)$ may have resulted from correspondences between stranding rates and fishing intensities, whereas others may have been coincidental. Our analyses determined only that there were significant positive correlations between $\ln(S + 1)$ and $\ln(E + 1)$, but they cannot prove there was a cause and effect relationship between fishing intensities and stranding rates. On the other hand, our results would be consistent with a cause and effect relationship. Although the positive correlations we detected were not significantly heterogeneous, they did tend to decrease in strength with depth, which may suggest a decreasing degree of statistical association between stranding rates and fishing intensities as depth increases. This tendency also could occur if sea turtles injured or killed in deeper waters were less likely to wash ashore than those injured or killed closer to the shoreline (Caillouet et al., 1991).

The significant positive correlations we detected between $\ln(S + 1)$ on $\ln(E + 1)$ were circumstantial evidence of a relation between sea turtle stranding rates and shrimp fishing intensities, but they did not demonstrate that shrimping caused the strandings. Nevertheless, they were consistent with previous findings that sea turtles are caught and killed incidentally in shrimping (National Research Council,

1990) and that some turtles incidentally caught during shrimping operations become stranded (Manzella et al., 1988; Fontaine et al., 1989). The surprising aspect of our findings comes from the expectation that TED regulations would lead to a reduction or elimination of the statistical association between sea turtle stranding rates and fishing intensities in the northwestern Gulf. To explain this continued statistical association, we offer the following hypotheses:

1 legal and properly installed TED's failed to eject all of the sea turtles caught incidentally in shrimp trawls;
2 sea turtles were captured and ejected repeatedly from trawls containing legal and properly installed TED's, and eventually succumbed to the stresses of repeated passage through such trawls;
3 sea turtles were captured incidentally in shrimpers' try nets that had no TED's;
4 violations of TED regulations resulted in incidental capture of sea turtles;
5 nonshrimping causes of sea turtle mortality were in synchrony with shrimping effort.

Legal and properly installed TED's may have failed to eject all of the sea turtles caught incidentally in shrimp trawls (hypothesis 1). Prior to June 1994, supporting floats were not required on bottom-opening hard TED's (Mitchell[4]). Tests by NMFS showed that use of such legal TED's without floats could result in sea turtle mortality (Mitchell[4]). Therefore, NMFS issued new rules to ensure sea turtle escape. Other NMFS studies have shown that sea turtles are sometimes caught in TED-equipped shrimp trawls (Renaud et al., 1990, 1991; Epperly et al., 1995). Each type of TED certified for use by the shrimp industry has been tested under an established scientific protocol (Federal Register, vol. 55, no. 195, p. 41882–41883, 9 October 1990). NMFS-certified TED's that were properly installed and "tuned" (adjusted) were required to be no less than 97% effective in ejecting incidentally captured sea turtles. The actual rate of ejection could vary below 97% under less than ideal shrimp trawling conditions.

There is no evidence that individual sea turtles were captured and ejected repeatedly from certified, properly installed TED's during commercial shrimp trawling operations (hypothesis 2). If they had been, they would have undergone repeated stress. To determine whether sea turtles are captured and ejected repeatedly from TED's during commercial trawling operations, underwater observations would be required and the sea turtles would have to be marked for repeated recognition. During TED certification trials conducted near Panama City, Florida, Kemp's ridley turtles, released into TED-equipped shrimp trawls and submerged for less than 8 min before ejection and surfacing, developed blood acidosis. The acidosis was, for the most part, metabolic (caused by accumulation of lactate) and to a lesser degree respiratory (caused by accumulation of CO_2)(Stabenau et al., 1991). The turtles released excess CO_2 when they hyperventilated after surfacing (Stabenau et al., 1991). Other research showed that at least 20 h were required for complete recovery from lactate acidosis in loggerhead sea turtles caught in shrimp trawls during sea turtle surveys in Port Canaveral Ship Channel, Florida (Lutz and Dunbar-Cooper, 1987). It is doubtful that a sea turtle in a state of severe blood acid-base disequilibrium, resulting from submergence and struggling to escape a shrimp trawl, would dive soon after release from a TED (Stabenau[5]). If it dived, the blood acidosis would be exacerbated. On the other hand, if the turtle remained at or near the surface it could take frequent breaths and recover from the acid-base disturbance. As standard practice, sea turtles submerged in shrimp trawls for less than 10 minutes during TED certification trials are allowed at least 48 h of recovery before being submerged in a second test (Fontaine[6]).

Sea turtles may have been captured incidentally in shrimpers' try nets (hypothesis 3) within which TED's were not required. Even though these small trawls are towed for relatively brief intervals, direct observations aboard shrimp trawlers have shown that sea turtles are caught incidentally in try nets (Renaud et al., 1990, 1991; Mitchell[4]).

Violations of TED regulations have been shown to result in incidental capture of sea turtles in shrimp trawls (hypothesis 4). For example, unprecedented numbers of sea turtles were stranded in Louisiana in 1993 and in Texas in 1994 and 1995, concomitant with concentrations of shrimp trawling. These stranding events were attributed, at least in part, to violations of TED regulations, including, but not limited to, various illegal alterations of TED's (Crouse, 1993a; Shaver, 1994, 1995; Steiner, 1994; Shrimp Trawling in the Southeastern United States Under the Sea Turtle Conservation Regulations, Endan-

[4] Mitchell, J. 1995. Pascagoula Laboratory, Southeast Fish. Sci. Cent., Natl. Mar. Fish. Serv., NOAA, P.O. Drawer 1207, Pascagoula, MS 39568-1207. Personal commun.

[5] Stabenau, E. 1994. Department of Physiology, School of Medicine, East Carolina University, Greenville, NC 27858-4354. Personal commun.

[6] Fontaine, C. 1995. Galveston Laboratory, Southeast Fish. Sci. Cent., Natl. Mar. Fish. Serv, NOAA, 4700 Ave. U, Galveston, TX 77551-5997. Personal commun.

gered Species Act, Section 7 Consultation, Biological Opinion, NMFS, 14 November 1994; Mitchell[4]). As a consequence, NMFS developed an Emergency Response Plan (Federal Register, vol. 60, no. 77, p. 19885–19886, 21 April 1995; Federal Register, vol. 60, no. 85, p. 21741–21745, 3 May 1995). This plan, a resurgence of sea turtle strandings along the Texas coast during the spring 1995 shrimping season (Shaver, 1995), and an ensuing ruling by Judge Samuel B. Kent (*Center for Marine Conservation vs. Brown*, C.V. No. G-94-660, U.S. District Court, Galveston, Texas) led to additional TED restrictions on shrimping seaward to 12 nautical miles.

There is little evidence to support hypothesis 5, that causes of strandings other than incidental capture of sea turtles in shrimp trawls were in synchrony with shrimping. It seems unlikely that a major nonshrimping cause of sea turtle mortality has escaped detection during the many years of study of factors causing sea turtle injury and mortality at sea (National Research Council, 1990; Kemp's Ridley Recovery Team[7]). Prior to our analyses, we deleted stranding records that represented known or likely causes (Table 1), even when some of these causes did not absolutely rule out incidental capture in shrimp trawls (Table 1). The records retained for analysis represented strandings for which no cause was known. Nevertheless, it is possible that causes other than shrimping contributed to the unexplained strandings that were retained for our analyses, because it is known that there are other minor causes of sea turtle mortality, some of which could have been in synchrony with shrimping.

The lower total number of strandings in the northwestern Gulf in 1990–93 as compared with 1986–89 (Tables 9 and 10) would be encouraging were it not for differences in STSSN coverage in 1990–93 and 1986–89. Schroeder (1989), Whistler (1989), and the National Research Council (1990) pointed out that temporal–spatial coverage of sea turtle strandings is rarely uniform because the STSSN depends for the most part on volunteers. During 1986–89, to supplement the efforts of volunteers, universities, and other agencies (Texas A&M University, the University of Texas, National Park Service, U.S. Fish and Wildlife Service, and Texas Parks and Wildlife Department), NMFS Galveston Laboratory personnel conducted systematic surveys at least once a month along accessible shorelines of beaches bordering the Gulf from the Mermentau River to the Rio Grande (Caillouet et al., 1991). During 1990–93, personnel at Galveston Laboratory focused their coverage only on subarea 18 during March–November; STSSN coverage in other areas of the northwestern Gulf in those years depended more on volunteers, universities, and other agencies than was the case in 1986–89. Therefore, the decrease in total number of strandings might have occurred because of a reduction in STSSN coverage, but the mandatory use of TED's and the decrease in total shrimp fishing effort, both on the upper and lower coasts (Table 2), cannot be ignored as possible contributing factors. The statistical association between stranding rates and fishing intensities persisted in 1990–93 despite the reduction in total strandings. It is essential that STSSN coverage of strandings be consistent, both spatially and temporally, to provide data sufficient to assess real trends in sea turtle strandings and to determine their relationship to natural as well as anthropogenic causes.

The statistical association between sea turtle stranding rates and shrimp fishing intensities in the northwestern Gulf is worthy of concern and further attention. Continued strandings of sea turtles demonstrate that the problem of sea turtle mortality at sea has not been solved (Henwood et al., 1992; Shaver, 1994, 1995). It is clear that further efforts will be necessary to solve this problem and thereby speed the recovery of sea turtle populations. Those efforts must include reduction or elimination of human-caused sea turtle mortality at sea (National Research Council, 1990; Henwood et al., 1992).

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Barotrauma-associated regurgitation of food: implications for diet studies of Hawaiian pink snapper, *Pristipomoides filamentosus* (family Lutjanidae)

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Abstract.—Juvenile (128–244 mm fork length) pink snapper, *Pristipomoides filamentosus*, were caught by hook and line from 60–90 m depths offshore of Kaneohe Bay, windward Oahu, Hawaii, during February–August 1994. About one-half of the 180 specimens were intercepted by scuba divers 15–18 m below the sea surface and individually "bagged" live before they were retrieved for the remaining distance to the surface. The other half were retrieved directly by fishing line to the surface ("unbagged"); these latter fish thus remained at a continual risk of prey loss from regurgitation while they were stressed by the full extent of pressure change. The retained stomach contents of bagged and unbagged fish were compared on the basis of volume and type of food and on the size of individual prey items. Bagged samples of juvenile snapper on average retained a 116% (95% CI=70–157%) greater volume of prey than unbagged snapper; bagged snapper also had more types and greater maximum body sizes of prey than did unbagged fish. These results are discussed in terms of designing quantitative diet studies for juvenile snapper and other deep-water physoclistous fishes.

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The diet and feeding habits of deep-water physoclistous fishes are usually described by using fish collected with gears (hook and line, set lines, trawls, nets, traps) that subject specimens to the stress of large reductions in ambient pressure (barotrauma) as they are retrieved. Numerous studies have derived estimates of stomach fullness, prey consumption or daily ration, and gastric evacuation rates (reviewed by Bromley, 1994) based on collections that include or exclude specimens with empty stomachs. Often overlooked is the distinction between naturally occurring empty stomachs and stomachs that have partially or totally everted their contents as a result of swimbladder expansion during gear retrieval or other procedures of capture (Kohler and Fitzgerald, 1969; Daan, 1973; Durbin et al., 1983; Rice, 1988; Hislop et al., 1991).

The Hawaiian pink snapper or "opakapaka" (*Pristipomoides filamentosus*) represents a major portion of the deep-slope (150–300 m) bottomfishery in Hawaii (Haight et al., 1993a). Juveniles inhabit a shallower (60–90 m), relatively narrow depth zone on insular shelves (Parrish, 1989; Ellis and DeMartini, 1995; Moffitt and Parrish[1]) but, nonetheless, experience barotrauma during conventional collection procedures (Parrish and Moffitt, 1993). Juveniles are discontinuously distributed, and localized patches of occupied habitat have recently persisted for at least five consecutive years (1989–93; Parrish et al.[2]). One hypothesis for the persistence of these patches of juveniles is the localized distribution of prey, which in turn might reflect static substrate characteristics or recurrent patterns of near-bottom water movements. Testing such hypotheses requires describing the diet of juveniles as well as the distribution and availability of prey organisms.

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As part of our studies of the foraging and distribution of juvenile pink snapper, we have been developing methods to quantify stomach contents with acceptable accuracy and precision. In this paper we describe and evaluate a method of collecting juvenile snapper for diet analysis that minimizes the problem of subsurface regurgitation of food as specimens are retrieved from depth.

Methods

Fish collection

Juvenile snapper were caught by hook and line from near-bottom depths of 60–90 m, about 3–4 km offshore of Kaneohe Bay, windward Oahu, Hawaii, on nine dates during the period February–August 1994. All fish were captured between about 0900 and 1500 h. On each date, at 15–18 m below the sea surface, about one-half of all fish (randomly selected) were "bagged" by scuba divers (using NOAA NITROX II [64% N_2, 36% O_2] to extend diving periods approximately twofold at these depths). Divers observed fish—underwater visibilities consistently exceeded 30 m—as they were reeled up to 15–18 m and subsequently to the sea surface and noted whether specimens regurgitated food just before or during the bagging process; if they did regurgitate, these fish were left "unbagged" (see below). Median time for collection (1055 h) was the same for both bagged and unbagged fish. Bagged fish were sealed live in individually marked canvas bags before they were retrieved the remaining distance to the surface. The other half of the fish (unbagged) were brought directly to the surface by the fishing line. All fish were reeled in at a rate of about 30 m per minute (Haight et al., 1993b). Once aboard ship, unbagged fish were also packaged individually in marked canvas bags. Fish were stored on ice in a cooler until they were frozen intact in their marked bags at the NMFS Honolulu Laboratory, 2–8 h after capture.

Stomach content analyses

Each frozen fish was thawed, removed from its bag, and the bag everted in the laboratory. The external body surface of each specimen and the inside surface of the bag were rinsed into a black paraffin-bottom dissecting tray. Any prey fragments in the fluid were collected. Gill rakers, esophagus, and pharynx (including vomerine and jaw teeth) of the specimen were examined for prey. Ruptured swim bladders were noted, and extent of stomach eversion according to a stomach eversion index (EvI) was recorded (on a scale from 1 [not everted] to 2 [partially everted] to 3 [fully everted]). Fish were then measured (mm fork length [FL]). Lastly, the stomach was excised and its contents saved, along with any prey items that were free in the coelom as the result of stomach rupture. All prey (regurgitated and present in the stomach) were pooled. Prey were then blotted damp on a paper towel, and a displacement volume (0.01 mL) was measured. Stomachs and prey were fixed in 3.7% formaldehyde (sea water buffered) for 1–2 months, then preserved in 60% EtOH. The eviscerated wet weight (EW) of each snapper was recorded to the nearest gram.

Prey were examined under a dissecting microscope at 8–50×and classified (when possible) to the level of suborder or order. The length (longest axis) of each prey item was recorded to the nearest millimeter.

Identifiable prey were divided a priori into four major types (Bowen, 1983) on the basis of probable microhabitat: 1) crustaceans—mostly shrimps and stomatopods of indeterminate epibenthic or lower water column habitats; 2) benthos—primarily demersal octopods, echinoids, and microgastropods representing mobile epifauna; 3) nekton—actively swimming water column fishes and squids; and 4) jellies—weakly mobile, gelatinous salps and heteropods.

Statistics

A nonparametric bootstrapping procedure was used to evaluate mean prey volume in bagged versus unbagged fish because we were interested in quantifying the magnitude of possible differences in prey volume between the two treatments, even though sampling dates were too few to evaluate normality accurately. The variables used for bootstrapping (n=1,000 iterations; Manly, 1991) were 1) the differences between the date-specific mean prey volumes for bagged and unbagged fish. Because sampling design alone might have incompletely controlled for body size and date effects on prey volume, we further evaluated 2) the differences between predicted and observed prey volumes in unbagged snapper. Predicted values for unbagged fish were calculated on the basis of prey volumes measured for bagged fish of the same weight and date, because prey volumes were positively related to body weight for bagged snapper only (see Results section). Predicted values for bagged fish were derived from stepwise multiple regression of prey volume on sampling date and body weight. For both 1) and 2), date-means were weighted by the number of sample fish on that date.

Standard nonparametric tests (Siegel and Castellan, 1988; SAS, 1988: Proc NPAR1WAY, Proc FREQ)

were used to compare prey composition and prey size between bagged and unbagged fish. All tests were two-tailed (α=0.05). The Bonferroni correction (α'=0.05/m; Manly, 1991, p. 52) was used to control type-I error for m = 3, 2 × 2 chi-squared tests of presence or absence of prey types between treatments. Data were too few to analyze by separate chi-squared tests for each date. A three-way G-test was inappropriate for simultaneous comparisons of prey types because the occurrences of types were interdependent.

Results

Fish specimens

A total of 180 juvenile snapper (88 bagged, 92 unbagged) were collected on the nine sampling dates. From 5 to 40 specimens were collected per date (numbers of bagged and unbagged fish were <15% different on six of the last seven dates). Median size of fish was 176 mm FL (range 128–244 mm) and 98 g eviscerated weight (EW, range 36–289 g). No significant difference existed between bagged and unbagged fish, and growth was clearly evident over the sampling period (Table 1). Few bagged (n=3) and unbagged (n=3) snapper had ruptured swimbladders, and both bagged and unbagged fish had equivalently high indices of stomach eversion (Table 1). Four specimens had completely empty stomachs, and all were unbagged fish. Regurgitated prey were typically evident inside the bags of bagged fish and on gill rakers or elsewhere in the pharynx of both bagged and unbagged fish. Divers witnessed unbagged snapper frequently regurgitating stomach contents between 15–18 m depth and the sea surface, as the volume of gases in swimbladders expanded by more than an atmosphere of pressure, equivalent to 40% of all bladder expansion between depths of 75 and 15 m. Snapper were never seen regurgitating prey below 18 m, although safety considerations precluded prolonged observations by divers at depths >18 m.

Prey volume

From bagged snapper, we collected an average 108% more prey (0.75 ±0.57 mL [SD], versus 0.36 ±0.24 mL for unbagged fish), on the basis of the unadjusted grand means of all nine date-means weighted by their respective sample sizes (Fig. 1; Table 1). The logarithm of prey volume was positively related to the logarithm of fish body weight for bagged fish (P<0.0001) and additionally differed among collection dates (P=0.04; forward stepwise regression, P=0.15 as inclusion level; Proc REG: SAS, 1988; R^2=0.98). Date effects thus represented more than just temporal differences in fish size. A fish body weight effect on prey volume was undetectable (P>0.95) for unbagged fish, for which only collection date was important (R^2=0.93). A general date effect increased monotonically over the sampling period.

Prey volumes for both bagged and unbagged snapper were evaluated on the basis of bootstrapped estimates for the last seven sampling dates on which

Table 1

Summary statistics for juvenile pink snapper, *Pristipomoides filamentosus*, caught by hook and line off Kaneohe Bay, windward Oahu, Hawaii, during February–August 1994. Values for fork length (FL, mm), eviscerated body weight (EW, g), and the stomach eversion index (EvI) are medians for the sampling date; number of fish (n) is the date-specific sample size.

	Bagged					Unbagged				
Sampling date	n	FL	EW	Time caught	EvI	n	FL	EW	Time caught	EvI
09 Feb	1	155	57	0935	3	4	190	118	0920	2
28 Feb	4	168	87	1206	2.5	2	165	98	1006	2
02 Mar	16	150	60	1130	2	16	153	63	1143	2
04 Mar	14	155	64	1120	3	16	187	101	1104	2
15 Jul	9	172	87	1112	2	8	170	84	1105	2
19 Jul	11	173	94	1045	2	12	166	85	1045	2
11 Aug	19	198	138	1050	2	21	202	154	1044	2
16 Aug	6	187	116	1112	3	3	202	150	1025	2
18 Aug	9	184	105	1055	2	10	186	112	1055	2
All dates	88	177	100	1057	2	92	175	97	1050	2

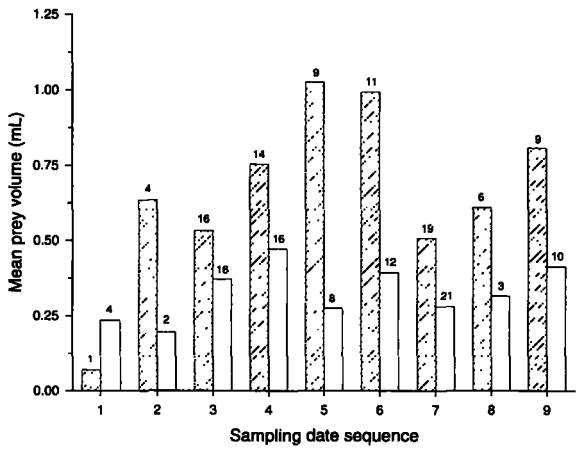

Figure 1

Mean prey volume for bagged (diagonal-line histograms) and unbagged (open histograms) juvenile pink snapper, *Pristipomoides filamentosus*, collected on each of nine dates during February–August 1994. Number of fish sampled is noted above histograms.

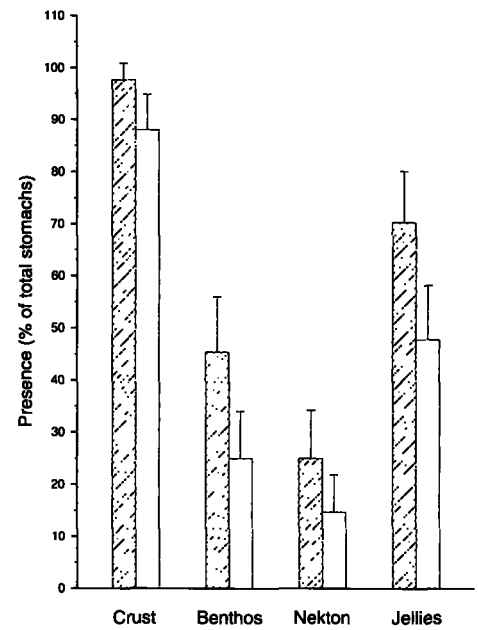

Figure 2

Percentage presence (1 standard error noted) for each of four major identifiable prey types (crustaceans, benthos, nekton, and jellies) for bagged (diagonal-line histograms) and unbagged (open histograms) juvenile pink snapper, *Pristimopoides filamentosus*, collected on nine dates during February–August 1994.

the smaller of the two sample sizes was nontrivial (≥3 fish, Table 1). Prey volumes bootstrapped without fish size and date adjustments averaged 112% (95% CI=72–152%) greater for bagged than for unbagged fish. For unbagged fish, predicted prey volumes (based on predicted values for bagged fish of the same body size and date) averaged 0.64 mL among dates, compared with observed prey volumes that averaged <0.30 mL. Bootstrapped differences of predicted minus observed prey volumes for unbagged snapper averaged +116% (95% CI=70–157%) or were 116% greater for bagged fish. Adjusted bootstrapped estimates thus were slightly larger than the bootstrapped estimates from unadjusted data.

Prey types

Three prey types (crustaceans, benthos, and jellies) were retained with greater relative frequency by bagged versus unbagged samples (2×2 Contingency χ^2 tests, $P<0.01$ for each of the three types; Fig. 2). A greater relative frequency of nekton for bagged (25%) versus unbagged (14%) snapper was only suggestive ($P=0.06$; Fig. 2). The proportion of fish with unidentifiable prey was similar in both bagged (49%) and unbagged (43%) fish (2×2 Contingency χ^2; $P=0.47$). Bagged fish in general retained greater numbers of major prey types (mean=2.9; median and mode=3) than did unbagged fish (mean=2.2; median and mode=2) (2-sample K-S test, $P<0.001$; Fig. 3).

Prey sizes

On average, the maximum size of prey retained by bagged samples was greater than the maximum prey size for unbagged samples (2-sample K-S test, $P<0.001$; Fig. 4). The minimum and median sizes of prey retained were equivalent, however, for bagged and unbagged (2-sample K-S tests, both $P>0.1$). Maximum prey size increased with fish body size for both bagged ($R^2=0.94$) and unbagged ($R^2=0.91$) snapper.

Discussion

Fundamental influences of ingestion

Two factors (fish body weight and date of collection) appear naturally to influence the amounts of prey consumed by juvenile snapper. The positive relation between fish size and prey volume was associated with snapper growth; juveniles averaged 50% greater body weight at the end versus the beginning of the 7-month period of study. Our observation of a monotonic temporal (date) effect in addition to the effect

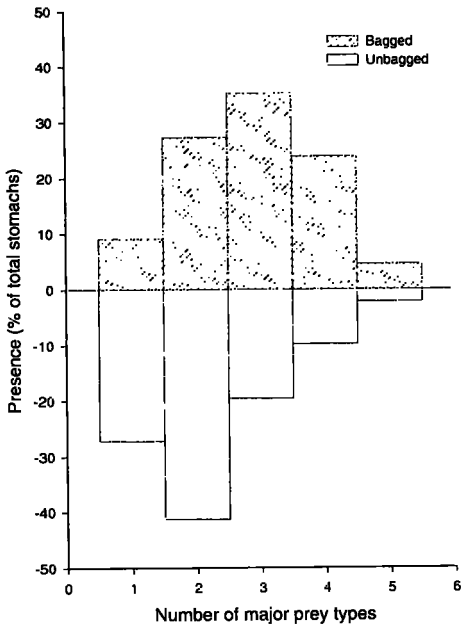

Figure 3

Frequency distributions for the major prey types (five, including unidentifiable category) present in bagged (above horizontal axis) and unbagged (below axis) juvenile pink snapper, *Pristimopoides filamentosus*, collected on nine dates during February–August 1994.

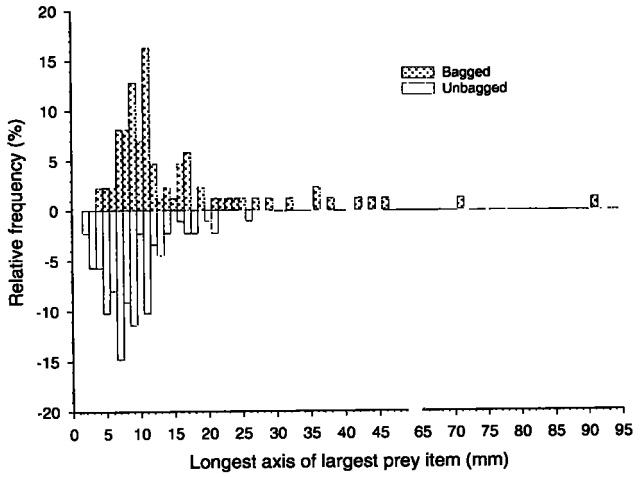

Figure 4

Frequency distributions of maximum prey sizes (all types, including unidentifiable category) for bagged and unbagged juvenile pink snapper, *Pristimopoides filamentosus*, collected on nine dates during February–August 1994.

of body size was not expected. It is possible that the date effect not related to size was caused by increases in the abundance or availability of prey between winter and summer.

In comparisons of prey volumes between bagged and unbagged specimens, the effects of body size and date of collection clearly need to be recognized, and adjustments made. Although this would seem intuitively necessary if sampling design does not control for fish body size and collection date, these factors influenced our results despite the fact that our sampling design specifically controlled for them. The possibility that the effects of body size and collection date may be too large to adjust statistically after-the-fact (if left uncontrolled by basic sampling design) should be taken into account in future studies.

Artifacts of regurgitation

Some food studies of physoclistous marine fishes (e.g. Bowman, 1986) have indicated or have strongly suggested that ingested prey are lost due to stomach eversion resulting from expansion of swimbladders when specimens are retrieved from even moderate (50 m) depths. This appears especially true for piscivores and other predators of large prey that have simple, undifferentiated stomachs (Treasurer, 1988).

Undetected regurgitation can lower the precision of estimates by adding erroneously empty or low-volume samples to the data set. There are also at least three ways in which undetected loss of stomach contents can bias dietary studies. These include 1) underestimates of the amount of food ingested, 2) underestimates of diet composition, including the taxonomic or functional variety of prey, and 3) size-selective regurgitation of prey. The latter can either inflate or reduce the effect of 1) depending on the nature of the size bias, which in turn may influence the precision of the estimates.

Precision of estimates

Total loss of stomach contents due to regurgitation occurred infrequently (4 out of 92 fish). However, the large reduction in prey volume for unbagged fish indicates that partial loss of prey because of regurgitation was a frequent occurrence. Partial prey loss did not inflate the variances of prey volume estimates for unbagged snapper; CV's (mean/SD·100%) of the date-specific estimates of prey volume were equivalent for bagged and unbagged fish (67% and 62%, respectively). Perhaps this reflects an effect of bias—selective loss of large prey—offsetting a decrease in

precision for unbagged fish. Species or collections in which the incidence of partial regurgitation is higher thus may be less precise, depending on whether loss of regurgitated prey is size-selective and in what manner so. High incidence of total regurgitation will be more likely to overwhelm size biases in retention and thereby lower precision.

Quantity and types of prey

Our observations for pink snapper document a general bias toward underestimating the total amount of food ingested by this species if partial or complete regurgitation goes undetected or is ignored. Because the number of different prey detected reflects the amount of material examined, underestimation of quantity should often underestimate prey variety as well, as our data illustrate. The observed underestimation for all four major prey types argues that our a priori classification of types, although subjective, was sufficient to detect a general bias resulting from regurgitation.

Sizes of prey

Size composition of prey can be biased by size-selective regurgitation. In the case of snapper, larger prey items were selectively regurgitated and lost by unbagged specimens. Large prey items might have been more recently ingested, despite likely crepuscular or nighttime periods of peak foraging (Haight et al., 1993b). The observed bias against retaining large prey may explain much of the underestimation of prey volume for unbagged snapper. Fishes with other feeding mechanism structures (e.g. different gill-raker size and spacing) may lack such a size bias, or regurgitation may result in the selective loss of smaller prey. Biases toward retaining larger prey can dampen the effect of regurgitation on underestimation of the total amount of prey.

Implications for diet studies

Depending on the specific research question, future studies of the food and feeding habits of juvenile pink snapper may benefit from the use of specimens collected at depth by divers. If simple comparisons of, say, the relative abundances of major prey types among fish collections are all that is needed, perhaps unbagged fish will suffice. Conversely, if longshore comparisons of large prey—perhaps comprising the bulk of the diet—are necessary, or if field estimates of total food intake or gastric evacuation rates are required, it is obvious that specimens retrieved directly to the sea surface will provide underestimates. Clearly, ingestion estimates for unbagged specimens will need to be adjusted for regurgitation loss, but collection date effects that are strongly nonlinear may make this difficult in practice. Further research is needed to develop methods for quantifying effectively the magnitude of regurgitation if collection date effects are nonmonotonic. Comparisons of diet among unbagged snapper captured at different depths will also be biased in terms of composition and size, as well as in terms of quantity of prey, because the amounts, diversity, and sizes of prey are interrelated and because the magnitude of regurgitation is influenced by extent of pressure change and hence depth of capture.

Bowman (1986) noted the progressive effects of depth on extent of regurgitation for other species. Prior explicit consideration of the interrelated biases resulting from regurgitation, on the composition, size, and quantity of prey has been lacking. The current consensus that diet descriptions require compound measures of both occurrence and bulk or mass data (Hyslop, 1980; Bowen, 1983; but see MacDonald and Green, 1983) reinforces the argument for critically evaluating prey data which may have been affected by barotrauma or other causes.

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Cohort abundances and daily variability in mortality of eggs and yolk-sac larvae of bay anchovy, *Anchoa mitchilli*, in Chesapeake Bay

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Abstract.—Eggs and yolk-sac larvae of bay anchovy, *Anchoa mitchilli*, were surveyed at seven sites in Chesapeake Bay on 12 days in July 1991 to estimate abundances and mortality rates of daily cohorts and the relative biomasses of adults that spawned them. An objective was to determine variability in abundance and mortality rates among sites and survey dates. Estimated abundances of eggs spawned each day and their hourly mortality rates were considered in relation to 1) in situ predator abundances, 2) environmental factors, and 3) initial egg and yolk-sac larval abundances. The mean initial abundance of bay anchovy eggs on each day during the 12 experiments was 6,630 eggs/m^2 (427.0/m^3). Mean initial abundance of yolk-sac larvae was 385 larvae/m^2 (24.6/m^3). Mean adult biomass at the survey sites, estimated from the egg productions, was 18.0 g/m^2 (1.16 g/m^3). A correlation analysis indicated that spawning by bay anchovy may be most intense in areas with high zooplankton biomass and where the ctenophore *Mnemiopsis leidyi*, a potential predator on eggs and larvae, was least abundant. Mean cohort instantaneous egg mortality was 0.066 eggs/h; on average, 73% of spawned eggs died before hatching. Yolk-sac larvae incurred a mean cohort instantaneous mortality of 0.053/h, i.e. 64% mortality during the first 24-h posthatch. Together, the mean egg and yolk-sac larval mortality rates indicated that >93% of bay anchovy daily cohorts die within 2 days after egg fertilization and before larvae reach the first-feeding stage. The range of cohort-specific mortality rates at a single station sampled on five consecutive days was equal to that observed at the seven sites. The high abundances, combined with high and variable cohort mortality rates, emphasize the probable importance of the egg and yolk-sac larval stages in the recruitment process of bay anchovy.

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Most marine and estuarine fishes are highly fecund and spawn pelagic eggs that suffer high mortalities (Dahlberg, 1979; McGurk, 1986; Pepin, 1991). Historically, an estimation of in situ mortality rates of fish eggs and yolk-sac larvae has been problematic because of their temporally and spatially patchy distributions (Fortier and Leggett, 1985; Heath, 1992). However, it is important to obtain such estimates because the magnitude and variability of mortalities potentially can affect recruitment levels and contribute to fluctuations in stock abundance (Houde, 1989a).

Bay anchovy, *Anchoa mitchilli*, is the most abundant fish in estuaries and bays along the east coast of the United States (Hildebrand and Schroeder, 1928; Bigelow and Schroeder, 1953; Houde and Zastrow, 1991). The species is euryhaline and occurs in habitats as diverse as tidal freshwater tributaries and continental shelf waters. In most estuaries, including the Chesapeake Bay, the bay anchovy is an important trophic link between plankton and piscivores (Baird and Ulanowicz, 1989; Luo and Brandt, 1993). Its eggs and larvae dominate summer ichthyoplankton collections from Chesapeake Bay, accounting for 99% of the

* Deceased.

eggs and ~70% of the larvae (Dovel, 1971; Olney, 1983).

Recruitment variability in anchovies is hypothesized to result from variable stage-specific mortality (Lasker 1985b; Smith 1985). If bay anchovy egg and yolk-sac larvae experience both high and variable stage-specific mortalities, the effect on annual recruitment could be substantial. Crude estimates of daily mortality of eggs and yolk-sac larvae ranged from 26% to 97% in Biscayne Bay, Florida, whereas mortality rates of feeding-stage larvae were lower, averaging 30%/d (Leak and Houde, 1987). To obtain reliable estimates of mortality during the short egg and yolk-sac larval stages (about two days total) of bay anchovy, it is necessary to sample repeatedly a daily cohort of eggs or yolk-sac larvae throughout a 24-h period. Our surveys followed that plan during twelve days on Chesapeake Bay in which mortalities were estimated in relation to biotic or abiotic factors that may have affected the rates. By restricting the study to cohorts of eggs and prefeeding yolk-sac larvae, the calculated mortalities must, therefore, have resulted primarily from causes other than starvation.

In Chesapeake Bay, bay anchovy is sexually mature at 40 mm fork length (FL), 10 months after hatching (Zastrow et al., 1991), and seldom lives beyond age 2 (Wang, 1992; Newberger and Houde, 1995). It is a serial spawner (Luo and Musick, 1991; Zastrow et al., 1991) and has a reproductive season in Chesapeake Bay that extends from May until September. Peak spawning occurs in July (Dalton, 1987) when virtually all females spawn nightly (Zastrow et al., 1991). Age-1 females produce most eggs (Zastrow et al., 1991), which hatch into yolk-sac larvae at approximately 20–24 h after fertilization. The yolk-sac larval stage also is short, with a duration of about 24 h (Houde and Zastrow, 1991).

The high abundances, serial spawning, and the presence of a single cohort of eggs on each day for this species allowed for repeated estimates of cohort-specific mortality rates within one season and for investigations into the factors that may affect variability in the rates. The four objectives of the study were as follows: 1) to estimate daily-cohort abundances and variability of bay anchovy eggs and yolk-sac larvae in selected areas of Chesapeake Bay; 2) to estimate mortality rates and variability of daily cohorts of bay anchovy eggs and yolk-sac larvae; 3) to relate densities of two potential predators—the scyphomedusan *Chrysaora quinquecirrha*, and the ctenophore *Mnemiopsis leidyi* (as well as environmental variables)—to anchovy egg and yolk-sac larval mortality rates; and 4) to estimate relative spawning-stock biomasses of bay anchovy at the experimental sites.

Materials and methods

Sampling design

After determining that anchovy eggs were present in test lifts of a plankton net, daily experiments were conducted at seven sites (Fig. 1) to estimate mortality rates of bay anchovy. Once a site had been selected, samples were obtained at 2-h intervals to estimate abundances of eggs and yolk-sac larvae. The sites were defined by the drift patterns of concurrent free-drifting mesocosm studies (Houde et al., 1994), which were initiated when the sites were selected. Each sample for this study was taken adjacent to free-drifting mesocosms. The mesocosms, which were 5 m in length and 1 m in diameter, acted as drogues and were assumed to drift with the water mass that was originally sampled. Each experiment consisted of 8 to 12 duplicate lifts of a plankton net. Water depths at the seven sites generally ranged from 10 to 25 m. Based upon the mesocosm drift tracks (Fig. 2), the mean area of the Bay included in an individual experiment was 59.8 km^2.

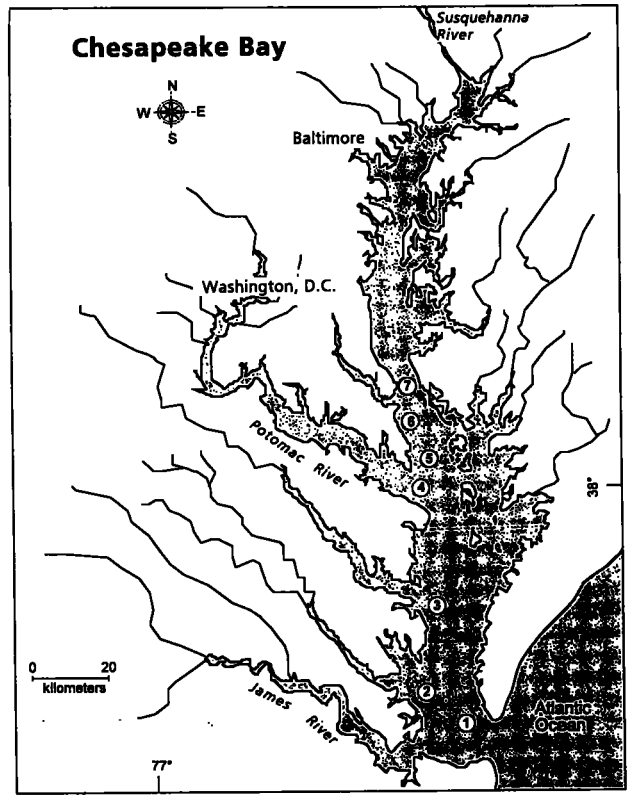

Figure 1
Chesapeake Bay and the seven sampling sites.

Collections

Collections were made from the research vessel RV *Henlopen* during the periods 2–9 July and 18–24 July 1991, the peak of the spawning season for bay anchovy. The lower Chesapeake Bay (sites 1–4) was surveyed on the first cruise and the mid-Bay (sites 5–7) was surveyed on the second cruise (Fig. 1).

Anchovy eggs and larvae were collected in a 40-cm diameter plankton net with 280-μm meshes. A flowmeter in the net mouth was used to determine the volume of water sampled. Vertical lifts of the net from near bottom (never deeper than 25 m) to the surface were made at 1 m/sec. The mean volume sampled in 312 net lifts was 3.00/m^3 (SD=1.38/m^3). Upon collection, samples were immediately preserved in 5% formalin-seawater. At each experimental site, sampling began between 0000 and 0400 h local time, shortly after peak spawning had occurred on each day. Duplicate samples were collected at 2-h intervals until approximately 2100 h. By sampling at 2-h intervals we documented declines in abundances of eggs and yolk-sac larvae from which mortality rates of daily cohorts were estimated. In this way, the level of mortality and its variability were determined for 12 daily cohorts.

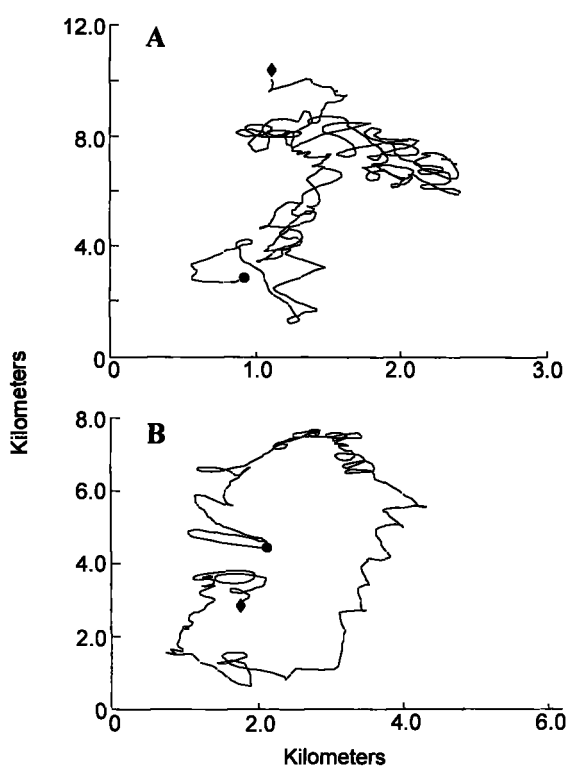

Figure 2

Vessel tracks from two surveys of bay anchovy egg and larval abundance in Chesapeake Bay. Samples were collected every 2 hours on the vessel track. (A) Track for site 6, 19 July 1991. (B) Track for site 3, 5 July 1991. The locations of sites are illustrated in Figure 1. ♦ = start; • = end.

Abundances of gelatinous predators were estimated from collections in a 60-cm, 280-μm mesh, opening and closing net. Collections were made in partitioned oblique tows: 1) from near-bottom to the pycnocline; and 2) from the pycnocline to the surface. They were made ~12 times daily adjacent to the drifting mesocosm array and concurrent with collections of anchovy eggs and larvae. Total biovolumes of *C. quinquecirrha* and *M. leidyi* >10 mm diameter in each sample were measured immediately upon collection.

Salinity, temperature, dissolved oxygen, and chlorophyll *a* fluorescence were determined from surface-to-bottom casts of a conductivity-temperature-depth (CTD) probe. Mean values during each 24-h experiment were based upon three to five CTD casts. Position data for plankton samples and CTD casts were logged by the vessel's navigation system to delineate drift tracks of the mesocosm deployments and the locations of sampling stations.

In the laboratory, fish eggs and larvae (yolk-sac and older) were removed from all samples. Eggs were identified and counted. Yolk-sac larvae were sorted, identified, and separated on the basis of ≥6 samples from each day's collections.

Settled volumes of zooplankton from the 40-cm net collections, determined from a minimum of three samples each day, were recorded and expressed as mL under 1 m^2 of bay surface. The zooplankton in the 280-μm mesh net potentially represented prey of adult bay anchovy, rather than prey of first-feeding larvae.

Egg and yolk-sac larval abundance

Densities (number/m^3) and abundances (number under 1.0/m^2) of anchovy eggs and yolk-sac larvae in each sample were estimated. Duplicate samples, collected between 0000 and 0600 h, were examined to determine the sample pair on each day which had the maximum abundance of eggs or yolk-sac larvae. Those samples provided an estimate of the mean "initial abundance" for each experiment. The decline in abundance over the next 18 to 20 h was a measure of mortality.

Some yolk-sac larvae are extruded through 280-μm meshes. However, abundances of yolk-sac larvae, which are of uniform length (approximately 2.0 mm), were not adjusted for extrusion in this analysis be-

cause mortality estimates presumably were not affected by consistent proportional losses. Adjustments to estimate actual yolk-sac larval abundances could be obtained by multiplying the uncorrected abundances by 2.3, the adjustment factor derived from paired collections in 280-μm and 53-μm mesh nets (MacGregor, 1994).

Mortality

Because bay anchovy eggs are abundant in Chesapeake Bay and hatch <24 h after being spawned, an intensive ichthyoplankton survey could derive mortality estimates for a daily cohort of eggs or yolk-sac larvae on the basis of the decline in their abundances on a single day. By using this approach, daily mortality rates were estimated. Hourly instantaneous mortality rates of eggs and yolk-sac larvae were estimated from a log-linear fit of the exponential model: $N_t = N_0\, e^{-Zt}$, where N_t is the abundance (number under 1/m^2) of a cohort at time t, N_0 is its initial abundance (number under 1 m^2), Z is the instantaneous mortality coefficient (per h), and t is the time elapsed (h) since the initial abundance estimate.

Estimates of daily cohort abundances and mortality rates of eggs and yolk-sac larvae were compared among days, an approach seldom possible in research on species with eggs that have longer development times. Some losses due to diffusion or transport of eggs and larvae out of the sampling areas may have occurred. However, such losses were minimized by the short period over which each cohort was sampled (≤1 d) and because sampling was directed by the drift of mesocosms that tracked the initially sampled water mass.

Egg production and adult biomass

We obtained an estimate of adult biomass from estimates of egg production, knowledge of adult fecundity, and spawning frequency. Egg production, when divided by relative fecundity (mean number of eggs spawned per gram of female), provides an estimate of adult female biomass (Saville, 1964). Biomass of serial-spawning fishes such as bay anchovy can be estimated by single-survey methods of egg production (Lasker, 1985a; Parker, 1985; Eltink[1]). Parker's (1985) formulation to estimate adult biomass is

$$B = E_d / (F_{bw} \times S \times R),$$

where B = adult biomass (g);
E_d = daily egg production;
F_{bw} = mean batch fecundity per female;
S = spawning fraction (i.e. the fraction of females that spawned on the sampling date); and
R = the proportion of the population that is female.

Batch fecundities and spawning fraction of bay anchovy were based upon estimates by Zastrow et al. (1991) who reported that batch fecundity (F_{bw}) was 687.1 ova per gram of ovary-free female weight and that spawning fraction (S) was 1.0 during July in Chesapeake Bay. We assumed that the proportion of adult females (R) was 0.5, on the basis of trawling data (Newberger and Houde, 1995), which indicated a mean female:male ratio of 1.02:1.00. Thus, relative adult biomass (g/m^2) at each site was about twice the relative female biomass.

Predators and other factors

Egg and yolk-sac larval abundances were examined in relation to environmental variables. Possible correlations between egg or yolk-sac larval abundances and biovolumes (mL/m^2) of two gelatinous predators (ctenophore *M. leidyi* and scyphomedusa *C. quinquecirrha*) were analyzed because Cowan and Houde (1992, 1993) and Purcell et al. (1994) indicated that these dominant species were important predators on bay anchovy eggs and larvae. Bay anchovy apparently is not cannibalistic (Klebasko, 1991), and other major predators have not been identified. Possible correlations between egg or yolk-sac larval abundances and zooplankton biomasses also were examined.

Statistical analyses

When assumptions for parametric tests were met, Analysis of Variance (ANOVA) was used to test for differences among daily surveys in initial egg abundances, zooplankton biomasses, and gelatinous predator biovolumes. An ANOVA also was used to determine if means of those variables differed among the five surveys carried out at site 5 (Fig. 1). When ANOVA results were significant, individual means were compared by using the a posteriori Student-Newman-Keuls (SNK) multiple-comparison procedure.

The estimates of hourly instantaneous mortality rates of eggs and yolk-sac larvae were the regression coefficients in the log-linear models relating $\log_e$ abundance to elapsed time. Egg mortality was calculated from collections made between 0200 and 2000 h because eggs hatch in ~20 h. Yolk-sac larval mor-

[1] Eltink, A. 1991. Horse mackerel egg production and spawning stock size in the North Sea in 1990. Int. Counc. Explor. Sea, Council Meeting 1991/H:27, 14 p.

tality was calculated from collections made between 0000 and 2400 h. Each of the duplicate samples was treated as a separate data point in regression analysis. An SNK test was applied following the regression analyses to determine which of the instantaneous mortality rates of eggs and yolk-sac larvae differed significantly from each other. In several cases the estimated mortality coefficients did not differ significantly from zero at the $P = 0.05$ level. These coefficients were retained in our overall analysis of mortality rates and comparisons among sites because we assumed that low, near-zero rates may occur and that such estimates did characterize low rates of loss at some sites.

Pearson product-moment correlation coefficients were calculated for mortality rates and selected biotic variables. Possible correlations between egg or yolk-sac larval mortality rates and initial abundances, zooplankton biomasses, and gelatinous predator biovolumes, were examined.

Results

Hydrography

Mean values of temperature, salinity, oxygen, and chlorophyll *a* fluorescence at 3-m depth are summarized in Table 1. Chlorophyll *a* fluorescence tended to increase in a south-to-north direction. Both temperatures and chlorophyll *a* fluorescence peaked at site 5 (Fig. 1). Depth profiles of salinity and oxygen, although not illustrated, indicated increasing stratification in a south-to-north direction and nearly anoxic conditions near-bottom at sites 5, 6, and 7.

Initial egg abundance and adult biomass

Initial egg abundances of daily cohorts during each of the 12 experiments were high and variable, ranging from 935 to 18,277 eggs/m^2 (Table 2). The mean initial abundance was 6,630 eggs/m^2 (427.0/m^3). The initial abundances of eggs differed significantly among experiment dates (ANOVA, $P<0.0002$) and probably among sites, although most sites were sampled on only one day. The highest initial egg abundance, 18,277 eggs/m^2, was observed at site 7, the northernmost site (Fig. 1).

The mean relative adult biomass (±2 standard error [SE]), estimated from the initial cohort abundances of eggs, was 18.0 g/m^2 (±8.0 SE). Biomass estimates varied widely among experiments and sites, ranging from 2.5 to 49.3 g/m^2 (Table 2).

Initial yolk-sac larval abundance

The mean initial abundance of cohorts of yolk-sac larvae was approximately 17 times less than initial

Table 1

Summary of sampling data for bay anchovy, *Anchoa mitchilli*, in Chesapeake Bay, 3–24 July 1991. Data include estimated relative biomass (B) of adult bay anchovy; mean daily biovolumes (mL/m^2) of *Mnemiopsis leidyi* (CTV), *Chrysaora quinquecirrha* (CHV), and zooplankton (ZP), mean daily temperature (TMP); salinity (SLT); oxygen concentration (OXY); and chlorophyll *a* fluorescence (FLR) at 3-m depth. Identical superscripts on means indicate no significant (P >0.05) difference (SNK pairwise comparison procedure). Locations of sites are indicated in Figure 1.

July date	Site	B g/m^2	CTV mL/m^2	CHV mL/m^2	ZP mL/m^2	TMP °C	SLT PSU	OXY mg/L	FLR mg/m^2
3	1	33.1	0.0^b	0.0^b	15.3^{ab}	26.4^a	22.3^a	8.04^a	0.82^b
4	2	15.0	0.0^b	0.0^b	16.4^{ab}	26.2^a	20.9^{ab}	7.87^a	1.53^b
5	3	10.6	0.0^b	0.0^b	17.1^{ab}	26.5^a	18.3^{bc}	9.35^a	1.10^b
7	4	2.5	484.4^a	128.4^a	7.2^b	26.6^a	14.6^{cd}	7.47^a	1.47^b
8	4	5.3	470.8^a	36.6^b	6.8^b	26.6^a	14.8^{cd}	6.44^a	0.90^b
18	7	49.3	32.5^b	41.8^b	20.3^a	27.3^a	14.3^{cd}	6.63^a	15.7^{ba}
19	6	15.5	24.4^b	35.7^b	15.0^{ab}	25.2^a	13.0^d	8.26^a	15.8^{ba}
20	5	19.6	30.6^b	6.8^b	10.6^{ab}	28.0^a	15.4^{cd}	6.01^a	11.0^{ba}
21	5	35.9	49.39^b	18.6^b	13.4^{ab}	28.0^a	15.4^{cd}	6.42^a	18.4^a
22	5	5.7	129.0^b	19.5^b	12.2^{ab}	28.5^a	15.3^{cd}	6.92^a	15.9^{ba}
23	5	9.2	278.6^{ab}	39.8^b	10.6^{ab}	26.6^a	13.9^{cd}	7.85^a	23.7^a
24	5	13.7	368.9^{ab}	22.3^b	18.8^{ab}	28.7^a	15.6^{cd}	5.41^a	25.3^a
Mean		18.0	155.7	29.1	13.6	27.1	16.1	7.22	11.0
Standard error		4.0	52.8	10.1	1.2	0.3	0.8	0.31	2.6

mean egg abundance. In the 12 experiments, initial yolk-sac larval abundances ranged from 56 to 781/m^2 with a mean of 385/m^2 (24.6/m^3 SE) (Table 2). Mean abundances differed significantly among experiments (ANOVA, $P<0.002$). The highest abundance of yolk-sac larvae was observed at site 7, where eggs also were most abundant (Table 2).

Table 2

Estimated hourly mortality rates and standard errors (SE) for egg (Z) and yolk-sac larvae (Z_L), initial egg abundances (N_0) and initial yolk-sac larval abundances (NL) of bay anchovy, *Anchoa mitchilli*, on 12 days during the period 3–24 July 1991. Identical superscripts on mortality rates and initial abundances indicate no significant ($P>0.05$) difference (SNK pairwise comparison procedure). Asterisks indicate that regression coefficients of $\log_e$ abundances regressed on time (h), from which Z and ZL estimates were obtained, differed significantly from zero at $P = 0.05$ level.

July date	Site	Z/h	SE$_Z$/h	N_0/m^2	n	r^2
Eggs						
3	1	*0.108^{ab}	0.027	12,214^{bc}	16	0.54
4	2	0.014^{ab}	0.015	5,521^{d}	18	0.05
5	3	0.001^{ab}	0.012	3,891^{d}	19	0.10
7	4	0.049^{a}	0.027	935^{d}	20	0.15
8	4	*0.062^{ab}	0.021	1,966^{d}	20	0.32
18	7	*0.081^{b}	0.020	18,277^{a}	19	0.50
19	6	0.042^{ab}	0.055	5,708^{cd}	19	0.04
20	5	*0.080^{ab}	0.013	7,245^{bcd}	20	0.67
21	5	0.020^{ab}	0.027	13,237^{ab}	20	0.02
22	5	*0.100^{a}	0.021	2,118^{d}	20	0.55
23	5	*0.045^{b}	0.012	3,402^{d}	20	0.44
24	5	*0.185^{b}	0.028	5,044^{cd}	20	0.77
Mean		0.066		6,630		
Standard error		0.014		1,462		

July date	Site	Z_L/h	SE$_{ZL}$/h	NL/m^2	n	r^2
Yolk-sac larvae						
3	1	*0.057^{ab}	0.049	422^{bc}	7	0.18
4	2	0.040^{b}	0.048	222^{d}	8	0.11
5	3	0.082^{b}	0.064	614^{ab}	9	0.19
7	4	*0.177^{ab}	0.018	162^{cd}	6	0.96
8	4	0.017^{ab}	0.052	56^{d}	7	0.02
18	7	*0.036^{b}	0.009	781^{a}	11	0.66
19	6	0.022^{ab}	0.019	605^{ab}	8	0.19
20	5	0.022^{a}	0.028	380^{bcd}	6	0.14
21	5	0.058^{ab}	0.027	430^{bc}	9	0.39
22	5	*0.072^{ab}	0.015	289^{bcd}	11	0.72
23	5	0.028^{b}	0.018	364^{bcd}	8	0.27
24	5	0.030^{ab}	0.021	299^{bcd}	8	0.25
Mean		0.053		386		
Standard error		0.012		56.7		

Gelatinous predator biovolumes

The above-pycnocline biovolumes of gelatinous zooplankters were highly variable among experiments, ranging from 0 to 612.8 mL/m^2 (Table 1). Ctenophore *M. leidyi* biovolumes ranged from 0 to 484.4 mL/m^2 and scyphomedusan *C. quinquecirrha* biovolumes ranged from 0 to 128.4 mL/m^2. The mean biovolume of *M. leidyi* was 4 times higher than that of *C. quinquecirrha*. Biovolumes of each species were highest at site 4 (ANOVA, $P<0.0001$), near the mouth of the Potomac River (Table 1; Fig. 1).

Zooplankton biomass

Zooplankton biovolumes from the 280-μm net ranged from 6.8 to 20.3 mL/m^2, mean = 13.6 mL/m^2. The two lowest zooplankton biovolumes (ANOVA, $P<0.02$) were observed at site 4 (Table 1; Fig. 1), where gelatinous zooplankton biovolumes were highest. The highest zooplankton biovolume occurred at site 7, coincident with highest anchovy egg and yolk-sac larvae abundances.

Egg and yolk-sac larvae mortality rates

The overall mean instantaneous mortality rate for eggs was 0.066/h. The estimates, which ranged from 0.001 to 0.185/h, represent stage-specific (20-h) mortalities of 2% to 98%. The highest egg mortality rates (>0.10/h) were estimated on 3, 22, and 24 July (Figs. 3 and 4; Table 2). If only the seven rates judged to be significantly different from zero ($P<0.05$) are included in the analysis, the mean mortality was 0.094/h (SE=0.017).

The overall mean mortality rate of yolk-sac larvae was 0.053 larva/h. The yolk-sac larval rates, which ranged from 0.017 to 0.177/h, represent daily mortality rates of 33.5 to 98.6%. The highest yolk-sac larval mortality rates (>0.07/h) were estimated on 5, 7, and 22 July. If only the four rates judged to be significantly different from zero ($P<0.05$) are included in the analysis, the mean mortality rate was 0.077/h (SE=0.035/h).

The mortality estimates differed among the daily surveys. Rates were estimated with low precision, possibly because the eggs and larvae were distributed in patches within each sampling site. The standard errors of yolk-sac larval mortality rates were relatively high at sites between the mouth of the Chesapeake Bay and the Potomac River (sites 1–4)

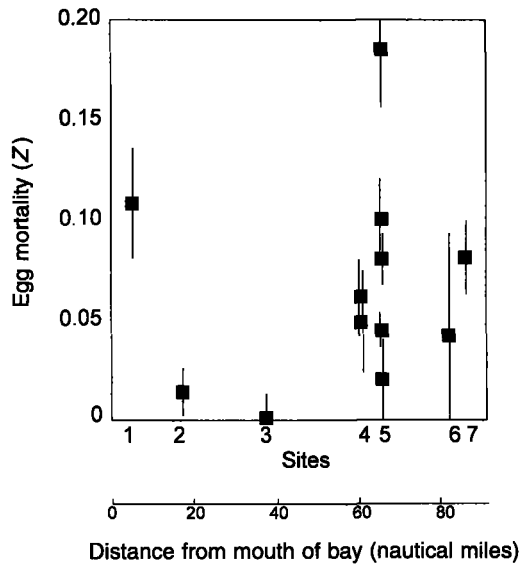

Figure 3

Instantaneous mortality rates (*Z*/h) of bay anchovy eggs collected at seven sites in Chesapeake Bay, July 1991. Locations of sites are illustrated in Figure 1. Vertical bars represent ±1 SE.

compared with sites farther north (Table 2; Fig. 1). Observed variability in mortality rates was approximately equal for eggs and yolk-sac larvae. Coefficients of variation (ratio of standard deviation to mean) were 0.73 and 0.79 for eggs and yolk-sac larvae, respectively.

The regression coefficients, which were the estimates of mortality rates, did not differ significantly from zero at the $\alpha = 0.05$ level in five of the twelve $\log_e$ egg abundance-on-time regressions and eight of the twelve yolk-sac larva regressions. The yolk-sac larval regressions were based upon relatively few data points, which contributed to their lower precision (Table 2). The nonsignificant ($P>0.05$) mortality coefficients corresponded to low, near-zero regression coefficients. Although not significantly different from zero, these coefficients were presumed to estimate mortality rates.

Correlations

There were several simple correlations among organism abundances, biovolumes, and mortality rates (Table 3). Most notable were 1) the positive correlation between yolk-sac larval mortality rate and *C. quinquecirrha* biovolume ($P<0.01$); 2) the positive correlations between egg abundance, yolk-sac larval abundance, and zooplankton biovolume ($P<0.05$); and 3) the negative correlations between both egg and yolk-sac larval abundances and *M. leidyi* biovolume ($P<0.05$).

Discussion

Daily cohorts of bay anchovy were demonstrated to suffer high and variable mortality during egg and yolk-sac larval stages. Our estimates of mortality rates indicate both day-to-day and regional variability in Chesapeake Bay. At site 5, which was sampled on five consecutive days, the range of egg mortality rates exceeded the range observed over all remaining sites. The high variability at a single site suggests that environmental conditions were changing daily. Variability in initial egg abundances indicated that numbers of adult spawners in the area also were changing on a daily basis.

Our egg-stage mortality rates ranged from 2% to 98%, and averaged 73%. Recent experiments in free-drifting mesocosms (Houde et al., 1994) conducted at the same sites and dates of surveys reported here have also provided estimates of mortality of bay anchovy eggs and yolk-sac larvae. The mesocosms, which included gelatinous predators, provided mean estimates of mortality that were essentially identical to those reported here. In Great South Bay, New York, Castro and Cowen (1991) reported that seasonal mortality rates of combined bay anchovy eggs and yolk-sac larvae ranged from 70% to 98%/d. If eggs in Great South Bay hatched in 20 h, the mortality rates on eggs alone may have ranged from 63.0% to 96.5%/d. In Biscayne Bay, Florida, Leak and Houde (1987) compared seasonal abundances of eggs and yolk-sac larvae of bay anchovy and estimated that

Table 3

Matrix of correlation coefficients for bay anchovy, *Anchoa mitchilli*, where *Z* is hourly egg mortality rate, *ZL* is hourly yolk-sac larvae mortality rate, *N* is initial abundance of eggs, *NL* is initial abundance of yolk-sac larvae, CTV is biovolume in mL/m² of *M. leidyi*, CHV is biovolume in mL/m² of *C. quinquecirrha*, ZP is zooplankton biovolume in mL/m². Asterisks indicate significant correlation ($P<0.05$).

	Z	*ZL*	*N*	*NL*	CTV	CHV
ZL	–0.19					
N	+0.07	–0.28				
NL	–0.12	–0.20	+0.66*			
CTV	+0.29	+0.30	–0.57*	–0.68*		
CHV	–0.04	+0.67*	–0.28	–0.26	+0.68*	
ZP	+0.22	–0.30	+0.58*	+0.70*	–0.59*	–0.49

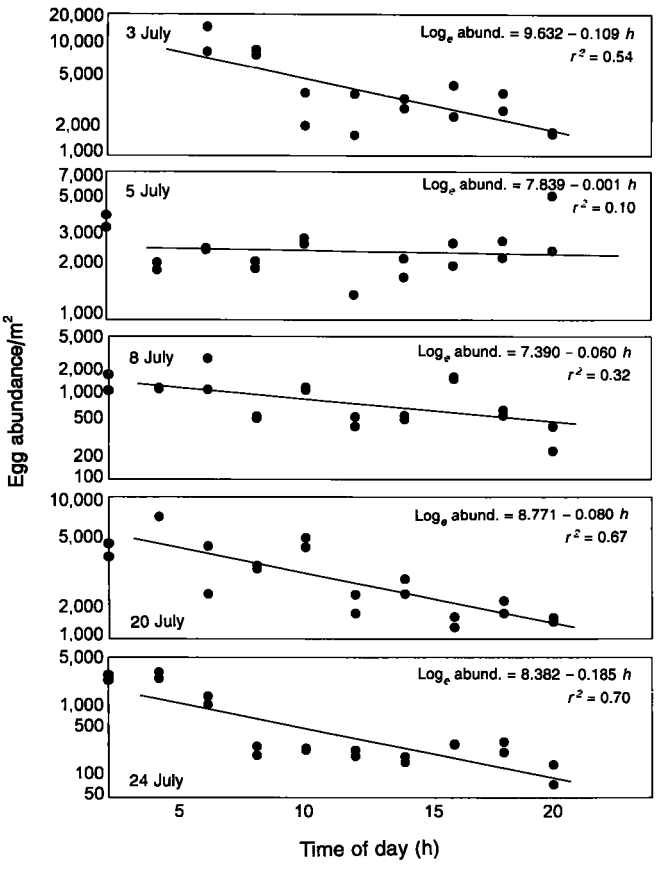

Figure 4

Regressions of $\log_e$ abundances on elapsed time in hours (t) for five experimental surveys of bay anchovy eggs in Chesapeake Bay during July 1991. The five regressions are examples which demonstrate the method to obtain mortality rates of eggs and yolk-sac larvae for the 12 surveys summarized in Table 2.

mean daily egg mortality was 86%, with a range of 26% to 97%.

Egg mortality rates of bay anchovy obviously are high. But, they are lower than predicted at their temperature of development (27°C), based upon Pepin's (1991) temperature-dependent mortality model, $Z = 0.030\ e^{0.18T}$, in which Z is the daily instantaneous mortality rate for marine fish eggs and T is temperature (°C). At 27°C the model predicts a mortality of $Z = 3.91$ (=0.16/h), a rate more than twice our mean estimate of $Z = 1.58$/d (=0.066/h). Pepin's (1991) model for marine fish eggs predicts mortality rates of $Z = 2.81$ to 4.63/d for temperatures in the range 25.23°C to 27.99°C which were observed during this study. These predicted mortality rates are higher than all except one of our estimated rates and are also higher than rates estimated for bay anchovy eggs by Leak and Houde (1987) in Biscayne Bay, Florida. Castro and Cowen (1991) determined mortality of bay anchovy eggs and yolk-sac larvae at lower average temperatures in Great South Bay. At their two-year mean of 23.4°C, they estimated a mean mortality rate of 2.36/d, a value rather close to Pepin's (1991) model-predicted 2.02/d. Pepin (1991) had suggested that species with short development times (i.e. high temperatures) may have lower than predicted daily mortality rates because of their relatively short exposure to predators.

Mortality rates for bay anchovy eggs are higher and perhaps more variable than rates reported for eggs of other anchovy species. Only the Peru anchoveta, *Engraulis ringens*, has been reported to experience similar daily egg mortality rates, a consequence of cannibalism by adult anchoveta and of high predation rates by other pelagic fish (Smith et al., 1989). The reported stage-specific egg mortalities of other anchovies, while high, probably do not exceed 50% to 60% (Dorsey and Houde[2]) and appear to be considerably lower than rates estimated for bay anchovy.

Instantaneous mortality rates for bay anchovy eggs also are higher than rates reported for most teleost fishes (Houde, 1989b; Houde and Zastrow, 1993). However, if stage-specific mortalities are compared, rather than daily rates, the bay anchovy resembles many fishes. For example, Harding et al. (1978) estimated that the mean mortality rate for plaice, *Pleuronectes platessa*, eggs was $Z = 0.075$/d in the Southern Bight of the North Sea at mean temperature 5.65°C. Egg-stage duration of plaice is about 22 days (Coombs et al., 1990). Thus, the stage-specific egg mortality is $Z_{cum} = 1.65$, equivalent to 81%, and similar to that of bay anchovy (Z_{cum}=1.32) despite the more than 20-fold difference in hourly rates (0.003 for plaice, 0.066 for bay anchovy).

Yolk-sac larvae are essentially embryos free of the chorion, and their expected mortality may be more comparable to eggs than to feeding-stage larvae. Our estimated mortality rates of bay anchovy yolk-sac larvae ranged from $Z = 0.41$ to 4.24/d (33.5 to 98.5%/d). The mean rate was $Z = 1.27$/d (72.0%/d), a value nearly equal to the egg-stage mortality rate. Because the yolk-sac larval stage of bay anchovy is approximately one day in duration, the daily mortality rate is

[2] Dorsey, S. E., and E. D. Houde. 1992. Daily variability in mortality of bay anchovy, *Anchoa mitchilli*, eggs in Chesapeake Bay. Int. Counc. Explor. Sea, Pelagic Fish Committee, Council Meeting 1992/H:17, 11 p.

equivalent to a stage-specific rate. At 27°C, the mean stage-specific mortality of bay anchovy yolk-sac larvae (Z=1.27) is higher than the mortality predicted (Z=0.77) from the temperature-dependent model of Pepin (1991) for yolk-sac larvae of marine fishes.

There was a high degree of spatial and temporal variability in the abundances of bay anchovy eggs. The initial abundances of eggs varied among days (i.e. experiments) and probably among sites. Because repeated experiments were carried out only at sites 4 and 5, it was not possible to critically analyze among-site differences in egg abundances or their mortality rates. Some of the variation may be explained by adult distributions and spawning strategy; Luo and Musick (1991) hypothesized that bay anchovy spawns preferentially in areas with plentiful adult food. Our study supports their hypothesis because zooplankton biovolumes were positively correlated with initial anchovy egg abundances. Additionally, the two lowest initial egg abundances in our study occurred at site 4, which also had lowest zooplankton biovolumes; the highest egg abundance was observed at site 7, where highest zooplankton biovolume occurred.

Our estimates of relative adult biomasses may be considerably higher than actual mean biomasses of bay anchovy in Chesapeake Bay because we had selected survey sites with high egg abundances. Our criterion for selecting sampling sites was the obvious presence of bay anchovy eggs in test tows. This criterion probably accounts for the high biomass estimates. Our mean biomass estimate, 1.16 g/m^3 (18.0 g/m^2), equates to approximately one adult anchovy per m^3. In a concurrent study of bay anchovy in the mid and upper Chesapeake Bay, acoustics-adjusted trawl abundances in July 1991 indicated a mean adult biomass of 0.58 g/m^3 (Wang and Houde, 1995).

Initial mean abundance of cohorts of yolk-sac larvae, uncorrected for the extrusion of a fraction of larvae through the 280-m net meshes, equaled 385.4/m^2 (24.6 [±6.0]/m^3). This unadjusted abundance was approximately 17 times lower than the initial mean abundance of egg cohorts. If yolk-sac larvae abundances were adjusted upward by the factor (2.3) required to correct them (MacGregor, 1994), the difference between initial egg and yolk-sac larvae abundances reduces to a factor of 5.8. The observed mean initial abundance of yolk-sac larvae, after adjustment, based upon our mean egg mortality rate (0.066/h), was still only 50% of that expected. However, because eggs hatch at ca. 2000 h and the initial yolk-sac larval abundance was estimated at ca. 0230 h, continuing mortality would have caused further declines in yolk-sac larval numbers for 6.5 h before samples were taken. Applying the mean yolk-sac larval mortality rate (0.053/h) to the 6.5-h period further reduced the mean discrepancy, although initial numbers of yolk-sac larvae were still 30% lower than expected. The cause of the remaining discrepancy, if real, was not identified but could have resulted if a fraction of the sampled eggs were infertile or dead.

Estimated biovolumes of two gelatinous predators of bay anchovy eggs and larvae, *M. leidyi* and *C. quinquecirrha*, were variable, probably patchy on temporal and spatial scales. Both have been demonstrated to be major consumers of bay anchovy eggs and larvae (Cowan and Houde, 1993; Purcell et al., 1994). There was a significant correlation between mortality of yolk-sac larvae and *C. quinquecirrha* biovolume (Table 3). Biovolumes of the two jellyfishes were highest at site 4, where lowest zooplankton biovolumes and lowest anchovy egg and larval abundances occurred. At the three southernmost sites (sites 1, 2, and 3 in Table 1), neither *M. leidyi* nor *C. quinquecirrha* were present. Despite their absence, there was no evidence that mortality rates of anchovy eggs or yolk-sac larvae were lower there than at sites with jellyfish present.

Spawning intensity by bay anchovy, indexed by initial abundances of egg cohorts, was lowest at site 4 where the gelatinous predator biovolumes were highest, raising a possibility that anchovy adults might avoid areas where zooplankton have been depleted on account of consumption by gelatinous predators. This suggests a mechanism that may indirectly reduce baywide predation mortality on anchovy eggs and larvae; this, in turn, is supported by the negative correlations between both egg and yolk-sac larval abundances and jellyfish biovolumes. The combined densities of *C. quinquecirrha* and *M. leidyi* were extremely high at site 4, near the mouth of the Potomac River, and possibly caused the depressed zooplankton biovolumes. Purcell (1992) noted that consumption by *C. quinquecirrha* depleted zooplankton in tributaries of Chesapeake Bay, but she reported smaller effects in the mainstem of the Bay.

An important conclusion of our study is that bay anchovy suffers highest mortality during its first two days after being spawned; on average, 73% of all spawned bay anchovy eggs in Chesapeake Bay died before hatching. Of the surviving 27%, approximately 72% perished during the 24-h yolk-sac larval stage. In July 1991 only 7.6%, on average, of each night's egg production survived until the first-feeding stage, which commences 2 days after hatching. Lasker (1985b) and Smith (1985) pointed out that fluctuations in yearly recruitment in engraulids may result from variable stage-specific mortality rates, which can be a consequence of interannual variability in both biotic and abiotic factors. Results of our study suggest that such factors also vary significantly on

much shorter, day-to-day, temporal scales and that interannual recruitment differences in species with life histories similar to bay anchovy could depend upon the variable conditions faced by daily cohorts during each summer's spawning season.

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Cannibalism and predation on fish larvae by larvae of Atlantic mackerel, *Scomber scombrus:* trophodynamics and potential impact on recruitment*

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Abstract.—Predation and cannibalism during larval life are potential determinants of recruitment and year-class strength in marine fish. We studied predation by larval Atlantic mackerel, *Scomber scombrus*, 3–14 mm in length, on conspecifics and other fish larvae over Sable Island Bank (Scotian Shelf) in July 1991. With increasing length, the diet of mackerel larvae shifted from copepod nauplii to copepods and fish larvae. Mackerel <5 mm selected strongly for copepod nauplii. Mackerel ≥6 mm preyed indifferently on copepods (i.e. in proportion to their abundance in the plankton) but selected strongly for fish larvae. The larval fish prey of Atlantic mackerel larvae comprised conspecifics (66%), yellowtail flounder, *Limanda ferruginea* (18%), silver hake, *Merluccius bilinearis* (12%), and redfish, *Sebastes* spp. (4%) larvae. Predation was stage-specific: only the newly hatched larvae of a given species were ingested. Based on a conservative estimate of the transit time of fish larvae in the gut (24 h), estimates of prey mortality by Atlantic mackerel larvae ranged from 7% to 57%/d (average 31%) of the standing stock of newly hatched larvae of suitable prey size. Piscivory was limited at densities of fish larvae <0.1/m^3. Predation on fish larvae by Atlantic mackerel larvae declined with increasing density of nauplii in the environment and with increasing number of alternative copepod prey ingested. Because the capacity of Atlantic mackerel larvae to digest fish larvae was limited, cannibalism was density independent and predation on other species was depensatory. Hence, despite its potential importance during the first days after hatching, cannibalism and predation by Atlantic mackerel larvae 3–14 mm long do not appear to contribute to the density-dependent regulation of Atlantic mackerel and other prey species.

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Several lines of indirect evidence suggest that predation is a major determinant of early survival in marine fish (Bailey and Houde, 1989): 1) the high mortality rate of eggs and yolk-sac larvae in the field (Fossum, 1988; Incze and Campbell, 1989); 2) the high estimates of predation mortality obtained by subtracting starvation mortality from total mortality (Hewitt et al., 1985; Leak and Houde, 1987); 3) the vulnerability of fast-growing, healthy larvae to predators in mesocosm experiments (Øiestad, 1985); 4) the wide range of potential predators of prerecruit fish in the sea (Hunter, 1984; Bailey and Houde, 1989); and 5) the variety of spawning strategies that can be interpreted as reducing the vulnerability of eggs and larvae to predators (Bailey and Houde, 1989). A recent field study comparing concurrent measurements of predation mortality and total mortality confirmed that predators such as medusae can have a significant impact on the early survival of bay anchovy, *Anchoa mitchilli*, in Chesapeake Bay (Purcell et al., 1994). Yet, in most ecosystems, the actual predators of fish larvae, the trophodynamics between predators and fish larvae, and the role of predation in regulating year-class strength remain unclear (Hunter, 1984; Anderson, 1988; Bailey and Houde, 1989; Heath, 1992).

Scombrid larvae often prey on the larval stages of their own and other fish species (Hunter and Kimbrell, 1980; Jenkins et al., 1984; Finucane et al., 1990; Young and Davis, 1990). In particular, Atlantic mackerel, *Scomber scombrus*, larvae capture fish larvae sometimes more than half their own length (Grave, 1981). The diet of Atlantic mackerel larvae changes markedly during ontogeny. First-feeding larvae may be phytophagous, young post-yolk-sac larvae feed primarily on copepod nauplii and copepodites, and Atlantic mackerel >6.5 mm in length add conspecifics and other fish larvae to their diet (Grave, 1981; Peterson and Ausubel, 1984; Ware and Lambert, 1985).

Because the probability of encounter between planktonic larvae increases with increasing density, Grave (1981) proposed that intracohort cannibalism could be a simple mechanism for the density-dependent regulation of year-class strength in Atlantic mackerel. In the present study, we examined the diet of Atlantic mackerel larvae and their selectivity for prey on Sable Island Bank (Scotian Shelf) in July

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1991. Cannibalism and predation on other fish larvae were studied in relation to larval fish density and the availability and consumption of alternative invertebrate prey. In particular, we searched for evidence that cannibalism and piscivory by Atlantic mackerel larvae were density dependent. Finally, we evaluated the potential impact of predation by Atlantic mackerel larvae on the early survival of fish larvae.

Methods

In spring, the northern component of the Northwest Atlantic stock of Atlantic mackerel migrates from the New England Continental Shelf and the Scotian Shelf towards the southern Gulf of St. Lawrence where the bulk of spawning takes place from early June to mid-August (Sette, 1943, 1950). Some spawning also takes place along the coast of Nova Scotia (Sette, 1943; Berrien et al., 1981). During a 27-month series of monthly ichthyoplankton surveys on Emerald, Western, and Sable Island banks (Fig. 1), Atlantic mackerel larvae were captured offshore, primarily over Sable Island Bank, in June, July, and August of 1991 and 1992. The larvae ranged from 2.7 to 13.7 mm standard length (SL)(unpreserved), corresponding to an approximate age span of 4 to 16 days (D'Amours et al., 1990). These lengths and ages indicate that the shallow waters west of Sable Island constitute a spawning ground for the species. The present study focuses on the trophodynamics of Atlantic mackerel larvae sampled in July 1991.

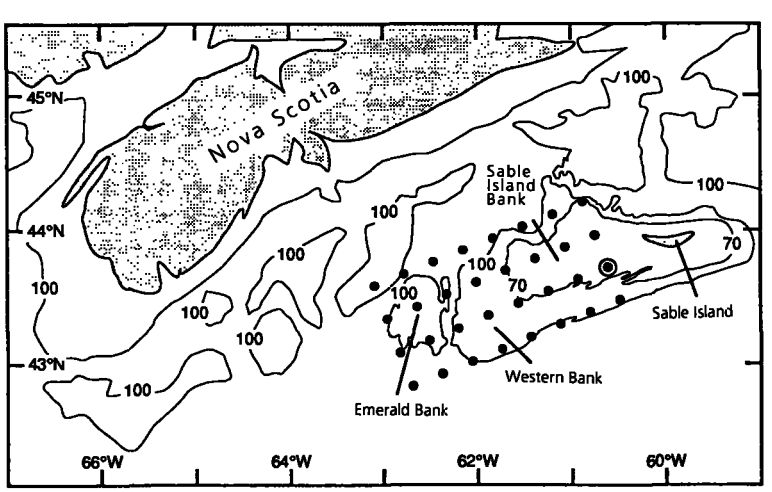

Figure 1

Location of the 32 rectangular midwater trawl (RMT) stations sampled for Atlantic mackerel, *Scomber scombrus*, larvae and their prey from 18 to 23 July 1991 on Emerald, Western, and Sable Island banks (Scotian Shelf). The vertical distribution of fish larvae was studied with the multi-net sampler on 24 and 25 July at the station marked with a circled black dot. Isobaths are in meters.

Sampling

Atlantic mackerel larvae and their prey were sampled from 18 to 23 July 1991 over a grid of 32 stations covering part of Emerald, Western, and Sable Island banks (Fig. 1). Three different plankton nets mounted on a rectangular midwater trawl (RMT) were used to collect young fish and zooplankton simultaneously. A main net (8-m^2 sweeping section, 1,600-μm mesh) captured juvenile fish; an intermediate net (2-m^2 sweeping section, 333-μm mesh) collected fish larvae and mesozooplankton; and a small net (0.0075-m^2 mouth, 64-μm mesh) sampled the microzooplankton prey of fish larvae. The RMT was towed once at each station in a multiple oblique trajectory from 0 to 75 m (or 5 m from the bottom at stations shallower than 75 m) for an average (± standard deviation [SD]) of 17 (±5) min at a speed of approximately 2 knots (1 m/s). A CTD (conductivity, temperature, and depth) probe and flowmeters linked to a computer allowed real-time monitoring of depth, water column temperature and salinity, and the volume of water filtered by each net.

On 24 July, a multi-net sampler (Eastern Marine Services E-Z-Net) mounted with 10 identical nets (1-m^2 mouth, 333-μm mesh) was used to determine the vertical distribution of fish larvae at the grid station (52-m depth) where the greatest density of fish larvae was found with the RMT (Fig. 1). Six casts were made at intervals of approximately four hours from 2115 h on 24 July to 2000 h on 25 July 1991. For each cast, 4 depth intervals of 10 m were sampled twice in the following order: 40–30, 30–20, 20–10, 10–0, 0–10, 10–20, 20–30, and 30–40 m. Nets were also opened on the downward (0–40 m) and upward (40–0 m) trajectories of the cast, providing two depth-integrated samples. The multi-net system was equipped with the same real-time monitoring system as that used on the RMT.

Most fish larvae (70%) were sorted immediately at sea and preserved in 95% ethanol. The remainder of the plankton sample, including undetected fish larvae, was preserved in 4% buffered formalin. A subset of 50 Atlantic mackerel larvae were videotaped on the ship for determination of morphometrics before preservation. Twenty-six of these (3.3 to 13.7 mm fresh SL) were preserved in ethanol and 24 (3.3 to 13.3 mm fresh SL) in formalin.

In the laboratory, all fish larvae remaining in the preserved samples were sorted and identified. All undamaged mackerel

larvae (n=1,667) were measured to the nearest 0.1 mm SL. Standard length of mackerel larvae preserved in ethanol and formalin was corrected for shrinkage by using the relationships between fresh and preserved measurements obtained from the subset of larvae videotaped at sea (r^2=0.98). The standard length of a random subset of the 3 other dominant larval fish species (51 silver hakes, 467 yellowtail flounders, 200 redfishes, preserved in ethanol) was measured. Mackerel lengths represent fresh measurements except those used for comparison with other species, in which case all lengths are ethanol-preserved measurements.

Gut content analysis

Undamaged Atlantic mackerel larvae were selected for gut content analysis. The digestive tract was separated from the body and dissected under a light microscope. Whenever possible, prey were identified and measured. The position of the prey in the tractus (foregut, midgut, and reargut) and the state of digestion of the prey (slightly, partly, and well digested) were noted. Because crustacean prey were flattened dorso-ventrally, cephalothorax length, rather than width, was measured. Fish larvae were particularly damaged by digestion and only a small proportion of them (36 out of 710) could be identified and measured directly under the light microscope.

Indirect identification of some digested fish larvae was based on discriminant analysis of their otoliths. To establish the discriminant function, between 18 and 29 ethanol-preserved specimens of each of the four dominant larval fish species sampled in July 1991 (Atlantic mackerel, silver hake, yellowtail flounder, and redfish), ranging in size from hatching length to 10 mm, were selected from the plankton collections and measured. The sagittae and lapilli of each fish were extracted and 8 measurements were taken on each of the 4 otoliths: longest and shortest diameter (LD and SD); longest and shortest radius (LR and SR); surface and perimeter (SU and PE); and longest and shortest diameter of nucleus (LN and SN). The discriminant function used 15 measures and ratios of measures (LR_S/LR_L, LN_S, SU_S/SU_L, PE_S/SU_S, PE_S/LD_L, SN_S/LN_L, SR_S/SD_L, LD_S/LR_L, SD_S/SD_L, LR_S/SU_L, SD_S/SR_S, SD_S/SN_L, SD_L, LN_S/SN_L, SR_S/SU_L), in order of decreasing discriminatory power, where the subscripts S and L refer to the sagitta and the lapillus, respectively (from the same side of the fish). The discriminant function, which was validated by using the known larvae, correctly classified between 67% and 89% of the larvae of each species (Table 1).

The discriminant function was used to identify an additional 38 (out of 710) digested fish larvae for which one undamaged sagitta and one undamaged lapillus (from the same side of the fish) were recovered. The length of identified fish larvae was back-calculated on the basis of the best polynomial regression between one of the otolith dimensions and the ethanol-preserved standard length for the known specimens of the species (LD_S, r^2=0.87 for Atlantic mackerel; LD_S, r^2=0.93 for silver hake; SR_S, r^2=0.80 for yellowtail flounder; SD_S, r^2=0.75 for redfish).

Table 1

Validation of the linear discriminant function used to identify fish larvae found in the gut of larval Atlantic mackerel, *Scomber scombrus*, sampled from 18 to 23 July 1991, southwest of Sable Island (Scotian Shelf). The discriminant function is based on the morphometry of the otoliths of known larvae (see text). Successful identification is the percentage of larvae of a given species correctly identified by the discriminant function. Type-1 error is the proportion of fish larvae incorrectly assigned to another species (H_0 rejected when it is true). Type-2 error is the proportion of fish larvae identified as a given species that were actually of another species (H_0 accepted when it is false).

	Silver hake	Yellowtail flounder	Atlantic mackerel	Redfish
Successful identification (%)	78	89	71	67
Type-1 error (%)	22	11	29	33
Type-2 error (%)	8	29	28	31
Sample size	54	38	58	36

Zooplankton were identified, enumerated, and measured in the RMT collections (64-μm and 333-μm net samples) that contained Atlantic mackerel larvae. The selectivity of Atlantic mackerel larvae for a category of prey was estimated by using Chesson's α (Chesson, 1978):

$$\alpha_j = (d_j / p_j) / \left(\sum d_i / p_i\right), \text{ for } i = 1, \ldots N,$$

where α_j is the selectivity for prey taxon j, N is the number of prey taxa, d_j and p_j are the frequencies of prey taxon j in the diet and the plankton respectively, and d_i and p_i are the same frequencies for the ith prey taxon. Copepod eggs in the diet of large fish larvae may have reflected the ingestion of egg-bearing females and, accordingly, eggs were not considered in the calculation of selectivity indices. Following Fortier and Harris (1989), α_j was first computed for each individual Atlantic mackerel larva captured in the RMT and then averaged by length classes (<5, 5 to <6, 6 to <7, 7 to <8, ≥9 mm). Variations in α reflect changes in the preference of the predator. α is not

affected by changes in the abundance of potential prey and is thus suitable for describing ontogenetic variations in prey selectivity and for comparing or averaging selectivity among stations with different prey densities (Pearre, 1982). A value of $\alpha_j > 1/N$ indicates that prey j is selected for, whereas $\alpha_j < 1/N$ indicates that the prey is rejected.

All dissected mackerel larvae (feeding and nonfeeding) were included in the determination of diurnal patterns of feeding activity. Larvae with empty guts occurred primarily during late-night and early-morning hours (0000–0800 h). These larvae were excluded from the calculations of feeding ratios (mean number of prey organisms per gut of feeding mackerel) or of piscivory (proportion of feeding mackerels with at least one fish larva in the gut). Note that the calculation of a feeding ratio for Atlantic mackerel larvae feeding on fish larvae was meaningless because the gut of mackerel larvae seldom (3% of all cases) contained more than one fish larva.

Results

Zooplankton and fish larvae

Copepods numerically dominated the zooplankton (Table 2). The cyclopoid *Oithona similis*, harpacticoid copepods, and the calanoid *Pseudocalanus* sp. were particularly abundant. The low mean densities of copepod eggs and nauplii (<2/L) may reflect the wide depth interval sampled by the RMT (0–75 m) because these organisms are often concentrated at the pycnocline or in the surface mixed layer.

Representatives of at least 18 genera of fish were collected (Table 2). Silver hake, yellowtail flounder, Atlantic mackerel, and redfish made up the bulk (98%) of the larval fish assemblage. Atlantic mackerel, silver hake, and yellowtail flounder larvae were found primarily over the shallow area of Sable Island Bank (Fig. 2). Redfish larvae were more evenly distributed in the sampling area than were the other species. Vertically, Atlantic mackerel, yellowtail flounder, and redfish larvae aggregated in the surface layer (<20 m) at night and moved deeper in the water column during the day (Fig. 3). In the morning and afternoon, Atlantic mackerel were concentrated in the thermocline at 10–20 m, whereas yellowtail flounder and redfish were found in or below the thermocline. At 2000 h, all four species were most abundant in the thermocline. During the day, the newly-hatched silver hake larvae were found primarily in the surface layer (0–20 m). Too few larvae were captured at night to confirm any diel migration pattern in this species.

Table 2

Mean density (± standard deviation) and percent composition of the zooplankton and larval fish assemblages at stations where Atlantic mackerel larvae, *Scomber scombrus*, were captured (n=14) from 18 to 23 July 1991, southwest of Sable Island (Scotian Shelf).

	Density	Percent
Invertebrates (no./m³)		
Copepods		
Oithona similis	2,048 ±1,226	29
Copepod nauplii	1,642 ±978	23
Harpacticoids	973 ±565	14
Copepod eggs	606 ±597	8
Pseudocalanus sp.	506 ±452	7
Temora longicornis	168 ±278	2
Calanus finmarchicus	153 ±163	2
Centropages sp.	85 ±107	1
Metridia lucens	12 ±20	<1
Eurytemora hirundoides	2 ±5	<1
Acartia sp.	1 ±2	<1
Calanus hyperboreus	<1	<1
Metridia longa	<1	<1
Tintinnids	690 ±838	10
Bivalve larvae	198 ±306	3
Gastropods	64 ±60	1
Appendicularians	29 ±39	<1
Polychaete larvae	6 ±15	<1
Chaetognaths	2 ±3	<1
Euphausiids	2 ±3	<1
Amphipods	1 ±3	<1
Decapod larvae	1 ±1	<1
Gelatinous zooplankton	<1	<1
Ichthyoplankton (no. 100/m³)		
Merluccius bilinearis, silver hake	17 ±52	37
Limanda ferruginea, yellowtail flounder	12 ±30	27
Scomber scombrus, Atlantic mackerel	11 ±23	24
Sebastes spp.,[1] redfish	4 ±10	10
Glyptocephalus cynoglossus, witch flounder	<1	<1
Melanogrammus aeglefinus, haddock	<1	<1
Scophthalmus aquosus, spotted flounder	<1	<1
Mallotus villosus, capelin	<1	<1
Ammodytes sp., sand lance	<1	<1
Hippoglossoides platessoides, American plaice	<1	<1
Lophius americanus, goosefish	<1	<1
Stichaeus punctatus, Arctic shanny	<1	<1
Urophycis sp., hake	<1	<1
Ulvaria subbifurcata, radiated shanny	<1	<1
Others[2]	1 ±1	2

[1] Includes *Sebastes mentella* and *Sebastes fasciatus*.
[2] Includes unidentified fish larvae, pleuronectids, gonostromatids, stichaeids, and *Cyclopterus lumpus* (lumpfish) in order of decreasing average density.

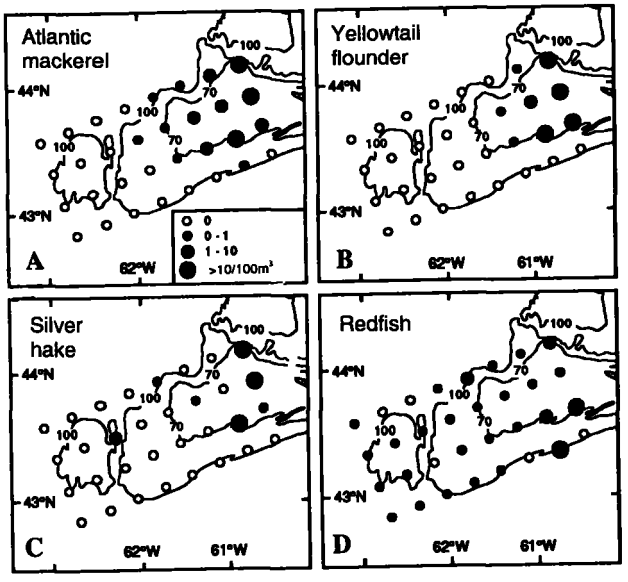

Figure 2

Distribution of the four most abundant species of fish larvae sampled with a rectangular midwater trawl (RMT) from 18 to 23 July 1991 on Emerald, Western, and Sable Island banks (Scotian Shelf).

Diet and feeding patterns in Atlantic mackerel larvae

The diet of Atlantic mackerel larvae changed markedly during early ontogeny (Table 3). Small larvae (<5 mm) fed almost exclusively on copepod nauplii. With increasing length, their diet shifted from nauplii to copepods (copepodites and adults) and fish larvae. Copepod eggs did not contribute substantially (<1% of the prey) to the diet of mackerel larvae <7 mm that preyed mainly on copepod nauplii. The increased proportion of copepod eggs in the diet of larvae ≥7 mm may have reflected the ingestion of egg-bearing female copepods such as *O. similis* or *Pseudocalanus* sp. Appendicularians were present in small proportion (<5%) in the diet of all length classes of larvae. The importance of fish larvae in the diet increased with the length of Atlantic mackerel larvae. The smallest Atlantic mackerel larva that had preyed on another fish larva was 3.3 mm (fresh SL).

The mean cephalothorax length of the copepod prey of Atlantic mackerel larvae increased threefold over the range of lengths studied (<5 to ≥9 mm, Table 3). Feeding incidence was high (≥75%) in all length classes of mackerel. The feeding ratio (all prey types considered) tended to decrease with length, a reflection of the increasing frequency of large prey such as fish larvae. The incidence of predation on fish larvae increased with larval mackerel size, from 12% in the smallest length class (<5 mm) to 69% in the largest length class (≥9 mm).

The mean number of invertebrate prey in the gut of Atlantic mackerel larvae was relatively constant from the second half of the night to late afternoon (1.9–3.5 prey per gut) and then jumped to 13 prey at dusk or soon after (Fig. 4A). This sharp increase in the number of invertebrate prey at dusk may represent an increase in copepod availability as the latter pass through the layer containing mackerel larvae during their nycthemeral migration towards the surface. The percentage of dissected Atlantic mackerel larvae with at least one fish larva in the gut tended to increase from the morning (<30%) to the afternoon and late evening (40–60%) (Fig. 4B).

The gut of Atlantic mackerel larvae usually contained no more than one fish larva (97% of cases). Forty-four percent (314 out of 710) of mackerel larvae containing a larval fish prey also contained at least one invertebrate prey. Most fish larvae were found in the midgut of Atlantic mackerel larvae throughout the diurnal period (Fig. 5A). The frequency of fish larvae in the foregut remained relatively constant during daylight hours, increased at dusk, and decreased in the second half of the night. Occurrence in the reargut was maximum in the early morning hours. In general, fish larvae in the gut of mackerel larvae were either partly or well digested (Fig. 5B). The percentage of Atlantic mackerel containing slightly digested fish larvae was low and relatively constant throughout the day. The frequency of partly digested fish larvae was high and tended to increase from early morning to late afternoon, whereas the frequency of well digested fish larvae declined.

Prey selectivity in Atlantic mackerel larvae

Atlantic mackerel larvae of all lengths fed selectively, but selectivity for a given prey type changed during ontogeny (Table 4). Selection for copepod nauplii was high in small larvae (<5 mm) but declined rapidly as predator size increased; larvae ≥7 mm selected against this prey. Despite their numerical importance in the diet, copepods were either selected against by larvae <7 mm or consumed in rough proportion to their availability in the plankton by larger larvae. Selection for fish larvae increased steadily with the length of Atlantic mackerel larvae and preference for this prey type was particularly strong in larvae ≥9 mm (Table 4).

When analyzed by size categories, copepod prey (nauplii + copepodites + copepods) <300 μm in cephalothorax length were selected (among the copepods) by larvae <7 mm, whereas copepods in the range 300–600 μm were selected against or consumed in near

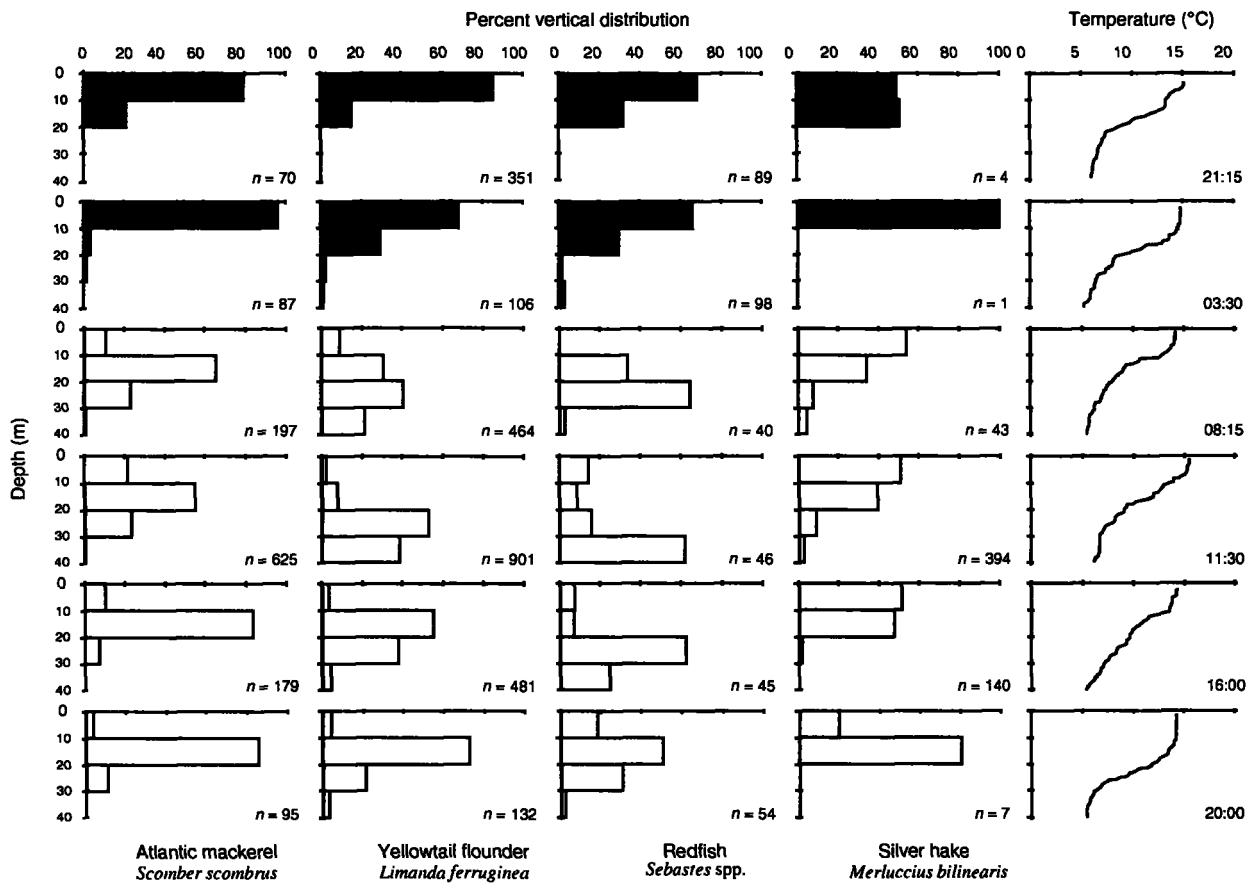

Figure 3

Diel changes in the vertical distribution of the four most abundant species of fish larvae captured with the multi-net sampler (24 and 25 July 1991) at the station (52-m depth) of the sampling grid where the greatest density of fish larvae was found. Black histograms represent nighttime percent distribution and white histograms, daytime percent distribution. Vertical profiles of temperature are shown on the right. Sample size (number of larvae) is given with the vertical distribution and sampling hour with the temperature profile.

proportion to their availability in the plankton by larvae of all lengths. Copepods ≥600 μm were selected for by larvae ≥7 mm (Table 5).

Out of the 710 fish larvae found in the gut of Atlantic mackerel larvae, 36 were identified visually and 38 were identified by discriminant analysis of their otoliths (Table 6). The species composition of the prey identified by either method was similar (Table 6). Assuming that the species composition of the 74 fish larvae identified represented the true composition of the assemblage ingested, conspecifics made up the majority (66%) of the fish larvae preyed upon by Atlantic mackerel larvae. Selectivity for a given species of larval fish prey was calculated for stations where ≥10 larvae were identified in the gut of Atlantic mackerel larvae. The results indicated little selection by mackerel larvae for any species of fish larvae ($\alpha \approx 1/N = 0.25$, where $N=4$ species) (Table 6).

Atlantic mackerel larvae preyed primarily on newly hatched larvae despite the availability of larger larvae in the plankton (Fig. 6). Only one conspecific prey >5 mm was found in the gut of mackerel larvae despite the availability of conspecifics in the plankton. Except for one larva 9 mm long, yellowtail flounder prey were <6.5 mm. The three redfish prey for which measurements are available were <5.5 mm. Atlantic mackerel apparently did not capture silver hakes >2.5 mm. The lengths of conspecifics, redfish, and silver hake prey corresponded to the range of lengths at hatching for these species (Fig. 6).

Predation by Atlantic mackerel larvae in relation to prey density

There was no consistent relationship between predation on invertebrates by Atlantic mackerel larvae

Table 3

Percent composition of diet and feeding statistics by length classes for larval Atlantic mackerel, *Scomber scombrus*, sampled southwest of Sable Island (Scotian Shelf) from 18 to 23 July 1991.

	Length class (mm)					
Prey taxa	<5	5–<6	6–<7	7–<8	8–<9	≥9
Copepod eggs	<1	<1	<1	18	46	37
Copepod nauplii	89	63	56	23	2	8
Copepods[1]	5	21	30	41	34	34
Appendicularians	4	7	4	5	2	1
Fish larvae	2	9	9	12	14	16
Others[2]	<1	<1	<1	1	2	4
Total number of prey	742	1,655	2,913	1,350	570	227
Total number of mackerel larvae	172	444	523	322	144	62
Feeding incidence (%)	75	87	92	88	88	86
Mean feeding ratio (prey per gut)	5.8	4.3	6.0	4.8	4.5	4.3
Incidence of piscivory (%)	12	39	54	57	63	69
Mean length of copepod prey (μm)[3]	190	253	289	405	657	597

[1] Copepodites and adult copepods.
[2] Include euphausiids, chaetognaths, gastropods, phytoplankton cells, cladocerans, amphipods, euphausiid nauplii, and crab larvae in order of decreasing frequency.
[3] Nauplii, copepodites, and adult copepods.

and the density of these prey in the environment. The feeding ratio for copepod nauplii (mean number of nauplii per gut) was not correlated with the density of nauplii in situ for any length class of Atlantic mackerel larvae ($P \geq 0.33$). The feeding ratio for copepods (copepodites and adults) was negatively correlated with the density of this prey for Atlantic mackerel larvae 6 to <7 mm ($P=0.03$, $n=7$) but not significantly correlated with prey density for other length classes (5 to <6 and ≥7 mm, $P \geq 0.67$).

In RMT collections, the relationship between the incidence of piscivory (proportion of feeding Atlantic mackerel with at least one fish larva in the gut) and the density of fish larvae of suitable prey size (sum of Atlantic mackerels and redfishes ≤5.5 mm, yellowtail flounders ≤6.5 mm, and silver hakes ≤2.5 mm) was adequately described by an Ivlev equation (Fig. 7, A–C). Incidence of piscivory was limited at densities of larval fish prey <0.1 larvae/m^3 and quickly reached a plateau as availability increased. The height of the plateau (maximum incidence of piscivory) increased with predator length. The parameters of the Ivlev equation varied little when the data from the multi-net collections were added to the RMT data set (Fig. 7, D–F).

Effect of alternative invertebrate prey on piscivory

In the present study, the absolute predation rate could not be assessed because the transit time for fish larvae

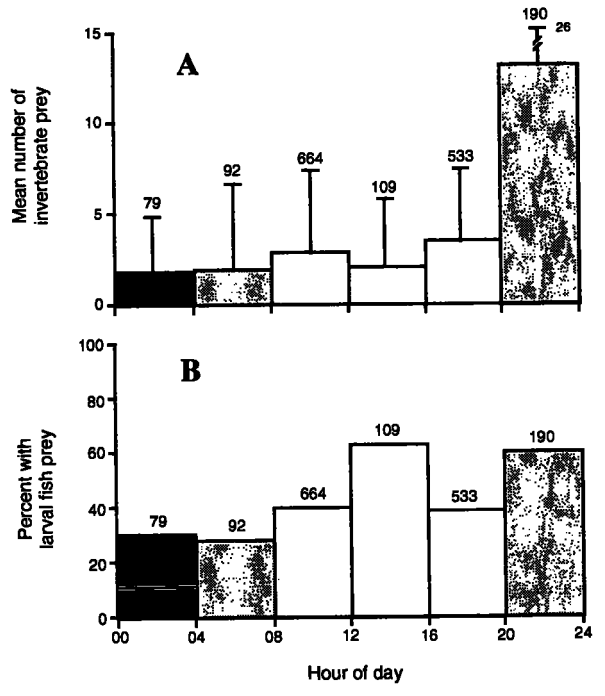

Figure 4

Daily feeding activity of larval Atlantic mackerel, *Scomber scombrus*. (**A**) Mean number (and standard deviation) of invertebrate prey per dissected gut. (**B**) Percentage of dissected mackerel larvae with at least one fish larva in the gut. Black histograms represent nighttime, gray histograms twilight, and white histograms daytime. Number above time class indicates the number of dissected mackerel larvae.

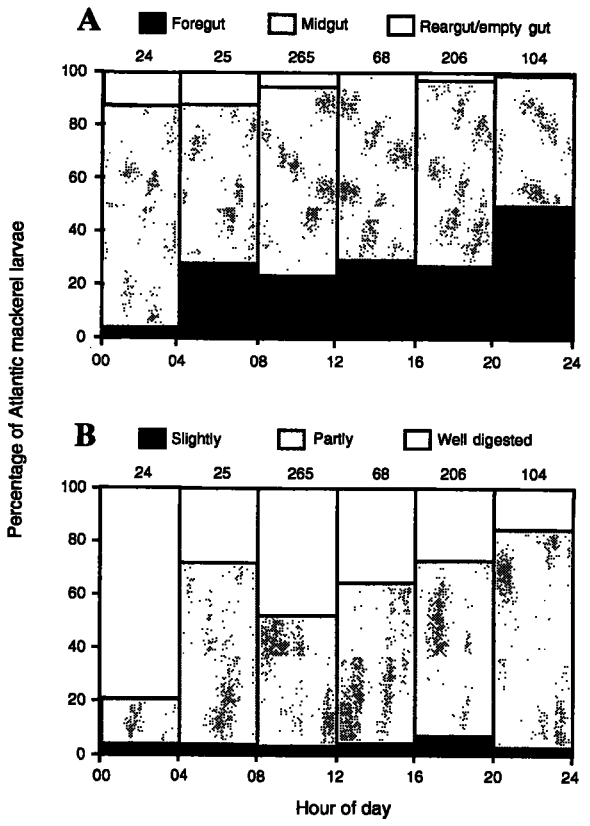

Figure 5

Diel changes in the position (**A**) and state of digestion (**B**) of larval fish prey in the gut of larval Atlantic mackerel, *Scomber scombrus*. Histograms represent the percentage of mackerel larvae with larval fish prey in a given position in gut (**A**) and the percentage of mackerel larvae with larval fish prey in a given state of digestion (**B**). Numbers above each time class indicate the number of Atlantic mackerel larvae dissected.

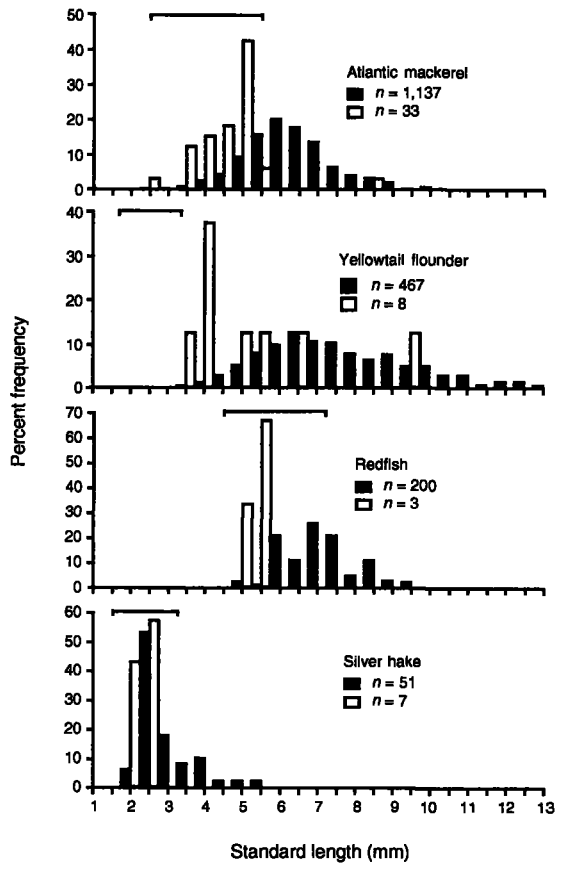

Figure 6

Frequency distribution of the standard length of ethanol-preserved fish larvae in the plankton (black histograms) and in the gut of larval Atlantic mackerel, *Scomber scombrus* (white histograms). Horizontal bars on top of histograms represent the range of hatching length (Fahay, 1983; this study).

in the gut of Atlantic mackerel larvae is unknown. However, assuming a digestion time of 24 hours, a relative daily predation rate (PR, in %/d) was defined as the proportion of all fish larvae of suitable prey size in a sample that was found in the gut of Atlantic mackerel larvae:

$$PR = (NP_g \times 100)/(NP_g + DP),$$

where NP_g = the density of fish larvae in mackerel gut per m^3 of water; and
DP = the density of larvae of suitable prey size in the plankton per m^3.

Predation rate by Atlantic mackerel larvae 3–14 mm long ranged from 7% to 57%/d (average of 31%/d) of the standing stock of the newly hatched fish larvae of suitable prey size (or 2% to 27%/d of all fish larvae). Daily predation declined linearly with increasing density of copepod nauplii (Fig 8A), the only other prey strongly selected for by Atlantic mackerel larvae (Table 4). Sample size for the regression was low (8) because few RMT collections (for which estimates of zooplankton density are available) contained enough Atlantic mackerel larvae to calculate a reliable index. Daily predation was not significantly correlated with the density of copepods (P=0.991) or the combined density of nauplii and copepods (P=0.658). Daily predation on fish larvae of suitable prey size decreased asymptotically as the average number of alternative copepod prey (nauplii + copepodites + adults) consumed by Atlantic mackerel larvae increased (Fig. 8B). The relationship was best described by a reciprocal model; 24% of the variance in daily

Table 4

Prey selectivity (α, Chesson, 1978) in larval Atlantic mackerel, *Scomber scombrus*, sampled southwest of Sable Island (Scotian Shelf) from 18 to 23 July 1991. α was calculated for each Atlantic mackerel larvae and averaged over length classes. A plus sign (+) indicates positive selection for prey ($\alpha > 1/N = 0.2$, where $N = 5$ prey taxa). Only samples containing at least 10 Atlantic mackerel larvae were considered in the calculations.

	Length class (mm)					
Prey taxa	<5	5–<6	6–<7	7–<8	8–<9	≥9
Copepod nauplii	+0.70	+0.33	+0.27	0.06	0.01	—
Copepods[1]	0.02	0.12	0.14	+0.24	+0.32	+0.28
Appendicularians	+0.22	+0.29	0.14	0.14	0.08	0.04
Fish larvae	0.05	+0.26	+0.44	+0.49	+0.53	+0.61
Others[2]	0.01	<0.01	0.01	0.07	0.06	0.07
No. of mackerel larvae	98	203	183	184	113	44

[1] Copepodites and adult copepods.
[2] Includes euphausiids, chaetognaths, gastropods, cladocerans, amphipods, euphausiid nauplii, and crab larvae in order of decreasing frequency.

Table 5

Selectivity for copepod (nauplii, copepodites, and adults) prey size in larval Atlantic mackerel, *Scomber scombrus*, sampled southwest of Sable Island (Scotian Shelf) from 18 to 23 July 1991. α (Chesson, 1978) was calculated for each Atlantic mackerel larva and averaged over length classes. A plus sign (+) indicates positive selection for size ($\alpha > 1/N = 0.2$, where $N = 5$ size categories). Only samples containing at least 10 Atlantic mackerel larvae were considered in the calculations.

	Length class (mm)					
Copepod size (μm)	<5	5–<6	6–<7	7–<8	8–<9	≥9
< 300	+0.94	+0.64	+0.40	0.10	0.01	0.02
300 < 400	0.04	+0.22	+0.26	0.14	0.03	0.04
400 < 500	0.02	0.08	0.12	0.08	0.05	<0.01
500 < 600	—	0.04	0.11	+0.25	0.16	+0.28
≥600	—	0.02	0.11	+0.43	+0.75	+0.66
No. of mackerel larvae	93	165	129	101	61	17

predation rate was explained by the consumption of alternative copepod prey. When one outlier point was removed, the fraction of the variance explained by the model increased to 46% (Fig. 8B).

Discussion

Selectivity for fish larvae in Atlantic mackerel larvae

Over 50% of feeding Atlantic mackerel ≥6 mm had captured at least one fish larva despite the absolute and relative (to other prey) scarcity of fish larvae of suitable prey size in the plankton (on average 0.14 fish larva/m^3 vs. 5,920 nauplii and copepods/m^3). By comparison, copepods were preyed upon in proportion to their relative abundance in the plankton. On the basis of the small percentage of larval fish prey that could be

Table 6

Species composition of larval fish prey found in the gut of larval Atlantic mackerel, *Scomber scombrus*, sampled southwest of Sable Island (Scotian Shelf) from 18 to 23 July 1991. Positive selection for prey ($\alpha > 1/N = 0.25$, where $N = 4$ species of larval fish prey) is indicated by a plus sign (+).

	Silver hake	Yellowtail flounder	Atlantic mackerel	Redfish
Number identified visually	6	3	27	0
Number identified by otoliths	7	6	22	3
Total number identified	13	9	49	3
Percent of grand total	18	12	66	4
Selectivity index	0.18	+0.31	+0.34	0.21

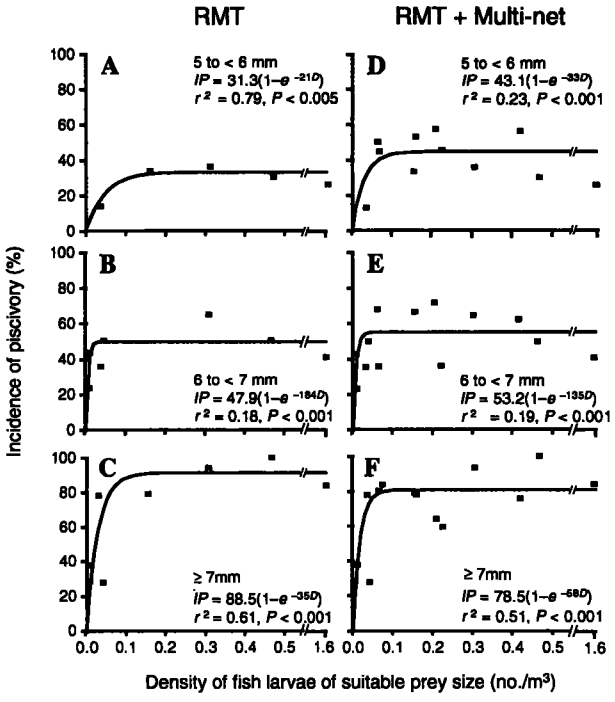

Figure 7

Incidence of piscivory (IP) in larval Atlantic mackerel, *Scomber scombrus*, as a function of the density of fish larvae of suitable prey size (D), by standard-length classes of mackerel larvae. (**A–C**) RMT collections only; (**D–F**) RMT and multi-net collections. The percentage of the variance (r^2) in the incidence of piscivory explained by the Ivlev function (Ivlev, 1961) and the significance level of the regression (P) are given. Note the broken scale on the abscissa.

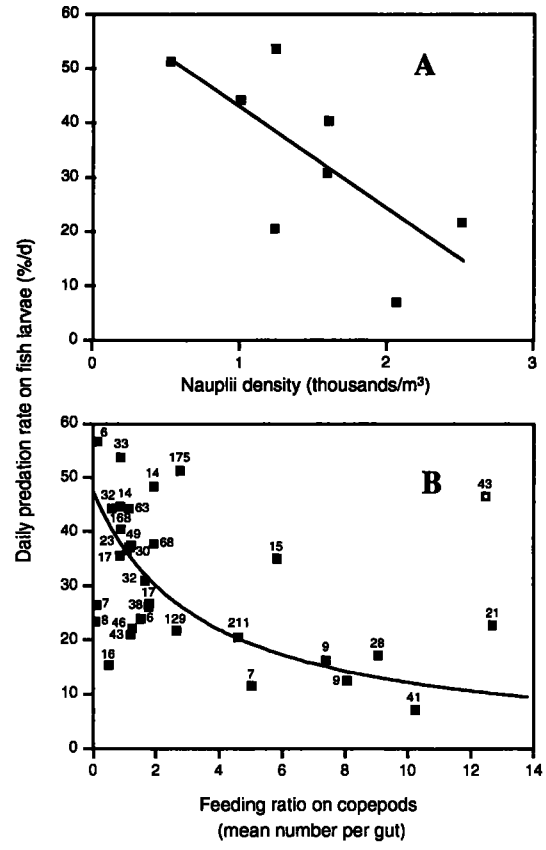

Figure 8

Estimated daily predation rate (PR, see text) of larval Atlantic mackerel, *Scomber scombrus*, on fish larvae of suitable prey size as a function of (**A**) the density of copepod nauplii (DN) in the environment ($PR = 61.6 - 0.0189DN$ [n=8, r^2=0.505, F=6.1, P=0.048]), and (**B**) as a function of the feeding ratio of Atlantic mackerel larvae for copepods (FR, all developmental stages), ($PR = 1/(2.1 + 0.612FR)$ [n=31, r^2=0.462, F=24.9, P<0.001]). In (B), each data point in the regression was weighted by the number of Atlantic mackerel larvae in the sample (given near each point). The outlier marked by the open symbol was excluded from the analysis.

identified (74 out of 710), Atlantic mackerel larvae exhibited little preference for any of the four dominant species of fish larvae available in July in the area studied.

Despite their relatively low frequency in the diet (2% to 16% by number), fish larvae represented an important fraction of the energy intake of Atlantic mackerel larvae. For example, most of the conspecifics ingested ranged from 3.0 to 5.5 mm in length, which translates into 20 to 200 μg in dry weight (Table 3 in Peterson and Ausubel, 1984). By comparison, the approximate dry weight of copepod prey (0.1–0.6 mm in cephalothorax length) ranged from 0.006 to 2 μg (Cohen and Lough, 1981). Thus, assuming that the nutritional value of copepods is four times that of fish larvae per unit biomass (Gotceitas and Brown, 1993), the energy intake represented by one fish larva corresponded to that of 2.5 to 25 of the largest copepods ingested. Pacific mackerel, *Scomber japonicus*, and Atlantic mackerel larvae are characterized by fast growth, high metabolism, and high food requirements (Hunter and Kimbrell, 1980; Peterson and Ausubel, 1984; Ware and Lambert, 1985). The width of ingested fish larvae closely matches the mouth width of Atlantic mackerel larvae (Ware and Lambert, 1985), and fish larvae are the largest prey ingested (Grave, 1981; Ware and Lambert, 1985; this study). Hence, fish larvae probably represent the most profitable prey available in the plankton to satisfy the high food requirements of Atlantic mackerel larvae.

Piscivores generally select small prey in laboratory experiments and consistently ingest smaller than average prey in field situations, a potential reflection of an inability to capture larger prey (Juanes and Conover, 1994, and references therein). In the

present study, Atlantic mackerel larvae 3–14 mm long preyed primarily on newly hatched fish larvae (conspecifics and others). This suggests that in the days following hatching, fish larvae quickly acquire enough motility to escape attack from Atlantic mackerel larvae in this size range. Thus, the predation rates estimated in the present study (7% to 57%/d of the standing stock of larvae of suitable prey size) would apply only over the relatively short period before the development of an efficient escape response. Growth during this period would determine cumulative predation mortality from co-occurring Atlantic mackerel larvae 3–14 mm in length. In the laboratory, survival to metamorphosis in Pacific mackerel larvae was positively correlated with growth over the period during which sibling cannibalism occurred (Hunter and Kimbrell, 1980).

Effect of prey density on predation by Atlantic mackerel larvae

Surprisingly few studies have related the feeding success of fish larvae in the sea to prey availability (Heath, 1992; Fortier et al., 1995). In the majority of these studies, there are indications that feeding was limited below some threshold density of prey. For example, the feeding ratio of larval Atlantic cod, *Gadus morhua*, was adequately described by an Ivlev equation, with feeding limited at nauplii concentrations <10/L (Ellertsen et al., 1989; Sundby and Fossum, 1990). The same model was used to describe stomach fullness and feeding incidence (proportion of predators with prey in the gut) in larvae of southern bluefin tuna, *Thunnus maccoyii*, as a function of zooplankton settled volume (Young and Davis, 1990; Heath, 1992). In this case, the feeding of larval tuna appeared limited at densities of approximately <0.5 prey/L (Heath, 1992). In ice-covered Hudson Bay, the feeding incidence and feeding ratio of Arctic cod, *Boreogadus saida*, and larvae of sand lance, *Ammodytes* sp. in relation to nauplii density were also adequately modeled by an Ivlev equation (Fortier et al., in press). Feeding was limited at densities <40,000 nauplii/m^2, corresponding approximately to <1.6 nauplii/L. In large enclosures, the growth of larvae of capelin, *Mallotus villosus*, was related to prey biomass by a function resembling an Ivlev function (Frank and Leggett, 1982).

In the present study, there was no indication that predation on copepod nauplii and copepods by Atlantic mackerel larvae was dependent on the density of these prey in the environment. This may indicate that naupliar (261 to 4,134/m^3) and copepod (1,170 to 7,190/m^3) densities were at or above the level at which feeding Atlantic mackerel larvae saturate. However, the relationship between the incidence of predation on fish and the density of fish larvae was adequately described by an Ivlev equation. Limitation began at prey densities <0.1 fish larva of suitable prey size per m^3. This threshold was only slightly less than the mean density of fish larvae of suitable prey size (0.14 larva/m^3), and predation on fish appeared limited in about 40% of our collections. Alternatively, Atlantic mackerel larvae preying on fish larvae appeared swamped by their prey in approximately 60% of the collections. Thus, the contracted production of large numbers of larvae in species such as yellowtail flounder and silver hake may reduce total cumulative predation by Atlantic mackerel larvae. Frank and Leggett (1982) suggested that the synchronized emergence of beach-spawned capelin larvae during onshore wind events in eastern Newfoundland resulted in the saturation of their predators and a reduction of percent predation mortality.

Effect of alternative prey on cannibalism and piscivory by Atlantic mackerel larvae

Controlled studies have invariably reported that the presence of alternative prey provides fish larvae with some protection from larval, juvenile, or small-bodied adult fish predators. In the laboratory, the rate of cannibalism on larvae by juvenile Cape anchovy, *Engraulis capensis*, decreased in the presence of alternative copepod prey (Brownell, 1985). Bay anchovy juveniles preferred newly-hatched (2-d-old) sea bream, *Archosargus rhomboidalis*, but shifted to copepods when the density of the latter increased (Dowd, 1986). The presence of alternative copepod prey strongly protected larval Atlantic mackerel (Kean-Howie et al., 1988) and Atlantic cod (Gotceitas and Brown, 1993) from predation by the three-spine stickleback, *Gasterosteus aculeatus*. The addition of *Daphnia magna* reduced by five to tenfold the predation rate of juvenile bluegill, *Lepomis macrochirus*, on larval white perch, *Morone americana* (Margulies, 1990).

In the present study, we found some evidence that the presence of alternative prey reduced the predation by Atlantic mackerel larvae on fish larvae (Fig. 8). The daily predation rate on fish larvae of suitable prey size (assuming a digestion time of 24 h) declined with increasing density of copepod nauplii (the only other prey, along with fish larvae, selected for by Atlantic mackerel larvae), but not with an increasing density of copepods. The evidence for a reduction of predation was stronger when the actual consumption of alternative prey rather than their density was considered (Fig. 8). On average, the daily predation rate on fish larvae of suitable prey size was reduced from 47% to 12%/d when the average number of copepod prey in the gut of Atlantic mack-

erel larvae increased from 0 to >10 prey. Given that copepods were not selected for, it appears that the time spent manipulating them or the satiation resulting from their ingestion, rather than a switch in prey preference, interfered with the predation by Atlantic mackerel on newly hatched fish larvae.

The noncompensatory nature of cannibalism and piscivory by Atlantic mackerel larvae

Cannibalism and interspecific predation have often been proposed as mechanisms for the density-dependent regulation of marine fish populations (Ricker, 1954; Rothschild, 1986). Because the probability of encounter between Atlantic mackerel larvae should increase with their density, Grave (1981) suggested that cannibalism could be a simple mechanism for the density-dependent (i.e. compensatory) regulation of year-class strength in this species. For compensatory mortality to occur, an increasing fraction of the prey population must be removed per unit of time as the abundance of prey increases. In the present study, the capacity of mackerel larvae 5–14 mm long to prey on conspecifics and other fish larvae increased initially (but at a decreasing rate) and then saturated quickly as prey density increased (Fig. 7). Our results suggest a type-II functional response (Holling, 1959) in which mortality is actually depensatory, a decreasing fraction of the prey population being removed per unit time as prey density increases. This would be the case when mackerel larvae prey on other species of fish larvae. In the case of cannibalism, percent mortality is expected to remain constant (i.e. density-independent) with increasing density of Atlantic mackerel larvae because both prey and predators increase in number.

As predation on other fish larvae appears depensatory and cannibalism seems density-independent, we conclude that piscivory by Atlantic mackerel larvae 3–14 mm long does not contribute to the density-dependent regulation of population size. In the laboratory, cannibalism by Pacific mackerel ceased when schooling developed at the time of metamorphosis (approximately 15.2 mm SL) (Hunter and Kimbrell, 1980). In St. Georges Bay, the longest Atlantic mackerel cannibal observed was 15.2 mm (Ware and Lambert, 1985), but Grave (1981) reported intense cannibalism in early juveniles 13–19 mm SL in the North Sea. Whether piscivory by Atlantic mackerel >14 mm SL is compensatory remains to be determined.

Potential impact of cannibalism and piscivory by Atlantic mackerel larvae on recruitment

While predation on conspecifics and other species of fish larvae by Atlantic mackerel larvae <14 mm is not compensatory, the resulting mortality may nevertheless have some important impact on year-class strength. The latitudinal and vertical distributions of Atlantic mackerel, yellowtail flounder, and silver hake larvae generally coincided on Sable Island Bank, and predation or cannibalism by mackerel larvae could be of significance during the early life of these species. As mentioned earlier, the actual mortality rate attributable to predation by Atlantic mackerel larvae cannot be determined without an estimate of the transit time of fish larvae in the gut. In the laboratory, half the gut content of Pacific mackerel larvae fed *Brachionus plicatilis* was evacuated in 2 h (Hunter and Kimbrell, 1980). In the North Sea, digestion time (from food intake to complete defecation of the last food remains) for Atlantic mackerel larvae 8–14 mm, feeding on copepods, cladocerans, and conspecifics was 8–10 h (Grave, 1981).

In the present study, there were several indications that the digestion of fish larvae by Atlantic mackerel larvae was a relatively slow process. First, a single fish larva was found in the gut of mackerel larvae in 97% of the cases. Second, the frequency of larval fish prey in the gut increased progressively during the day (Fig. 4), an unlikely result if digestion and evacuation were rapid. Third, the proportion of fish larvae in the fore- and midgut of mackerel larvae remained high during the day, suggesting a slow transit time due to the large size of the prey (Fig. 5). Finally, the high frequency of partly or well-digested fish larvae (>90%) in contrast to slightly digested material, also suggested that fish larvae remained for a long time in the gut. All our observations are consistent with a continuous search for fish larvae, saturation of the digestive tractus upon the capture of a larva, slow digestion completed during the night, and evacuation in the early morning. Thus, although the time between capture and complete assimilation of a fish larva could be faster than we estimate, our results suggest a digestion time of 24 h.

The impact of predation by Atlantic mackerel larvae was limited primarily to newly hatched fish larvae. Assuming a conservative 24 h for the time between capture and evacuation, the percent mortality rate of fish larvae of suitable prey size attributable to predation by Atlantic mackerel larvae ranged from 7% to 57%/d (average of 31%/d). A value of 8 h for digestion time (Grave, 1981) would triple these estimates. Recent studies have often reported high mortality rates for the period just before and after yolk resorption when the swimming abilities of the fish are still poorly developed: 80%/d in jack mackerel, *Trachurus symmetricus* (Hewitt et al., 1985), 56% and 60%/d in capelin (Fortier and Leggett, 1985; Taggart and Leggett, 1987). For Atlantic mackerel,

Kendall and Gordon (1981) calculated an average mortality rate of 35%/d (SD=20%/d) for larvae <13 mm, whereas Ware and Lambert (1985) reported a rate of 42%/d for larvae <8 mm. Thus, according to our conservative estimate of digestion time, predation by Atlantic mackerel larvae (average 31%/d) would represent a sizable fraction (>38%) of the total mortality typically experienced by newly hatched larvae in the sea. This is consistent with an estimate of 41% for the fraction of the total mortality of newly hatched bay anchovy that could be attributed to predation by medusae (Purcell et al., 1994). According to our highest estimate (average 93%/d), predation by Atlantic mackerel larvae could wipe out populations of newly hatched co-occurring species in a few days, and all the mortality of newly hatched Atlantic mackerel could be attributed to cannibalism.

Atlantic mackerel larvae can dominate the larval fish assemblage over large areas in spring and early summer. For example, the species represented from 62.2% to 76.9% of the ichthyoplankton in the neritic, transitional, and oceanic zones of the Celtic Sea in the spring of 1980 (Horstman and Fives, 1994). We conclude that, in these areas, predation by Atlantic mackerel larvae could represent a significant survival bottleneck for co-occurring species in the days after hatching.

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Catchability coefficient for rockfish estimated from trawl and submersible surveys

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Abstract.—A bottom-trawl catchability coefficient was estimated for rockfish by comparing trawl catch rates to densities estimated from a manned submersible. A total of 16 comparisons were completed in 1989 and 1991 at depths of 180–283 m. Pacific ocean perch, *Sebastes alutus*, was the target species and accounted for 72% of the rockfish caught in the trawl. The seafloor area sampled by the trawl was calculated from the distance between the wingtips of the net and the distance the net traveled across the seafloor. The seafloor area sampled from the submersible was calculated from the distance the submersible traveled and the lateral range of visibility. A larger volume of water was sampled from the submersible because counts of rockfish included fish to 7 m above the seafloor, whereas the vertical opening of the trawl was 1.8 m; approximately 50% of the rockfish observed from the submersible were >1.8 m above the seafloor. Even though a larger volume of water was sampled from the submersible, catchability coefficients of 0.97 and 1.27 were estimated for minimum and maximum detection probabilities of rockfish from the submersible. Apparently, rockfish dove or were herded horizontally into the opening of the net. Density estimates of rockfish and other groundfish species are feasible from a submersible, and these estimates can be used to determine bottom-trawl catchability coefficients.

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Bottom-trawl surveys are used to estimate absolute abundance of most groundfish species in Alaska. The method is founded on the basic assumption that catch per unit of effort (CPUE) is a function of stock density. CPUE is converted to biomass from the area swept by the trawl and the sampling efficiency of the gear (catchability coefficient) (Alverson and Pereyra, 1969). The basic equation relating population size to CPUE is

$$P_{ij} = C_{ij} / qf_{ij},$$

where i = time period;
j = location or area;
P = exploitable population size in weight;
C = catch in weight;
q = catchability coefficient; and
f = fishing effort (Alverson and Pereyra, 1969).

Because there is no simple method of measuring catch efficiency, a catchability coefficient of 1.0 is used to convert CPUE data to biomass in bottom-trawl surveys (assuming a 100% catch efficiency across the horizontal spread of the net [wingtip to wingtip]). However, if fish are distributed above the headrope, are buried in the substrate, swim out of the path of the trawl, or escape through the net, the catchability coefficient is <1.0 and abundance is underestimated. Conversely, if fish are herded into the trawl by the bridles and trawl doors and do not escape above or under the net, the catchability coefficient is >1.0 and abundance is overestimated. Catchability coefficients depend on biological factors such as sensory capabilities as well as behavioral responses of the target species, and environmental factors such as light, temperature, and bottom type (see Gunderson, 1993, for an overview). A wide range of catchability coefficients were estimated in studies that monitored efficiency of bottom trawls: Harden-Jones et al. (1977) attached acoustic tags to flatfish and monitored their behavior in response to trawl gear; 61% of the fish in the path of the net were captured. Main and Sangster (1981) observed the catch process of several groundfish species from a towed underwater vehicle; each species responded differently with regard to net avoidance, escapement, and herding by the bridles and doors. Korotkov[1] observed groundfish behavior in front of a bottom trawl from an underwater towed apparatus; catchability coefficients of 0.1 to 0.4 were estimated, depending on trawl rigging and trawl orientation to the bottom. These studies relied on species that could be tagged or on species located at shallow depths where ambient

[1] Korotkov, V. K. 1984. Fish behaviour in a catching zone and influence of bottom trawl rig elements on selectivity. Int. Counc. Explor. Sea, Council Meeting 1984, paper/B:15, 14 p.

light was available for observations. In this study catchability coefficients are estimated for rockfish that inhabit deep depths where ambient light is minimal and that cannot be tagged because of gas bladder expansion when sampled. Catchability coefficients are estimated by comparing trawl catch rates with counts from a manned submersible.

Pacific ocean perch, *Sebastes alutus*, was the target species of this study. Biomass estimates of Pacific ocean perch in the Gulf of Alaska, based on bottom-trawl surveys conducted triennially, were 214,827, 138,003, and 460,755 metric tons for 1987, 1990, and 1993 (Heifetz et al.[2]). These extreme changes in biomass are unlikely, given the slow growth and low mortality rates of *Sebastes* spp. (Heifetz et al.[2]). To improve Pacific ocean perch biomass estimates from bottom-trawl surveys, manned submersibles and bottom trawls have been used since 1988 to study their substrate association and spatial distribution, and the efficiency of bottom trawls for sampling them. Most Pacific ocean perch observed from a submersible were concentrated on smooth substrates in groups of 2–200 fish (Krieger, 1993). Counts of Pacific ocean perch from a manned submersible in 1989 were compared with catch rates from trawl hauls, and a catchability coefficient of 2.1 (SE=0.4) was estimated for the distance between the wingtips of the net. This catchability coefficient was considered preliminary for three reasons: 1) only nine submersible-trawl comparisons were made; 2) no fish were assumed captured while the trawl was retrieved; and 3) all fish were assumed counted within the viewing range from the submersible (Krieger, 1993). The catchability coefficient estimated in this study is based on an increased number of submersible versus trawl comparisons and on improved density estimates from trawl catch rates and submersible counts.

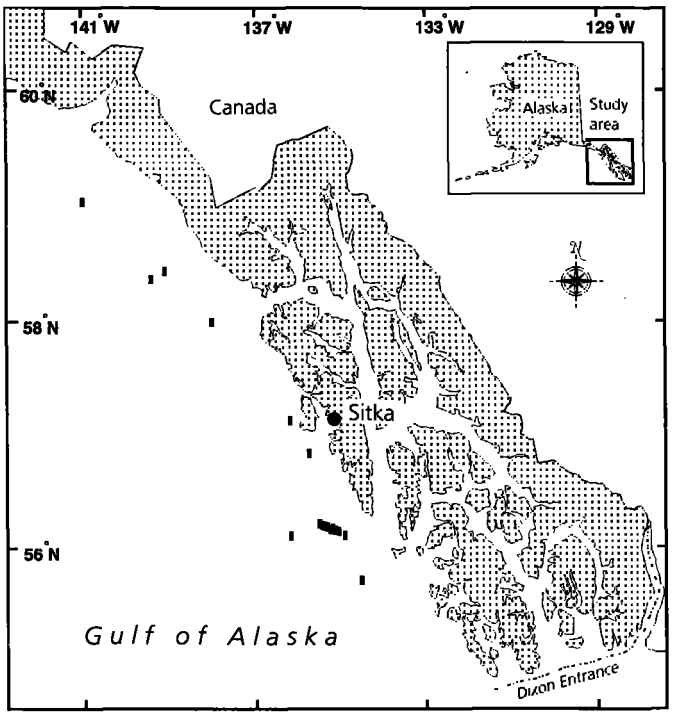

Figure 1

Locations of submersible dive sites that were sampled with bottom trawls in the eastern Gulf of Alaska, 1989 and 1991.

Materials and methods

Sampling of submersible counts and trawl catch rates for Pacific ocean perch were conducted in August 1989 and 1991 on the outer continental shelf in the eastern Gulf of Alaska (Fig. 1). The sampling strategy was to count rockfish from the submersible along four parallel transects, and then intersect the four transects with a bottom trawl. Each transect was determined by following a compass heading for 15 min, and there were 5 min of travel between transects. Trawl hauls were considered successful only if the gear was retrieved intact (no tears in the net or broken cables) and the trawl intersected at least three of the four submersible transects. Submersible dives and bottom trawling were completed during daylight at 180–283 m depths. The time between dives and trawls was <4 h for 13 of the 16 comparisons. Substrates consisted of pebble or sand, interspersed with cobble <0.5 m in diameter and boulders 0.5–5.0 m in diameter.

Submersible

We used the two-man submersible *Delta* chartered by the National Oceanic and Atmospheric Administration, National Undersea Research Center. This battery-powered submersible is 4.7 m long, dives to 365 m, and travels 2–6 km/h for 2–4 h. It is equipped with halogen lights and internal and external video cameras. In addition, it has a magnetic compass, directional gyro compass, underwater telephone, and transponder that allow tracking of the submersible from a surface vessel. The pilot maintained the submersible within 0.5 m of the bottom, while a scien-

[2] Heifetz, J., D. M. Clausen, and J. N. Ianelli. 1994. Slope rockfish. *In* Plan Team for the Groundfish Fisheries of the Gulf of Alaska (eds.), Stock assessment and fishery evaluation report for the groundfish resources of the Gulf of Alaska as projected for 1995, Sect. 5. North Pac. Fish. Manage. Counc., P.O. Box 103136, Anchorage AK 99510.

tist counted rockfish through a starboard porthole 0.5 m above the bottom of the submersible. Rockfish counts and behavior were audio- and video-recorded for subsequent analysis. Rockfish densities were derived from the number of fish counted and the seafloor area searched. This area was calculated from the distance the submersible traveled and the estimated lateral range of visibility from the starboard porthole. The observer estimated that lateral visibility ranged from 3 to 7 m, depending on water clarity. The ability of the observer to estimate distance was tested by three methods: 1) a length of pipe marked at meter intervals was laid on the seafloor and observed on two dives; 2) a hand-held sonar gun provided distance readouts to rock formations located at the maximum visibility range on six dives; and 3) the submersible's sonar provided distance readouts when the seafloor became visible during descents and when the seafloor disappeared from view during ascents. Observer estimates of distance were consistently within 1 m of actual distances. Accuracy to within 1 m was possible because constant illumination was provided entirely by the submersible lights, and water clarity was consistent at each site. The pilot assisted in counting fish >4 m above the seafloor from a panoramic view 2 m above the scientist. The pilot could see at least 10 m above the seafloor.

Identification of Pacific ocean perch from the submersible was not always possible because they look similar to three other red rockfish species: redstripe rockfish, *S. proriger*; sharpchin rockfish, *S. zacentrus*; and harlequin rockfish, *S. variegatus*. Therefore, rockfish density estimates from submersible counts and from trawling include these three species in addition to Pacific ocean perch. Most rockfish observed from the submersible, however, were identified as Pacific ocean perch by their symphyseal knob and body shape. Trawl sampling confirmed their dominance: 72% of the rockfish caught were Pacific ocean perch.

A detection probability (DP) from the submersible was estimated by measuring angles to targets with a clinometer. Clinometer readings were collected from a fixed height above the seafloor to red sea stars, *Luidiaster* spp., on the seafloor; sea stars were selected as targets because their color was similar to red rockfish and they were abundant, stationary targets. The DP was assumed to equal 1.0 near the submersible and to decrease to zero at some distance from the submersible. The DP was computed as the ratio of the observed and expected density of targets. The observed population density was computed as

$$P_i = N_i / D_i ,$$

where N_i is the observed count in angle interval i, and D_i is the distance along the seafloor corresponding to angle interval i. The expected density was computed as the average observed density within the full-detection range (the range where the observed density did not decrease).

Bottom trawling

Trawl gear consisted of a 400-mesh Eastern otter trawl equipped with 55-m bridles between the net and 1.5 × 2.1-m doors weighing 386 kg each. The average distance between the wingtips (15.8 m) and the trawl doors (45.0 m) was determined during four trawl hauls by using mensuration gear. Krieger (1993) used a wingtip spread of 14 m, based on previous net measurements of the 400 Eastern trawl, to estimate the preliminary catchability coefficent (NMFS, 1993). A net height (foot-rope to head-rope) of 1.8 m is based on previous mensuration gear measurements of 1.4–1.8 m (NMFS, 1993).

Trawl catches were processed for total number and weight by species. Rockfish density estimates were derived from the number of rockfish captured and the seafloor area swept by the net. The seafloor area swept was the distance trawled multiplied by the horizontal spread of the net. Trawl distances (0.93–1.74 km/haul) and trawl speeds (5.0–6.5 km/h) were calculated from position fixes with a global positioning system (GPS). Trawl periods ranged from 10 to 18 min, depending on trawl speed and trawl distance needed to intersect the submersible transects. At the completion of the 10–18 min trawl period, vessel speed was reduced while the trawl was retrieved. To determine the sampling capabilities of the trawl during retrieval, catch rates from six "standard" trawl hauls were compared with catch rates from seven "retrieval" trawl hauls. A "standard" trawl haul was followed by a "retrieval" trawl haul at randomly selected sites separated by <3 km distance by using the same trawl depths, cable ratios, and vessel speeds as those for trawling at the submersible sites. "Standard" trawl hauls consisted of the net sweeping the seafloor for 10 min at 5.5–6.0 km/h and then being retrieved at reduced vessel speed. "Retrieval" trawl hauls consisted of the net sinking to the seafloor and then being retrieved immediately at reduced vessel speed. A sonar net-sounder was used to determine when the net departed the seafloor. GPS fixes and the rate of cable retrieval were used to determine the speed of the trawl during retrieval.

Data analysis

Rockfish density estimates from submersible counts and trawl catch rates were based on the total sea-

floor area sampled, but were not adjusted for the larger water column sampled from the submersible; submersible personnel surveyed to 10 m above the seafloor, whereas the net sampled to 1.8 m above the seafloor. A catchability coefficient was estimated by comparing the average density from trawl catch rates to the average density from submersible counts. The bootstrap resampling method (Efron, 1982; Efron and Tibshirani, 1986) was used to test the statistical significance of the difference and to estimate a confidence interval for the catchability coefficient. A bootstrap sample was created by sampling 1,000 times with replacement. The statistical significance of the difference (P) between submersible and trawl comparisons was computed by tallying how many of the 1,000 bootstrap replicates were greater than zero; P is for a two-sided test.

Results

Sampling during trawl retrieval

During trawl retrieval, the net remained in contact with the seafloor an additional 7–9 min. The speed of the net along the seafloor during retrieval was 4–5 km/h—a combination of the vessel moving slowly forward and retrieval of the cable. Catch rates for Pacific ocean perch averaged 34.9/1,000 m^2 during "standard" trawling and 29.8/1,000 m^2 during "retrieval" trawling (Table 1) and were not significantly different (2-sided t-test, $P>0.5$). Apparently, the net continued to sample effectively during retrieval; therefore, trawl catch rates included the seafloor area swept during trawl retrieval.

Detection probability from submersible

Observed densities of sea stars began decreasing 3.4 m from the submersible; therefore, the expected density was the average density of targets within the 3.4-m full-detection range. Assuming DP = 1.0 within 3.4 m, we calculated a DP of 0.77 for the entire 5.3-m range of visibility, which implies that about 3/4 of the sea stars were counted within the range of visibility. Sea stars were more difficult to detect than were rockfish because of differences in body shape; the flat bodies of sea stars blended into the seafloor, but the fusiform bodies of rockfish extended above the seafloor. Therefore, the 0.77 DP for sea stars is considered a minimal DP for rockfish and catchability coefficients are calculated for both a 0.77 DP and a 1.0 DP.

Comparison of submersible counts with trawling catch rates

Sixteen dive sites were successfully sampled by bottom trawling (Table 2). The average rockfish densities were 21.7/1,000 m^2 from trawling, and 22.4/1,000 m^2 (DP=0.77) and 17.1/1,000 m^2 (DP=1.0) from submersible counts, resulting in catchability coefficients of 0.97 (95% confidence interval: 0.70–1.32) and 1.27 (95% confidence interval: 0.91–1.73) for the area swept between the trawl wingtips. No significant difference was detected between density estimates from the submersible and trawl for either the 0.77 DP (P=0.95) or the 1.0 DP (P= 0.13).

Discussion

The 0.97 and 1.27 catchability coefficients are considerably less than the 2.1 (SE=0.4) catchability coefficient reported by Krieger (1993), mainly because they include the area sampled during trawl retrieval. The 0.77 DP from the submersible and the increased estimate of net width also contributed to lower estimates of catchability coefficients.

If rockfish did not react to the trawl gear, density estimates from submersible counts would have exceeded those from trawl catch rates because approxi-

Table 1

Number of rockfish caught, distance trawled, and estimated catch rates during standard (10 min + retrieval) and retrieval trawling using a 400 Eastern otter trawl at depths of 180–283 m in the eastern Gulf of Alaska.

	Distance (km)		
Number caught	Trawling (10 min)	Retrieval (7–9 min)	Catch rate (number/1,000 m^2)
2,263	1.10	0.63	82.53
1,267	0.96	0.74	47.02
778	0.93	0.63	31.46
660	1.06	0.65	24.35
416	1.02	0.78	14.58
274	1.15	0.69	9.40
Standard trawling mean = 34.89			
686		0.62	69.81
677		0.74	57.72
304		0.69	27.80
240		0.78	19.41
204		0.63	20.43
131		0.74	11.17
21		0.63	2.10
Retrieval trawling mean = 29.78			

Table 2

Density (number/1,000 m²) of rockfish estimated from submersible counts and trawl catch rates at 16 sites in the eastern Gulf of Alaska, 1989 and 1991. Submersible densities are for detection probabilities (DP) of 1.0 and 0.77.

	Submersible				Trawl		
			Density (number/1,000 m²)				
Site	Count	Area (1,000 m²)	DP=1.0	DP=0.77	Caught	Area (1,000 m²)	Density (number/1,000 m²)
1	1,040	12.0	86.7	113.0	2,902	26.3	110.3
2	747	12.3	60.7	79.2	884	26.3	33.6
3	380	13.9	27.3	35.6	1,134	30.2	37.6
4	391	17.3	22.6	29.5	1,419	37.6	37.7
5	230	12.1	19.0	24.8	848	30.2	28.1
6	187	15.3	12.2	15.9	339	30.8	11.0
7	222	16.8	13.2	17.2	1,244	33.4	37.2
8	117	13.7	8.5	11.1	658	35.8	18.4
9	136	12.9	10.5	13.7	426	29.2	14.6
10	79	13.6	5.8	7.6	352	32.9	10.7
11	55	14.4	3.8	5.0	31	34.4	0.9
12	38	13.6	2.8	3.6	158	37.6	4.2
13	16	17.6	0.9	1.2	115	38.3	3.0
14	1	7.1	0.1	0.2	10	33.3	0.3
15	1	5.1	0.2	0.3	6	39.2	0.2
16	0	14.1	0.0	0.0	0	26.3	0.0
Mean			17.1	22.4			21.7

mately 50% of the rockfish were distributed above the 1.8-m height sampled by the net. The similar density estimates imply that rockfish dove to within 1.8 m of the seafloor or were herded horizontally into the net opening by the bridles and doors. Herding of fish by trawl doors and bridles has been documented for several semidemersal species by using acoustic tags (Harden-Jones et al., 1977), direct observations from a towed submersible (Main and Sangster, 1981), and underwater video (Glass and Wardle, 1989). For Pacific ocean perch, herding and diving in response to trawl gear was indicated in studies using sonar and variable bridle lengths. Sonar recordings of Pacific ocean perch indicated that the fish were diving as a fishing vessel passed over them (Kieser et al., 1992) and were diving in response to trawl gear (Nunnallee[3]). Herding was indicated in two studies where increased bridle lengths resulted in increased catch rates of Pacific ocean perch: catch rates increased 2.79- and 3.24-fold when 36.6-m bridles were increased 27.4 m and 54.9 m (Harling and Davenport, 1977), and catch rates were about 2.5 times higher for a net with 33% longer bridles, even though its vertical and horizontal opening was smaller (Wilkins and Weinberg, 1987).

This study demonstrates that estimates of fish density are feasible from a submersible and that these estimates can be used to determine bottom-trawl catchability coefficients. Rockfish were ideal for counting within the illuminated area because they were brightly colored, solitary or loosely grouped, not hidden by rugged habitat, usually motionless, and generally distributed within 7 m of the seafloor (Krieger, 1993). Most rockfish remained oriented into the current while the submersible passed, indicating minimal response to the submersible. The only movements observed were those of individual fish moving out of the direct path of the submersible and those of a few groups moving toward the submersible. Counts of fish within these groups were not hindered, because the fish swam slowly and maintained their spacing and orientation. The pilot observed similar behavior on all sides of the submersible. In addition to rockfish, density estimates appear feasible for numerous invertebrate species and groundfish species, including shortspine thornyhead, *Sebastolobus alascanus*, and several flatfish species.

The value of comparing in situ observations of groundfish with trawl catches has been documented

[3] Nunnallee, E. P. 1991. An investigation of the avoidance reactions of Pacific whiting (*Merluccius productus*) to demersal and midwater trawl gear. ICES Council Meeting 1991, paper/B:5, Sess. U., Fish Capture Committee, 17 p.

in other studies. Uzman et al. (1977) compared submersible counts with trawl catches of fish and invertebrates and concluded that continuous visual assessment of the benthos provides the best approximation of species abundance and diversity. Adams et al. (1995) compared remotely operated vehicle counts with trawl catches of groundfish and concluded that for strongly bottom-associated groundfish, ROV abundance estimates were significantly higher and were less variable than bottom-trawl abundance estimates.

Application to stock assessment

The catchability coefficient estimated in this study with a 400 Eastern trawl may not be directly applicable to Alaska trawl surveys that use a Nor'eastern trawl. The main differences between the Nor'eastern trawl and 400 Eastern trawl are net height and footrope design: the Nor'eastern net height is 6–10 m and roller gear (36–cm rubber bobbins separated by 10-cm rubber disks) is attached to the footrope, whereas the 400 Eastern has a maximum 1.8-m net height with no roller gear on the footrope. The 15–17 m wingtip spread of the Nor'eastern is similar to the 15.8 m average spread of the 400 Eastern trawl, whereas the 47–57 m door spread of the Nor'eastern is wider than the average 45-m door spread of the 400 Eastern. The Nor'eastern trawl is assumed to be more efficient for capturing rockfish because of its higher vertical opening. Roller gear attached to the Nor'eastern trawl may either increase or decrease catch efficiency of rockfish. A repeat of this study using the Nor'eastern trawl is recommended for determining a catchability coefficient for Alaska trawl survey data.

Accurate indexing of Pacific ocean perch seems possible from bottom-trawl surveys because of their substrate preference and susceptibility to bottom-trawl gear. Pacific ocean perch concentrate on trawlable substrates (Krieger, 1993) and were effectively sampled in this study. Assuming that fish occupy the water column above the opening of the trawl and inhabit untrawlable areas, Balsiger et al. (1985) reported that CPUE data from bottom-trawl surveys probably underestimate Pacific ocean perch biomass. Submersible studies, however, indicate Pacific ocean perch biomass may be overestimated from bottom-trawl surveys for two reasons: 1) the catchability coefficient of the survey trawl may exceed 1.0 for the distance between the wingtips; and 2) only trawlable substrates where Pacific ocean perch are concentrated are sampled during surveys, but CPUE from trawlable substrates is applied to untrawlable substrates.

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Description of pelagic larval and juvenile stripetail rockfish, *Sebastes saxicola* (family Scorpaenidae), with an examination of larval growth

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Abstract.—Pigmentation, morphometrics, head spination, fin development, and meristic characters were described and illustrated for the developmental series of larval and pelagic juvenile (4.7–38.2 mm standard length) stripetail rockfish, *Sebastes saxicola*. Pigment patterns were sufficiently distinct to differentiate larval and juvenile *S. saxicola* from other *Sebastes* species occurring in the study area (central California). Early larvae of *S. saxicola* were identified by the presence of pigment on the postanal ventral midline and the nape and by the lack of pigment on the lower jaw and the pectoral fins. Late larval *S. saxicola* had areas of intense pigment along the dorsal, lateral, and ventral midlines. Juvenile *S. saxicola* were identified by their distinctive bar pattern and meristic characters. Examination of otolith characters indicated that the extrusion check radius of *S. saxicola* differed from that of other *Sebastes* species examined. Otolith characters, used in combination with pigment patterns, readily separated larval *S. saxicola* from other *Sebastes* species. Calculated growth rates for *S. saxicola* were slower than most previously reported growth rates for other *Sebastes* species.

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Rockfishes (*Sebastes* spp.) are important to the commercial and recreational fisheries of the northeastern Pacific. In 1993, they accounted for approximately 18% 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). Sixty-one species of rockfish are reported from California alone (Eschmeyer et al., 1983). Management of the fishery has been plagued by taxonomic problems. The need to separate adult rockfish landed by the fishery has long been recognized (Phillips, 1964; Chen, 1971). Larvae and juveniles are far more difficult to separate than are adults, but the need to differentiate them is growing with their use as subjects of 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 *S. saxicola*.

Stripetail rockfish, *Sebastes saxicola*, are small (maximum size 39 cm) and occur on soft bottom at depths of 46–421 m (Eschmeyer et al., 1983). This species accounts for less than 1% of the commercial groundfish catch by weight (Pearson[3]), perhaps because of its small size. It is one of the more abundant groundfish species off Santa Cruz, California (Adams et al., 1995), and is generally common in waters be-

[1] PFMC (Pacific Fishery Management Council). 1994. Status of the Pacific coast groundfish fishery through 1994 and recommended acceptable biological catches for 1995. Pacific Fishery Management Council, Portland, OR, 118 p.

[2] Ralston, S., J. R. Bence, M. B. Eldridge, and W. H. Lenarz. 1993. Estimating the spawning biomass of shortbelly rockfish (*Sebastes jordani*) in the region of Pioneer and Ascension Canyons using a larval production method, 32 p. National Marine Fisheries Service, Southwest Fisheries Science Center, 3150 Paradise Drive, Tiburon, CA 94920.

[3] Pearson, D. E. 1994. National Marine Fisheries Service. 3150 Paradise Drive, Tiburon, CA 94920. Personal commun.

tween 100–149 fathoms off the central California coast (Gunderson and Sample, 1980). This study describes the development of *S. saxicola* from pre-extrusion larvae to the pelagic juvenile stage and describes the age and growth of larval *S. saxicola*.

Methods

Specimens of pelagic larval and juvenile *S. saxicola* were obtained from cruises conducted aboard the NOAA RV *David Starr Jordan* and the Moss Landing Marine Laboratories RV *Ed Ricketts*. Specimens were taken with Manta nets (0.505-mm mesh), bongo nets (0.505-mm mesh), a 5-m^2 Methot-Isaacs-Kidd (MIK) trawl (2-mm mesh and a 0.505-mm codend), and a 26 × 26 m midwater trawl (12.7-mm stretched mesh codend liner). Manta nets were used during surveys in January and February 1992, bongo nets in January and February 1992 and January 1994, MIK trawls in March 1992 and 1993, and midwater trawls in May and June 1990–93. Specimens taken with Manta nets, bongo nets, and MIK trawls were preserved in 95% EtOH, whereas specimens from midwater trawls were frozen. Pre-extrusion larvae were obtained from three adult females in February 1994 and preserved in 95% EtOH. All samples were collected off central California between Cypress Point (36°35'N) and Salt Point (38°35'N).

We examined and measured 197 *S. saxicola* larvae and juveniles from 3.3 mm notochord length (NL) to 43.9 mm standard length (SL). Specimens greater than 19.9 mm SL were identified by meristic characters (Chen, 1986; Matarese et al., 1989; Moreland and Reilly, 1991; Laroche[4]); melanophore patterns were recorded. Specimens less than 20 mm SL were initially identified by pigment patterns developed from a size-series based on pre-extrusion pigment patterns and 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 taken only on fish larger then 15 mm SL.

We measured snout to anus length, head length, snout length, eye diameter, body depth at the pectoral-fin base, pectoral-fin length, pectoral-fin base depth, and parietal spine length on 28 specimens from 3.3 mm NL to 20.9 mm SL. Terminology for morphometrics followed Richardson and Laroche (1979).

Eighteen specimens from 6.2 mm NL to 20.9 mm SL were stained with Alizarin Red S and examined for head spination. Terminology for head spination followed Richardson and Laroche (1979).

Otoliths were removed from 58 *S. saxicola* larvae (4.2 mm NL to 19.7 mm SL) and aged according to procedures in Laidig et al. (1991). In addition, otoliths from five species (*S. atrovirens*, *S. auriculatus*, *S. maliger*, *S. rastrelliger*, and *S. semicinctus*) and two species complexes (the copper complex [*S. atrovirens*, *S. carnatus*, *S. caurinus*, and *S. chrysomelas*] and the gopher complex [*S. carnatus* and *S. chrysomelas*]) were removed for comparison of otolith characters with *S. saxicola* (Laidig and Ralston, 1995). These five species and two complexes were chosen for similarity in pigment patterns with preflexion *S. saxicola*; *S. rastrelliger* was also selected for its similar pigmentation in postflexion fish. In addition, otoliths were removed and examined from 15 *Sebastes* larvae of unknown species with pigment patterns similar to *S. saxicola*, but with pigment present on the axillary surface of the pectoral fins.

Results

General development

Larvae were extruded at a size of 3.3–5.2 mm NL. Notochord flexion began at approximately 5.8 mm NL and was completed by 8.0 mm SL. The full adult complement of pectoral-fin rays developed during late-stage flexion and early postflexion (16 rays, Table 1). By 7.0 mm NL, anal-fin rays had begun to form and a full adult complement (7 rays, Table 1) was present in 90% of the fish by 8.0 mm SL. The dorsal, pectoral, and pelvic fins began to form around 7.5 mm NL and a full adult complement (dorsal=12 rays, pectoral=16, pelvic=5, Table 1) was present by approximately 9.0 mm SL. Lateral line pores first appeared around 17 mm SL and a complete series was apparent by approximately 38 mm SL. Because we had only a few specimens above 38 mm SL, we were unable to obtain accurate lateral line pore counts.

Morphometrics

Changes in body shape in *S. saxicola* were related to notochord flexion (Table 2). As the larvae began flexion, they became more stout-bodied, as evidenced by the increase in body depth at the pectoral-fin base. During flexion, the pectoral-fin length increased as the full adult complement of fin rays was attained (Table 2). The parietal spine length increased until approximately 10 mm SL when spine growth ap-

[4] Laroche, W. A. 1987. Guide to larval and juvenile rockfishes (*Sebastes*) of North America. Box 216, Enosburg Falls, VT 05450. Unpubl. manuscr., 311 p.

Table 1

Frequency of occurrence of dorsal-, anal-, and pectoral-fin ray counts and gill-raker counts in larval and juvenile stripetail rockfish, *Sebastes saxicola*.

Character	Count	Frequency of occurrence	Percent occurrence
Dorsal-fin rays	11	2	1.4
	12	136	91.8
	13	10	6.8
Anal-fin rays	6	4	2.5
	7	153	95.0
	8	4	2.5
Pectoral-fin rays	15	14	10.4
	16	117	86.6
	17	4	3.0
Gill rakers	28	2	3.1
	29	6	9.2
	30	15	23.1
	31	15	23.1
	32	22	33.8
	33	3	4.6
	34	2	3.1

peared to cease. All other measurements showed a marked increase after flexion was completed (Table 2).

Head spination

Head spines first began to appear during flexion (Table 3). By 9 mm SL, the postocular, parietal, pterotic, inferior posttemporal, inferior and superior opercular, 1st inferior and 1st superior infraorbital, and all preopercular spines were present. By approximately 10 mm SL, the supracleithral, nuchal, 2nd inferior intraorbital, and nasal spines were formed. By 20 mm SL, the preocular, superior posttemporal, and tympanic spines formed. The cleithral, 3rd superior infraorbital, and 3rd inferior infraorbital spines were not present in larvae less than 21 mm SL. Supraocular and coronal spines did not occur at any size.

Pre-extrusion pigmentation

Pre-extrusion larvae had pigment along the ventral midline extending from the anus to myomere 23 or 24 (second and third most posterior myomeres). This pigment was typically strong, with 2–4 melanophores per myomere (Fig. 1A). Pigment consisting of 6–16 melanophores was also located along the dorsal midline from approximately myomeres 15–23. The dorsal and posterior surfaces of the gut cavity were also heavily pigmented. In addition, in 72% of the larvae very small melanophores (1–5 in number) were observed on the ventral surface of the gut cavity. A single melanophore was located in the nape region of the head in 80% of specimens (Fig. 1A).

Body pigmentation

After extrusion, melanophores along the dorsal midline increased in number and size (Fig. 1B). This increase was most noticeable in the advancement of pigment in the anterior direction (there was little or no advancement posteriorly). At approximately 12 mm SL, the nape and dorsal midline pigments merged to form a solid line along the dorsal body surface. This dorsal body pigment increased in intensity as larvae grew.

A distinct pattern of five body bars (numbered 1–5 from anterior to posterior) was apparent in juveniles greater than 25 mm SL. Body-bar 1 began to appear in the nape region at 13 mm SL (Table 4; Fig. 1D). This bar extended from the dorsal midline to the operculum and was fully formed by approximately 24 mm SL. The next bar to form was body-bar 4 (an inverted triangle under the soft dorsal fin), which appeared at 17 mm SL (Fig. 1E), and was completely developed by approximately 35 mm SL (Table 4; Fig. 1F). Body-bar 2 was the next bar to form (from the spinous dorsal fin to the dorsal surface of the gut), appearing at approximately 19 mm SL and becoming fully developed by 33 mm SL. Body-bars 3 and 5 (from the spinous dorsal fin to the anus and an inverted triangle on the caudal peduncle, respectively) were the last bars to form; both appeared at approximately 20 mm SL and were fully developed at 38 mm SL (Fig. 1F).

The postanal ventral midline melanophores near the anus were lost soon after extrusion (Fig 1B). By 6 mm NL, the anteriormost melanophores were located approximately three myomeres posterior to the anus. The anterior melanophores decreased in number with increased fish length until approximately 10 mm SL. At this size, postanal ventral midline pigment began to advance anteriorly with increased fish size. In addition, pigment intensified to form a very dark area extending from the middle of the anal fin posteriorly to the first few ventral pterygiophores of the caudal fin. In larger juveniles (greater than 25 mm SL), the postanal ventral midline pigment became less intense and only a few melanophores remained near the anal fin articulations (Fig. 1, E and F).

Pigment on the lateral midline began to develop in 6 mm NL fish with a few melanophores near the caudal peduncle (Table 4; Fig. 1B). As fish length increased, the lateral midline pigment increased and became most intense at approximately 20 mm SL,

Table 2

Morphometrics (mm) of stripetail rockfish, *Sebastes saxicola*. Fish undergoing flexion are shown between the dashed lines. — = measurements not taken.

SL (mm)	Snout–anus length	Head length	Snout length	Eye diameter	Body depth	Pect.-fin length	Pect.-fin base depth	Parietal spine length
3.3	1.15	0.70	0.08	0.29	0.51	0.18	0.15	0.00
3.9	1.35	0.74	0.05	0.30	0.47	0.23	0.17	0.00
4.1	1.42	0.71	0.07	0.28	0.48	0.18	0.16	0.00
4.1	1.41	0.76	0.09	0.33	0.50	0.25	0.16	0.00
4.4	1.61	0.79	0.07	0.36	0.63	0.22	0.20	0.00
4.6	1.53	0.72	0.07	0.29	0.57	0.24	0.15	0.00
4.7	1.77	0.88	0.13	0.36	0.64	0.29	0.21	0.00
4.7	1.72	0.85	0.14	0.40	0.71	0.25	0.18	0.00
4.7	1.71	0.85	0.09	0.34	0.62	0.20	0.21	0.00
5.0	1.66	0.85	0.13	0.34	0.63	0.20	0.21	0.00
5.0	1.73	0.80	0.09	0.32	0.52	0.26	0.16	0.00
5.1	1.76	0.90	0.22	0.39	0.73	0.26	0.19	0.00
5.8	—	1.8	0.4	0.7	1.2	—	0.4	0.2
6.2	3.2	2.2	0.6	0.8	1.5	0.4	0.5	0.3
6.9	3.6	2.2	0.6	0.8	1.6	0.6	0.6	0.3
7.3	3.6	2.5	0.7	0.8	1.7	0.7	0.6	—
8.1	4.0	2.5	0.7	0.9	1.8	0.7	0.6	0.4
8.7	4.5	2.8	0.9	1.0	1.9	0.9	0.7	0.5
9.1	5.3	3.0	0.9	1.1	2.4	1.3	0.7	0.5
10.2	6.0	3.5	1.1	1.2	2.9	1.5	0.9	0.5
10.4	6.1	3.7	1.1	1.3	2.8	1.6	0.8	0.3
11.3	6.5	3.9	1.2	1.2	3.0	1.9	0.9	0.4
12.2	7.0	4.2	1.2	1.5	3.2	2.2	1.1	0.3
13.4	7.7	4.5	1.4	1.5	3.7	2.5	1.1	0.5
14.3	8.0	4.9	1.3	1.5	3.9	3.2	1.1	0.4
16.4	9.3	5.5	1.3	1.8	4.5	3.9	1.3	0.4
18.4	10.4	6.3	1.5	2.2	4.9	4.5	1.5	0.4
20.9	12.4	7.5	2.5	2.4	5.4	4.9	1.6	0.3

forming a line stretching from the posterior caudal peduncle (sometimes onto the caudal fin) to the posterior edge of the operculum. After 20 mm SL, pigment on the body intensified (mostly above the lateral midline), causing the lateral midline pigment to become much less evident (Fig. 1E). By 35 mm SL, the lateral midline pigment was virtually indistinguishable as it merged with the body pigment and the five body bars (Fig. 1F).

The hypural region remained mostly unpigmented until approximately 15 mm SL, when pigment formed on the posterior edge of the hypural plates (Fig. 1D). At 20 mm SL, when body-bar 5 became noticeable, the hypural region was highly pigmented (Fig. 1E).

Fin pigmentation

The pelvic and pectoral fins were relatively unpigmented in the larval and pelagic juvenile stages. Pigment was noted in the pelvic fins of only two fish. In these two fish, pigment occurred at the base of the rays of the left pelvic fin. In larger individuals, a few melanophores were noted on the pectoral fin, but these were not in a consistent area of the fin and did not constitute a regular pattern (Table 4). In addition, the axillary surface of the pectoral fin remained unpigmented throughout development.

Pigment on the dorsal fin began appearing at 17 mm SL with a few melanophores on the spinous fin. Melanophores appeared first on the anterior portion of the spinous dorsal fin and spread along the entire fin length as fish size increased. By 25 mm SL, most of the length of the spinous dorsal fin had some pigment, and melanophores were just beginning to appear on the soft dorsal fin (Fig. 1E). By 38 mm SL, the spinous dorsal fin was completely pigmented and the soft dorsal fin had a distinctive pattern. This pattern consisted of two horizontal pigment bands: the first was located just ventral to the tips of the soft fin rays, and the second at the fin ray bases. In addi-

Table 3

Development of head spines in stripetail rockfish, *Sebastes saxicola*. "1" means spine was present and "0" means spine was absent.

	Standard length (mm)																	
Spines	6.2	6.9	7.3	8.1	8.5	8.7	9.1	9.7	10.2	10.4	11.3	12.2	13.4	14.3	15.4	16.4	18.4	20.9
Nasal	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1
Preocular	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1
Supraocular	0	0	0	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	1	1	1
Coronal	0	0	0	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	0	0	0	0	0	0	0	1	1
Parietal	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Nuchal	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1
Pterotic	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Posttemporals																		
Superior	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
Inferior	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Supracleithral	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1
Cleithral	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Operculars																		
Superior	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Inferior	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1
Preoperculars																		
1st Anterior	1	1	1	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	1	1	1
3rd Anterior	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
1st Posterior	0	0	0	0	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	1	1	1
3rd Posterior	1	1	1	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	1	1	1
5th Posterior	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Infraorbitals																		
1st Inferior	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
2nd Inferior	0	0	0	0	0	0	0	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	0	0	0
1st Superior	0	1	1	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	0	1	1
3rd Superior	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4th Superior	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1

tion, there was an unpigmented area at the base of the first two soft rays and the last spine (Fig. 1F).

Pigment began appearing on the anal fin at approximately 30 mm SL. Pigment intensified quickly, and by 38 mm SL a pattern had developed, consisting of a band through the middle of the fin and extending from the first anal spine to the last ray (Fig. 1F).

The caudal fin remained unpigmented until approximately 38 mm SL, when pigment began forming near the base of the rays. On the largest fish examined (43.9 mm SL), pigment was observed sporadically on a few fin rays.

Head pigmentation

Pigment on top of the cranium began forming soon after extrusion (Table 4). Four to five melanophores were present by 5 mm NL. The number and size of melanophores increased with increased fish size and by 7 mm NL, the head had become highly pigmented (Fig. 1B). Nape pigment also increased from one melanophore to five or six melanophores by 6 mm NL (Fig. 1B). At around 7 mm NL, nape pigment was overgrown by muscle tissue and became embedded. After flexion, pigment again appeared on the surface of the nape area. This pigment intensified with increased fish size.

At 7 mm NL, pigment began to develop on the anterior portion of the head between the eyes. As fish size increased, more pigment was added to this area. Pigment began forming on the upper jaw at approximately 8 mm SL. By 10 mm SL, pigmentation on the upper jaw and the anterior section of the head was well developed and could not always be differenti-

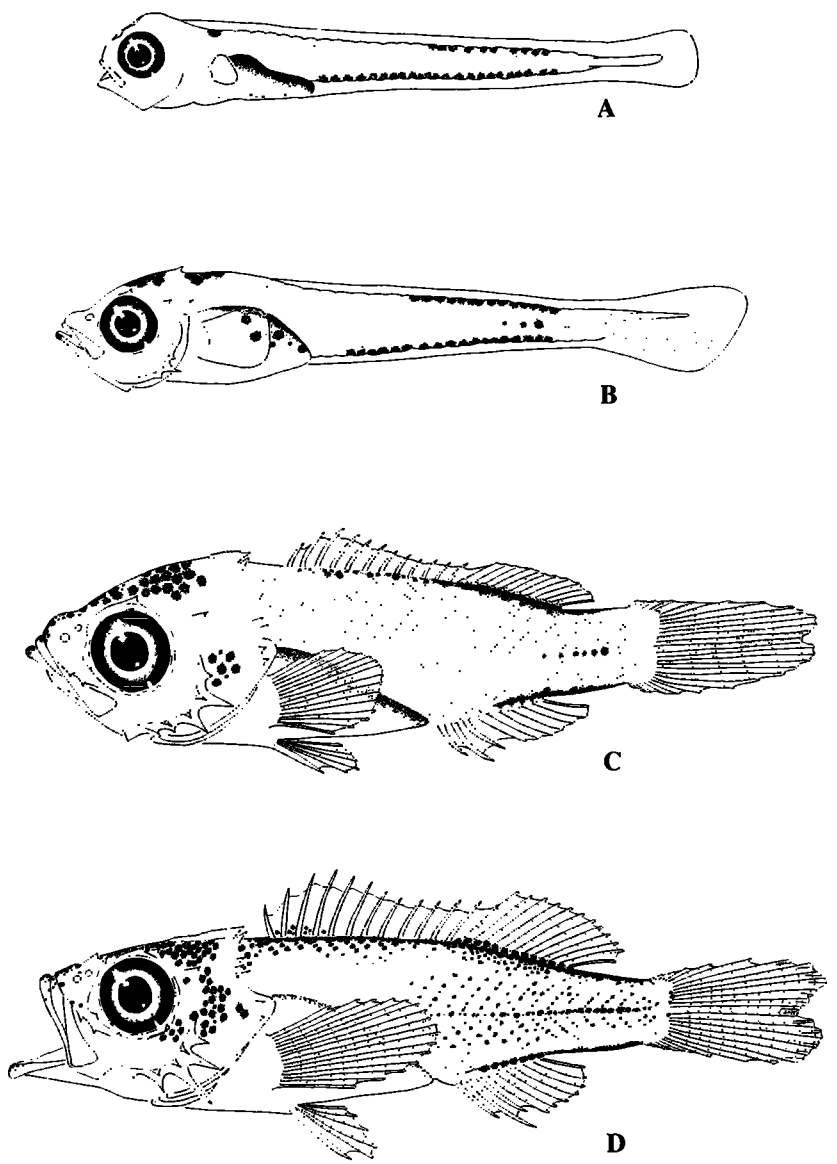

Figure 1

Developmental series of stripetail rockfish, *Sebastes saxicola*. (**A**) 4.7 mm NL pre-extrusion larvae; (**B**) 6.0 mm NL larvae; (**C**) 9.9 mm SL larvae; (**D**) 17.8 mm SL larvae; (**E**) 25.9 mm SL pelagic juvenile; (**F**) 38.2 mm SL pelagic juvenile.

ated (Fig. 1C). At this time, pigment on the cranial region and the anterior section of the head also merged, forming a solid pigment line extending from the upper jaw to the posterior side of the cranium (Fig. 1C).

Pigment began forming on the tip of the lower jaw at approximately 5 mm NL (Table 4). With increased development, pigment spread posteriorly along the jaw. At 30 mm SL, the upper and lower jaw pigments merged to encircle the mouth (Fig. 1F).

Pigment on the operculum began forming at 8 mm SL (Table 4; Fig. 1C). More melanophores were added to this region creating a large area of pigment by 12

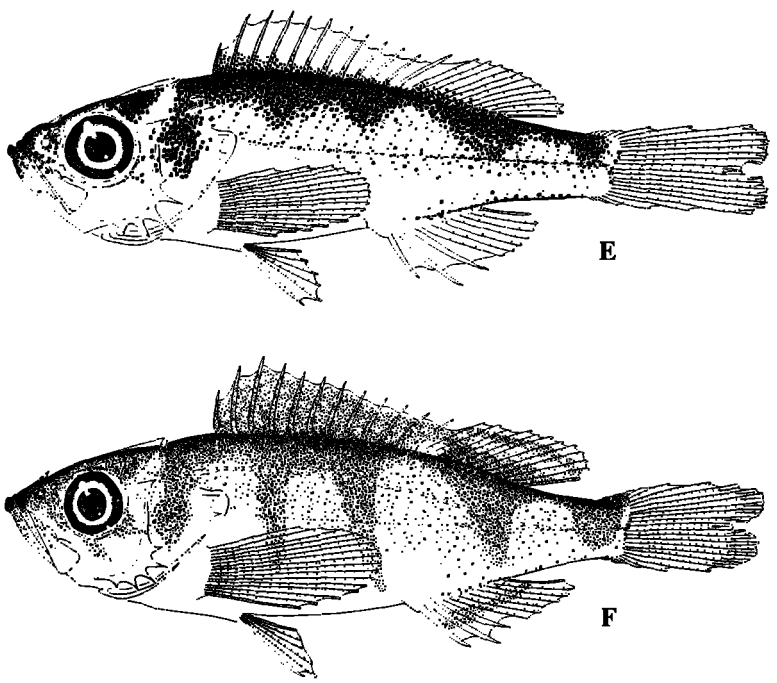

Figure 1 (continued)

mm SL. This pigment area intensified with increased fish size and merged with body-bar 1 at 22 mm SL (Fig. 1F).

Pigment along the ventral and posterior regions of the eye orbit began forming at 12 mm SL (Table 4). This pigment intensified and developed into two cheek bars. The more dorsal cheek bar formed first at 14 mm SL. By 36 mm SL, this bar extended from the eye orbit across the preopercle to the operculum, ending just below the operculum pigment (Fig. 1F). The more ventral cheek bar began forming at 28 mm SL at the base of the eye orbit and extended ventrally. At 44 mm SL, this bar was not completely formed.

Otolith examination

The extrusion check radius for *S. saxicola* ranged from 11.0 to 13.6 μm, averaging 11.9 μm (standard deviation [SD]=0.526 μm)(Fig. 2). The extrusion check radius of *S. saxicola* was not significantly different from the copper (P=0.132; extrusion check radius=10.5 μm; SD=0.354 μm) and gopher complexes (P=0.056; extrusion check radius=10.6 μm; SD=0.288 μm). Three species had extrusion check radii significantly larger (P<0.05) than those of *S. saxicola* (*S. rastrelliger* at 14.0 μm, SD=0.389;

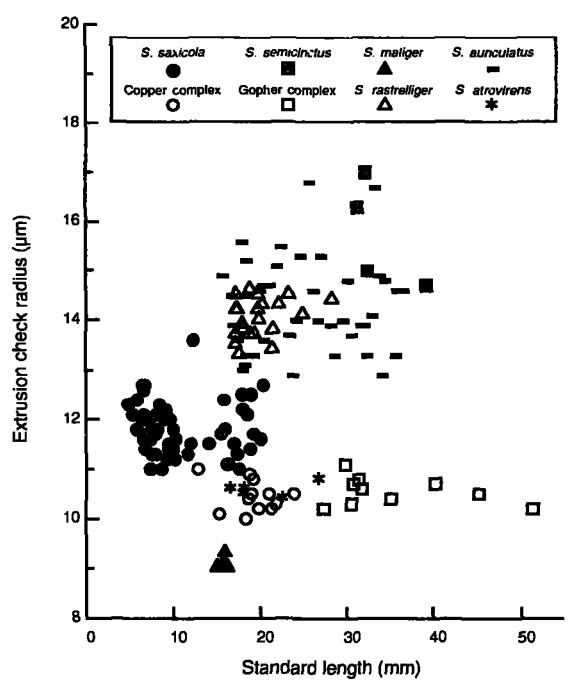

Figure 2

Comparison of extrusion check radius between stripetail rockfish, *Sebastes saxicola*, and other species.

Table 4

Proportions of stripetail rockfish, *Sebastes saxicola*, with melanophores present at various pigment loci averaged over 1.0 mm (range=+/– 0.5 mm) and 2.0 mm (range=+/– 1.0 mm) size bins. SL = standard length in mm. Definitions of pigment loci are given below.

SL	N	LJ	EYE	HEAD	FACE	OPER	CHK	NAPE	DORS	VENT	MID	HYP	DFIN	AFIN	PEC	PEL	B1	B2	B3	B4	B5
4	2	0.0	0.0	0.0	0.0	0.0	0.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
5	2	0.5	0.0	1.0	0.0	0.0	0.0	1.0	1.0	1.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
6	14	0.4	0.0	1.0	0.3	0.0	0.0	0.7	1.0	1.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
7	17	0.5	0.0	1.0	0.9	0.1	0.0	0.3	1.0	1.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
8	14	1.0	0.0	1.0	0.9	0.9	0.0	0.6	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
9	15	1.0	0.0	1.0	1.0	1.0	0.0	0.7	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
10	8	1.0	0.1	1.0	1.0	1.0	0.0	0.9	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
11	15	1.0	0.1	1.0	1.0	1.0	0.0	1.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
12	12	1.0	0.3	1.0	1.0	1.0	0.0	1.0	1.0	1.0	1.0	0.1	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0
13	10	1.0	0.1	1.0	1.0	1.0	0.0	1.0	1.0	1.0	1.0	0.2	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0
14	10	1.0	0.7	1.0	1.0	1.0	0.6	1.0	1.0	1.0	1.0	0.2	0.1	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0
15	7	1.0	0.8	1.0	1.0	1.0	0.7	1.0	1.0	1.0	1.0	0.4	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0
16	8	1.0	1.0	1.0	1.0	1.0	0.7	1.0	1.0	1.0	1.0	0.5	0.0	0.0	0.0	0.0	0.1	0.0	0.1	0.1	0.0
17	3	1.0	1.0	1.0	1.0	1.0	0.9	1.0	1.0	1.0	1.0	0.3	0.3	0.0	0.0	0.0	0.7	0.0	0.0	0.3	0.0
18	4	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.3	0.0
19	2	1.0	0.5	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.5	0.0	0.0	0.0	0.5	0.4	0.0	0.5	0.0
20	2	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.5	0.0	0.5	0.0	1.0	1.0	0.5	1.0	0.5
22	8	1.0	0.9	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.5	0.0	0.0	0.0	0.5	0.4	0.4	0.5	0.4
24	5	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.0	0.0	0.0	0.6	1.0	0.4	0.6	0.4
26	6	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.0	0.0	0.0	1.0	1.0	0.8	1.0	1.0
28	6	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.2	0.0	0.0	1.0	1.0	1.0	1.0	1.0
30	3	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.7	0.2	0.0	1.0	1.0	1.0	1.0	1.0
32	4	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.8	0.0	0.0	1.0	1.0	1.0	1.0	1.0
34	4	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.8	0.0	0.0	1.0	1.0	1.0	1.0	1.0
36	6	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.8	0.7	0.0	1.0	1.0	1.0	1.0	1.0
38	5	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.6	0.0	1.0	1.0	1.0	1.0	1.0
40	4	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.7	0.0	1.0	1.0	1.0	1.0	1.0
44	1	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.0	1.0	1.0	1.0	1.0	1.0

LJ=anterior tip of the lower jaw, EYE=posterio-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, PEL=pelvic fin, B1=body-bar 1 (most anterior), B2=body-bar 2, B3=body-bar 3, B4=body-bar 4, B5=body-bar 5 (on peduncle)

S. auriculatus at 14.3 μm, SD=0.939 μm; *S. semicinctus* at 15.8 μm, SD=1.085 μm). The two remaining species had extrusion check radii significantly smaller ($P<0.05$) than that of *S. saxicola* (*S. maliger* at 9.1 μm [SD=0.141 μm] and *S. atrovirens* at 10.6 μm [SD=0.148 μm]).

The extrusion check radius from individuals with axillary pectoral-fin pigment varied from that of *S. saxicola* (Fig. 3). The difference between extrusion check radius in all the larvae with axillary pigment (11.08μm; SD=1.79μm) and *S. saxicola* was not significant. However, when the larvae with axillary pigment were separated into two groups (one with extrusion check radius greater than 13 μm and the other with extrusion check radius less than 11 μm), the extrusion check radius of each group (13.46 μm [SD=0.055 μm] for the larger and 9.89 μm [SD= 0.532 μm] for the smaller) was significantly different from that of *S. saxicola* and from each other ($P<0.001$).

A linear model provided the best fit for the relationship of total otolith radius versus SL (r^2=0.967) (Fig. 4). A power curve was used to fit the relationship of SL and age (r^2=0.927)(Fig. 5). The model predicted that a fish would be 4.5 mm NL at extrusion (age=0), which is similar to what we observed.

Discussion

Sebastes saxicola have unique pigment patterns which allow them to be distinguished from other *Sebastes* spp. Of the 51 *Sebastes* spp. with published illustrations of pre-extrusion or the recently extruded larvae that occur in the study area, 10 are similar to *S. saxicola* (Morris, 1956; Moser et al., 1977; Stahl-Johnson, 1985; Matarese et al., 1989; Moreno, 1990; Wold, 1991; Sakuma and Laidig, 1995; Laroche[4]). Pre-extrusion *S. saxicola* larvae can be separated

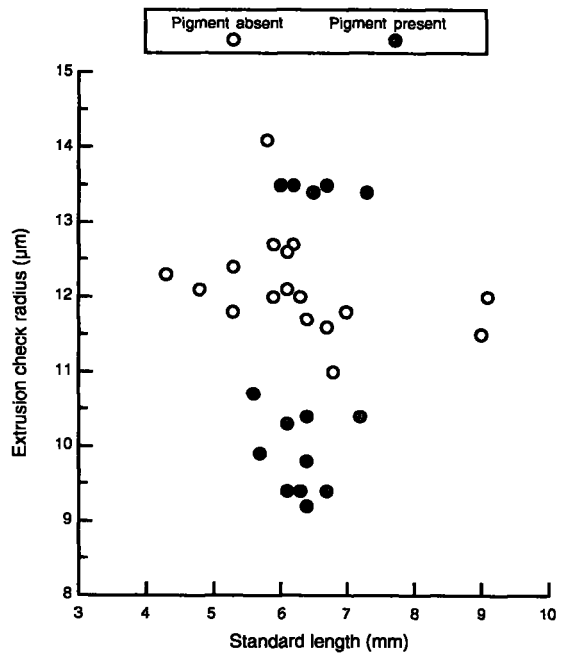

Figure 3

Comparison of extrusion check radius between stripetail rockfish, *Sebastes saxicola* (open circles), which has no axillary pectoral fin pigment, and other *Sebastes* spp. that are similarly pigmented except for the presence of axillary pectoral-fin pigment.

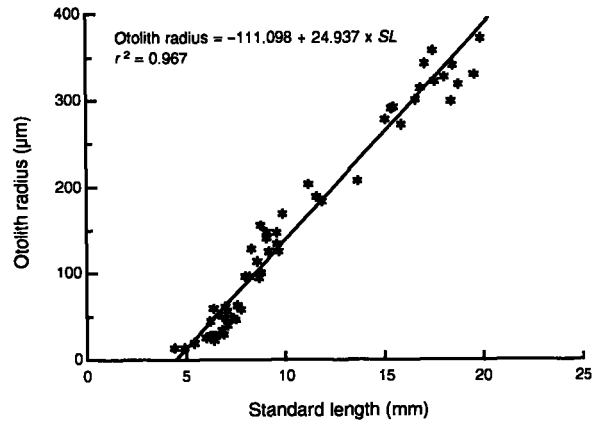

Figure 4

Plot of total otolith radius and standard length of all aged stripetail rockfish, *Sebastes saxicola* (n=58). Solid line indicates predicted values from linear model.

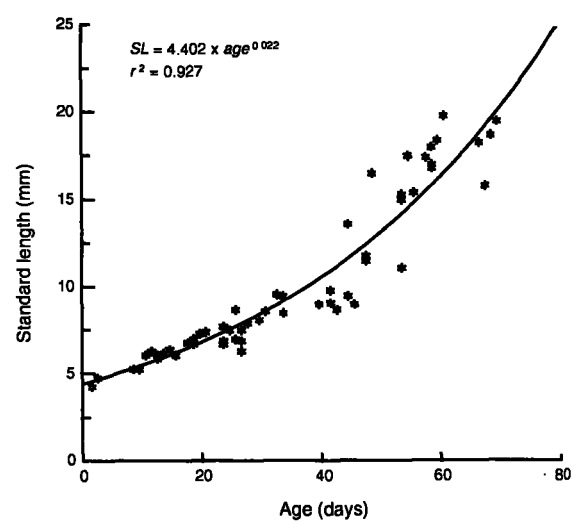

Figure 5

Plot of standard length and age of all aged stripetail rockfish, *Sebastes saxicola* (n=58). Solid line indicates predicted values from model (power curve).

from these 10 species by the extent of pigment along the ventral midline of the tail (i.e. the ventral midline pigment extends almost to the anus), the presence of the single nape pigment, and the absence of pigment on the pectoral fin and lower jaw.

As larval *S. saxicola* increase in length, they become readily distinguishable from most other *Sebastes* species. By early flexion, *S. saxicola* pigment patterns may be confused with only six other rockfish species (*S. atrovirens*, *S. carnatus*, *S. chrysomelas*, *S. maliger*, *S. rastrelliger*, and *S. semicinctus*) (Moreno, 1990; Wold, 1991). The pigment patterns of these six species are not completely described in all larval stages; thus direct comparisons with *S. saxicola* are not possible.

Sebastes saxicola can be separated from these six species on the basis of otolith characters, a technique used by Laidig and Ralston (1995). The size of the extrusion check radius for *S. saxicola* is significantly different from that for *S. atrovirens*, *S. maliger*, *S. rastrelliger*, and *S. semicinctus* (Fig. 2), as well as that for each group of larvae that had axillary pectoral-fin pigment (extrusion check radii greater than 13 µm and less than 11 µm [Fig. 3]). The extrusion check radii of the two groups with axillary pigment correspond well with the copper and gopher complexes (smaller radius) and *S. rastrelliger* (larger radius). Both *S. carnatus* and *S. chrysomelas* have axillary pectoral-fin pigment (Moreno, 1990; Wold, 1991). Thus, the presence of axillary pigment and the difference in size of the extrusion check radius could be used to separate the gopher complex from *S. saxicola*.

Sebastes saxicola can be separated from other *Sebastes* spp. greater than 10 mm SL on the basis of meristic characters and pigment patterns. The average fin ray counts of 12 dorsal rays, 7 anal rays, and 16 pectoral rays (Table 1) are similar to those reported by Moreland and Reilly (1991), who found this combination of meristic counts typical only for *S. saxicola*. The strong lines of pigment on the lateral, dorsal, and ventral midlines help to distinguish late larval *S. saxicola* from other *Sebastes* spp. As the larvae transform into juveniles, the distinctive bar pattern becomes evident (Fig. 1, E and F). In later stage juveniles, body-bars 3 and 4 become quite distinct and allow for field identification.

The growth of *S. saxicola* is similar to that of other *Sebastes* spp. occurring in the study area (Laidig et al., 1991; Woodbury and Ralston, 1991). The growth rate (as determined by the power curve model) for the first 40 days for *S. saxicola* is 0.125 mm/d, which is slightly slower than that reported for other species. Sakuma and Laidig (1995) found that *S. goodei* had a growth rate of 0.135 mm/d for the first 40 days, whereas Laidig et al. (1991) found that the growth rate of *S. jordani* in the first 20 days was approximately 0.165 mm/d. As *S. saxicola* larvae develop, their growth rate increases to 0.367 mm/d (for days 40–70). The change from slower growth to faster growth for *S. saxicola* occurs at approximately 9 mm SL (Fig. 5), which corresponds to the end of flexion. During flexion, the notochord turns up and the hypural plates form, creating the caudal fin. During this period, little growth in length is recorded, but the fish appears to grow in depth (Table 2). This period of slow apparent growth is similar to that found for *S. jordani* (Laidig et al., 1991).

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Vertical distribution of euphausiid life stages in waters adjacent to Baja California

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Abstract.—Vertical distribution of euphausiids on opposite sides of Baja California, off Point Eugenia to the west (June 1961) and in the central sector of the Gulf of California to the east (May 1965), are described from day and night sets of samples. Off Point Eugenia, the thermocline was shallow (20 m) toward the coast, characteristic of upwelling in late spring. In the Gulf, the Salsipuedes Channel showed well-mixed water whereas the Guaymas Basin had a stratified profile of temperature and oxygen. Lower abundances of the larger euphausiids during day throughout the water column, compared with night, are attributed to net avoidance. When a thermocline was present, two basic migration patterns were observed: 1) species crossing the thermocline (*Nyctiphanes simplex* and most *Euphausia* spp.) and 2) species remaining at or beneath the thermocline (*Euphausia gibboides* and *Nematoscelis difficilis*). On the basis of distribution at night, the youngest larvae and adults of *N. simplex* were in the mixed layer at the coastal station off Point Eugenia; more advanced stages of development were at mid-depth, between 0 and 50 m, suggesting an upwelling-downwelling cell of circulation. Inside the Gulf, abundant metanauplii and ovigerous females of *N. difficilis* occurred only in the upper layers of Salsipuedes Channel, whereas in Guaymas Basin and Point Eugenia, the youngest larvae were within the thermocline. The decrease of oxygen with depth did not reach the critical values observed in the more tropical eastern Pacific but, in general, where values of $[O_2]$ were <1 mL/L, the abundance of euphausiids was low.

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Early studies of euphausiids in the California Current showed a coincidence between their vertical distribution and the vertical movement of a mid-depth layer of organisms from which sonic scattering was reflected (the deep scattering layer in Boden, 1950; Barham, 1957). Interaction of this layer with shoaling of the sea floor was described by Isaacs and Schwartzlose (1965). Vertical migration, or lack of it in certain species, has been related to daytime avoidance of nets by euphausiids off California and northern Baja California (Brinton, 1967). For a given species, variation in the extent of vertical migration, and range of nonmigrators, has been related to the depth of the thermocline and distributions of dissolved oxygen (Brinton, 1967, 1979; Youngbluth, 1976). In the margins of the eastern tropical Pacific (ca. 20–22°N), a shoaling oxygen minimum layer constrains the vertical ranges of warm-temperate euphausiid species with a replacement by tropical species tolerant of oxygen deficiency (Longhurst, 1967; Brinton, 1979). Seasonal variability in vertical migratory behavior has been also observed. In La Jolla Bight near San Diego, differences in patterns of vertical migration of *Euphausia pacifica* and the copepod *Calanus pacificus* were observed between upwelling and downwelling periods (Koslow and Ota, 1981).

These and subsequent studies dealing with vertical migration in different taxa have shown variable responses to environmental stimuli. For example, in euphausiids, the influence of light (Boden and Kampa, 1967; Bright et al., 1976), proximity of the bottom (Cochrane et al., 1994), and temperature and salinity (Wiebe and Boyd, 1978) have been described. The selective advantage of remaining at depth during the day is usually considered an adaptation for escape from predators (Zaret and Suffern, 1976; Ohman et al., 1983; Bollens et al., 1992) or an energetic benefit (McLaren, 1963, 1974; Enright, 1977).

The present study describes for the first time the vertical distribution of euphausiids in the central sector of the Gulf of California and off Point Eugenia (28°N) during spring. In the Gulf of California, deep basins, island channels, and, in particular, low $[O_2]$ within subtropical latitudes all suggest possibilities for interesting variability in vertical distribution of fauna. However, information on the subject is restricted to the vertical distribution of euphausiids and pelagic red crab, *Pleuroncodes planipes*, at the entrance of the Gulf, as part of an eastern Pacific transect (Brinton, 1979). Inside the Gulf, only the submergence of the copepod *Calanus pacificus californicus* to depths of 200–300 m during summer has

been reported by Fleminger (in Brinton et al., 1986). Point Eugenia is of biogeographical interest because species of temperate, tropical, and central Pacific regions may occur together relatively near to the coast (Boden et al., 1955; Brinton 1962, a and b).

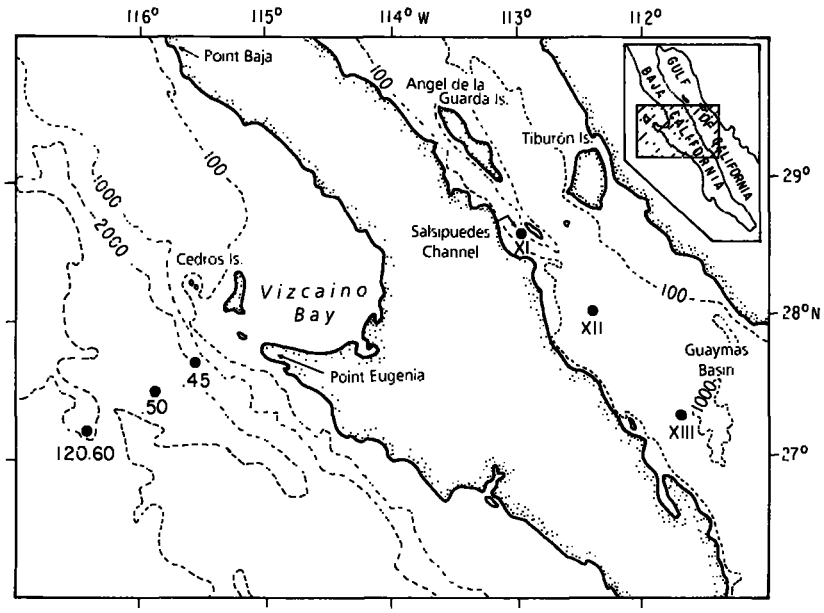

Figure 1

Sampling stations (•) off Point Eugenia, Pacific Coast of Baja California. Isobaths are in fathoms.

Methods

Samples used in this study were collected from a three-station transect off Point Eugenia, Pacific coast of Baja California (*Zigpac II* cruise, 12–18 June 1961), and from three stations from the central part of the Gulf of California (*El Golfo II* cruise, 15–20 May 1965) (Fig. 1). In both cruises of RV *Alexander Agassiz*, two series of tows (one during the day and one at night) were made with an opening-closing net as described by Brinton (1967). The net was 1 m in diameter, 2.35 m long, and used 0.505-mm mesh with 0.25-mm mesh in the codend bag as well as a 40-cm long section at the front of it. Off Point Eugenia, nets were hauled horizontally at discrete depths (0, 10, 25, 50, 75, 100, 150, 200, 300, 400, and 500 m) for 30 min. In the Gulf of California, hauls were oblique and nets equipped with flowmeters. In the upper 150 m, five hauls were made through strata of 30 m; below 150 m, five hauls were made through strata of 135 m.

Euphausiids were identified, counted, and grouped as adults (males and females), juveniles, and larvae. The entire sample was used except in cases of abundant *Nyctiphanes simplex* and *Euphausia recurva*, where subsamples were obtained with a Folsom splitter. Between 200 and 400 individuals per life phase were typically counted. Larvae of *Nematoscelis difficilis* and *N. simplex* were sorted by developmental stages as defined by Gopalakrishnan (1973) and Lavaniegos (1992). The biogeographic provinces of Brinton (1962a, 1979), based on affinity to water masses, were used in the classification of species.

Abundance at a particular depth is expressed as individuals (ind)/m^3, and total abundance in the water column as ind/m^2 of ocean surface. In horizontal hauls, the depth of tow was taken as the middle depth of the layer. In oblique hauls, the thickness of the layer was the difference between depths of opening and closing of net. Statistical comparisons were not made because of absence of replicate tows. Data on temperature, salinity, and dissolved oxygen were obtained from standard Nansen-bottle casts and processed by California Cooperative Oceanic Fisheries Investigations. Data from the Gulf of California are published (SIO Data Report[1]).

Results

Hydrographic vertical profiles

In the outer coast of Baja California, physical conditions in June 1961 were typical for late spring (Reid et al., 1958; Hickey, 1979; Huyer, 1983). Near the coast (station [st.] 120.45), the mixed layer was 20 m (Fig. 2). The station most distant from the coast (st. 120.60) showed a thicker mixed layer (50–60 m) and warmer temperatures between depths of 20–150 m than did the other stations. Salinity in the surface layer showed low values (33.5–33.8 ppt), influenced by more northern California Current water. Near the coast (st. 120.45), a shallow oxycline and values of salinity >34.0 ppt at 75–100 m depth resulted from the influence of Intermediate Equatorial water.

The Gulf of California is influenced by northerly winds during spring and summer. However, tides,

[1] SIO Data Report. 1967. Physical and chemical data report: CalCOFI Cruise 6505 (*El Golfo* II). SIO Reference 67-16. Scripps Institution of Oceanography, La Jolla, CA, 92093.

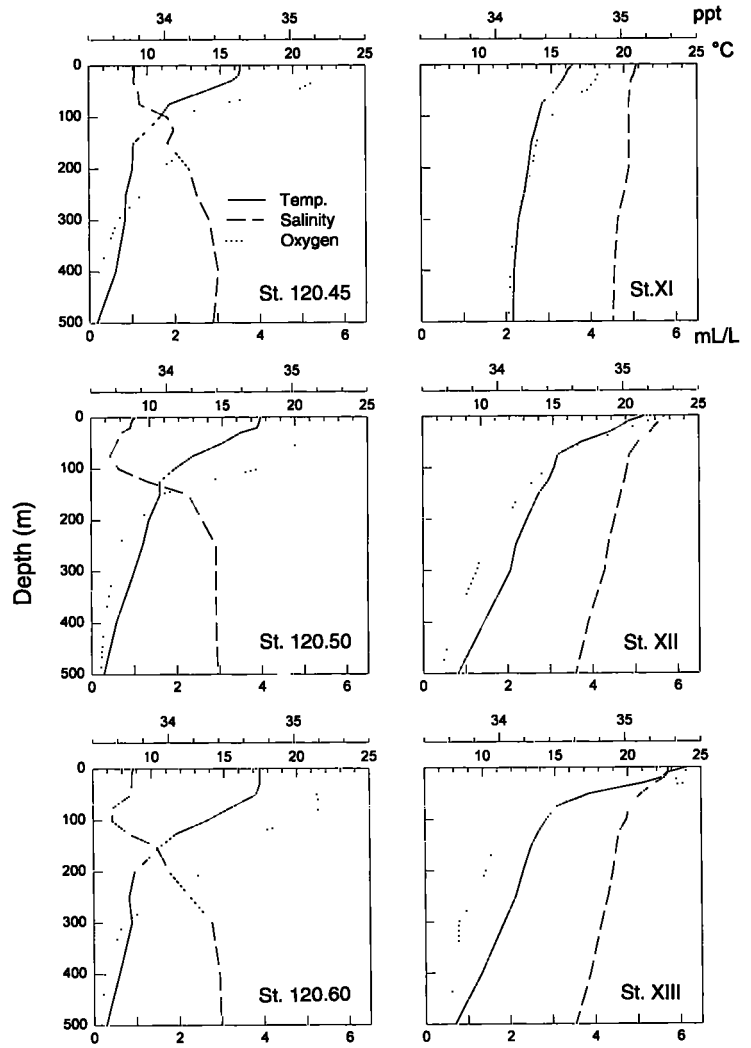

Figure 2

Depth profiles of temperature (°C), salinity (ppt), and dissolved oxygen (mL/L) for Point Eugenia (left) and the Gulf of California (right) stations.

air-sea fluxes, and propagation of internal waves enhance mixing of the water (Roden and Groves, 1959; Badan-Dangon et al., 1985; Bray and Robles, 1991). Strongest tidal currents have been recorded in the Ballenas Channel (west of Angel de la Guarda Island) and Salsipuedes Channel (Fig. 1). Here the water column is well mixed above 500 m during spring tides (Bray and Robles, 1991) as observed in May 1965 (st. XI, Fig. 2). In contrast, the Guaymas Basin profiles (sts. XII and XIII) showed gradients of temperature and oxygen that were particularly strong above 100 m. Temperature in the top 50 m showed differences of 2–4°C among the three sampling stations. Surface salinity showed values >35.0 ppt, characteristic of the Gulf water mass, produced in the northern gulf and flowing and mixing rapidly southward.

Vertical distribution of euphausiids

Off Point Eugenia, the greatest number of species was of the Central Pacific group. These, however, had relatively low abundances, <10 ind/m^2 per species, excepting *Euphausia recurva* and, at one station, *E. hemigibba* (Table 1). This group was absent in the Gulf of California.

The most abundant species in both study regions was *Nyctiphanes simplex* (Tables 1 and 2). This spe-

Table 1

Abundance integrated to surface (ind/m^2) per species off Point Eugenia. (METP = marginal of the eastern tropical Pacific (sensu Brinton 1962a, 1979).

Biogeographic group	Species	St. 120.60		St. 120.50		St. 120.45	
		Night	Day	Night	Day	Night	Day
Transition zone	*Euphausia gibboides*	26	19	123	6	12	4
	Nematoscelis difficilis	1	3	98	10	60	23
	Nyctiphanes simplex	5	1	674	79	836	588
	Thysanoessa gregaria	<1	1	4	3	9	4
METP	*Euphausia eximia*	2	10	13	13	8	3
	Nematobrachion flexipes	1	<1	<1	1	1	<1
	Stylocheiron affine	1	1	2	<1	5	<1
Subarctic	*Euphausia pacifica*	—	—	73	18	20	21
Equatorial	*Nematoscelis gracilis*	<1	—	—	—	—	<1
Central epipelagic	*Euphausia hemigibba*	9	1	1	—	<1	1
	Euphausia mutica	2	—	1	—	<1	—
	Euphausia recurva	33	30	64	1	33	4
	Nematoscelis atlantica	<1	—	<1	—	—	—
	Stylocheiron suhmii	—	<1	—	—	—	—
	Thysanopoda astylata	<1	<1	<1	—	—	<1
Central mesopelagic	*Nematobrachion boopis*	—	<1	—	—	—	—
	Nematoscelis tenella	<1	<1	<1	—	<1	—
	Stylocheiron elongatum	<1	—	<1	<1	—	—
	Stylocheiron longicorne	1	1	2	1	3	1
	Stylocheiron maximum	<1	<1	<1	<1	<1	<1
	Thysanopoda orientalis	<1	—	<1	<1	<1	<1
	Total	79	66	1,054	132	987	650

Table 2

Abundance integrated to surface (ind/m^2) per species in the central sector of the Gulf of California. (METP = marginal of the eastern tropical Pacific, ETP = eastern tropical Pacific (sensu Brinton 1962a,1979).

Biogeographic group	Species	St. XI		St. XII		St. XIII	
		Night	Day	Night	Day	Night	Day
Transition zone	*Nematoscelis difficilis*	324	217	604	178	344	163
	Nyctiphanes simplex	274	619	1,778	1,314	11,082	585
METP	*Euphausia eximia*	—	—	2	—	10	2
	Nematobrachion flexipes	—	—	<1	—	—	—
ETP	*Euphausia distinguenda*	—	—	<1	1	—	1
	Euphausia lamelligera	—	—	<1	1	1	21
	Total	598	836	2,385	1,494	11,437	772

cies is a warm-temperate endemic, occurring typically in nearshore waters of the southern part of the California Current (Brinton, 1962a) and in the Gulf of California (Brinton and Townsend, 1980). Other abundant species of the group identified as the "California Current's transition zone" was *Nematoscelis difficilis*, which was even more abundant in the Gulf than at the California Current stations. *Euphausia gibboides*, *Thysanoessa gregaria* (transition zone), and the subarctic-warm temperate *E. pacifica* were not observed in the Gulf.

Tropical species were scarce along both coasts of the peninsula, as expected during the time of sampling (Brinton, 1979; Brinton and Townsend, 1980). In this group, *E. eximia* and *Nematobrachion flexipes* were common off Point Eugenia and in Guaymas Basin. *Euphausia lamelligera* and *E. distinguenda* were observed in Guaymas Basin only. The tropical-subtropical *Stylocheiron affine* was taken only at Point Eugenia.

Expected trends of low abundances during daytime were observed and are believed to be due to net avoidance during the hours of light. High abundance was usually accounted for by larvae of epipelagic species when most of the population was in the upper 100 m at night. Larvae of *N. simplex* accounted for 90% or more of the euphausiids in the richest samples. Off Point Eugenia their distribution was greater toward the coast and in the upper 50 m (Fig. 3). Night occurrences of calyptopes and early furcilias (C–F_3 in Fig. 3) were almost exclusively at st. 120.45, with most at the surface; the oldest furcilias (F_4–F_6) and juveniles were well represented at st. 120.50, down to 50 m. The old larvae descended to 200 m during daytime. The occurrence of mature adults at the surface at the nearshore station may be associated with nearshore grouping to mate and spawn. Inside the Gulf few larvae of *N. simplex* occurred at Salsipuedes Channel (st. XI, Fig. 4). Moreover, all larval stages were found at Guaymas Basin, where furcilias at st. XII were restricted to the first 30 m during night; the larval calyptopes were dispersed in the upper 100 m. Adults were more abundant at st. XIII, peaking at 30–60 m (there was no sample for 0–30 m) during night and at 135–270 m in the light hours.

Vertical distribution of *Nematoscelis difficilis* larvae off Point Eugenia, as with *Nyctiphanes simplex*, was restricted to coastal stations, with a shallower range nearshore (st. 120.45) than at st. 120.50 (Fig. 5). In contrast to *N. simplex*, *N. difficilis* larvae avoided the upper layer, and juveniles and adults peaked at 100 m depth during nighttime (Fig. 5). Mating and spawning may have occurred in and below the thermocline near the coast, because most of the females with spermatophore attached or carrying external eggs were found between 75 and 200 m during the night (st. 120.45). In the Guaymas Basin, a more extended vertical range, from 55 to 420 m, was observed for adults of this species (Fig. 6). Interestingly, in Salsipuedes Channel, certain of the adults were near the surface, particularly gravid females. These may have been shedding newly hatched metanauplii in the upper layer, where many were found. A progression toward more advanced larval stages from north to south was observed.

Larvae of other species were found only off Point Eugenia. These were of the four most abundant species of *Euphausia* (Fig. 7). Three (*E. gibboides*, *E. recurva*, and *E. eximia*) included larval calyptopes

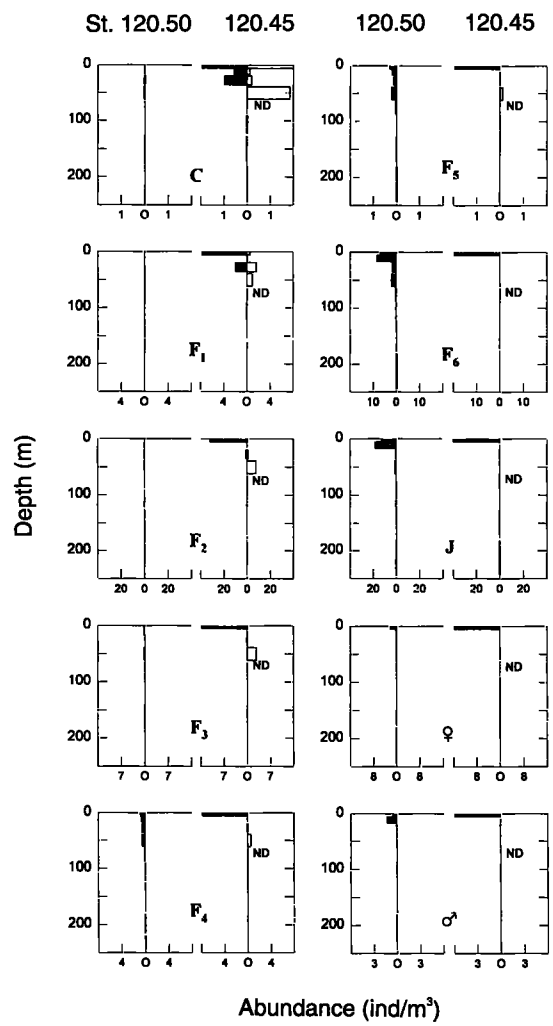

Figure 3

Vertical distribution of life stages of *Nyctiphanes simplex* off Point Eugenia at night (solid bars) and day (open bars). C = calyptopes; F_1–F_6 = furcilia stages; J = juveniles; ND = no data. Note the different scales used for abundance among stages.

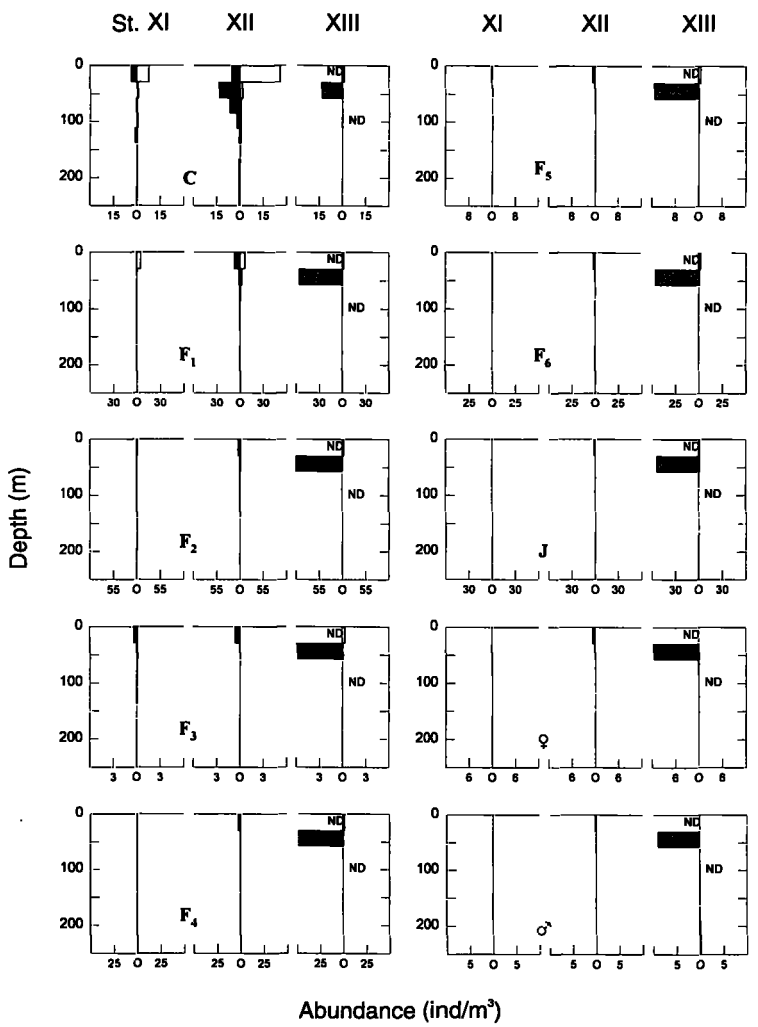

Figure 4

Vertical distribution of life phases of *Nyctiphanes simplex* in the Gulf of California. C = calyptopes; F_1–F_6 = furcilia stages; J = juveniles; ND = no data.

whereas *E. pacifica* larvae were advanced furcilias. Though the larvae of nighttime epipelagic species (*E. recurva*, *E. eximia*, and *E. pacifica*) occupied upper strata during both day and night, larvae of *E. gibboides* showed the same tendency as *N. difficilis* in avoiding the surface layer.

Few postlarvae (juveniles and adults) of epipelagic species were caught during daytime, particularly of *E. gibboides*, making it difficult to compare day and night vertical distributions. However, the other *Euphausia* species (Fig. 7) may have been migrating daily, on the basis of specimens found between 200 and 400 m during daytime, compared with their nighttime presence near the surface (Tables 3 and 4). *Thysanoessa gregaria* and *Stylocheiron affine* did not appear to migrate; they were not present in the upper 100 m during day and night (Fig 8).

The main part of the population of the three mesopelagic species did not occur above 100 m (Fig. 8). Larvae of *Stylocheiron longicorne* and *S. maximum* were at 100 m (except at st. 120.60 during the day) and of *Thysanopoda orientalis* at 200 m (Table 3). Off Point Eugenia and in Guaymas Basin virtually no euphausiids were found below 400 m depth. At those depths, dissolved oxygen was <1 mL/L at both locations (Fig. 2). In Salsipuedes Channel, oxygen values below 400 m was >2 mL/L, and some postlarvae of *N. difficilis* were found as deep as 700–800 m.

Discussion

The vertical distribution of the six most abundant species of euphausiids off Point Eugenia, June 1961, showed differences between day and night. Three of them (*Nyctiphanes simplex*, *Nematoscelis difficilis*, and *Euphausia eximia*) were important species in the central Gulf of California in May 1965. In both regions, when a thermocline was present, two basic kinds of distribution were apparent: 1) species found above and below the thermocline (*Nyctiphanes simplex* and most *Euphausia* species); and 2) species that remain in or below the thermocline (*E. gibboides* and *Nematoscelis difficilis*). In the absence of confirming replicated tows, the differences could also be interpreted as local patchiness. Similar patterns, however, were found during January–February of 1964 (Brinton, 1967) off Pt. Banda (32°N), Dana Pt. (34°N), and Pt. Reyes (38°N). During winter, upwelling is weak and the difference in depth of the thermocline between offshore and onshore stations is less than in summer. Though transects of winter 1964 extended farther offshore than in the present study, the trend of migrating species to be concentrated into depth ranges that were narrower nearshore was observed in both studies. A more northern study, off Cape Mendocino (40°N) and Cape Blanco (43°N) during July–August 1970, also showed this trend (Youngbluth, 1976).

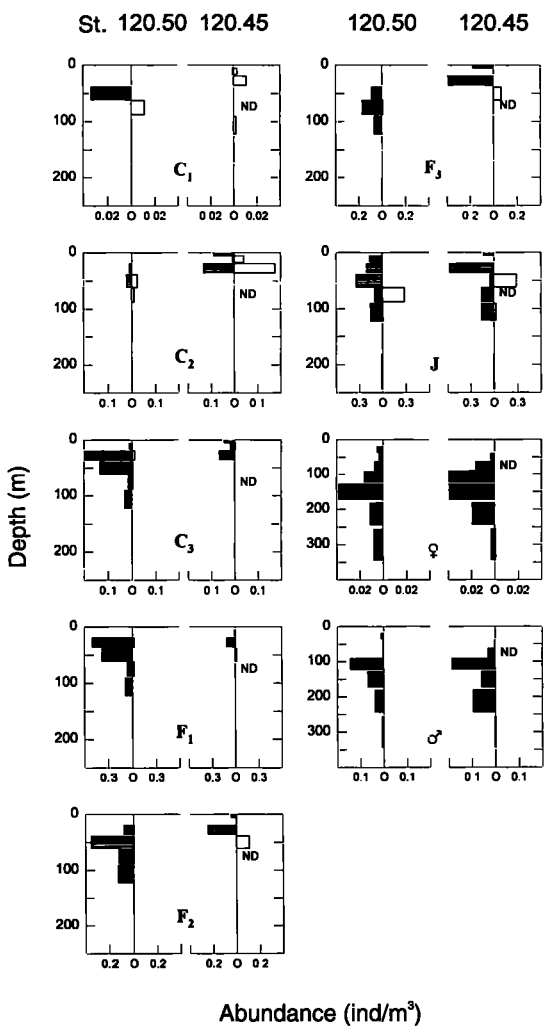

Figure 5

Vertical distribution of life stages of *Nematoscelis difficilis* off Point Eugenia. C_1–C_3 = calyptopis stages; F_1–F_3 = furcilia stages; J = juveniles; ND = no data.

In the Gulf of California, wind-driven upwelling occurs along the mainland coast in winter and on the peninsular coast in summer (Roden and Groves, 1959; Badan-Dangon et al., 1985). However, tides dominate the circulation of water near the midriff islands (Angel de la Guarda and Tiburón), including the Salsipuedes Channel, where currents up to six knots (2.76 m/s) have been measured (Alvarez et al., 1984; Bray and Robles, 1991). In this well-mixed area, the water column is cold, relatively rich in oxygen, and the vertical distribution of *Nematoscelis difficilis* was unique in that many adults were present in the upper 100 m at night. A migratory behavior to mate or shed the hatching metanauplii could be occurring, but an absence of a thermocline, acting as a barrier, could promote this behavior. In the earlier (1964) California Current study, near the coast the juveniles and adults of *N. difficilis* showed a bimodal vertical distribution (a peak near the surface and another in or below the thermocline), whereas offshore, the nocturnal distribution showed only the deep mode (Brinton, 1967). *N. difficilis* was therefore considered a vertical migrant, although a capability of daytime net avoidance was noted. In the congener *N. megalops*, from the northwestern Atlantic, differences between day and night were explained as due to daytime net avoidance (Wiebe and Boyd, 1978; Wiebe et al., 1982). Unfortunately, no replicate data for the Salsipuedes Channel station are available. This appeared to be an important area for reproduction of this species in May 1965; many metanauplii and first larval calyptopes were found in the upper layer, coincident with ovigerous females.

Though larvae of many species were found off Point Eugenia, most were late furcilias. Only the transition-zone group *N. simplex*, *N. difficilis*, and *E. gibboides*; the more tropical *E. eximia*; and the central Pacific *E. recurva* showed evidence of local reproductive activity, as suggested by the abundance of younger larval stages. Of these, differences in vertical distribution were between species with stage

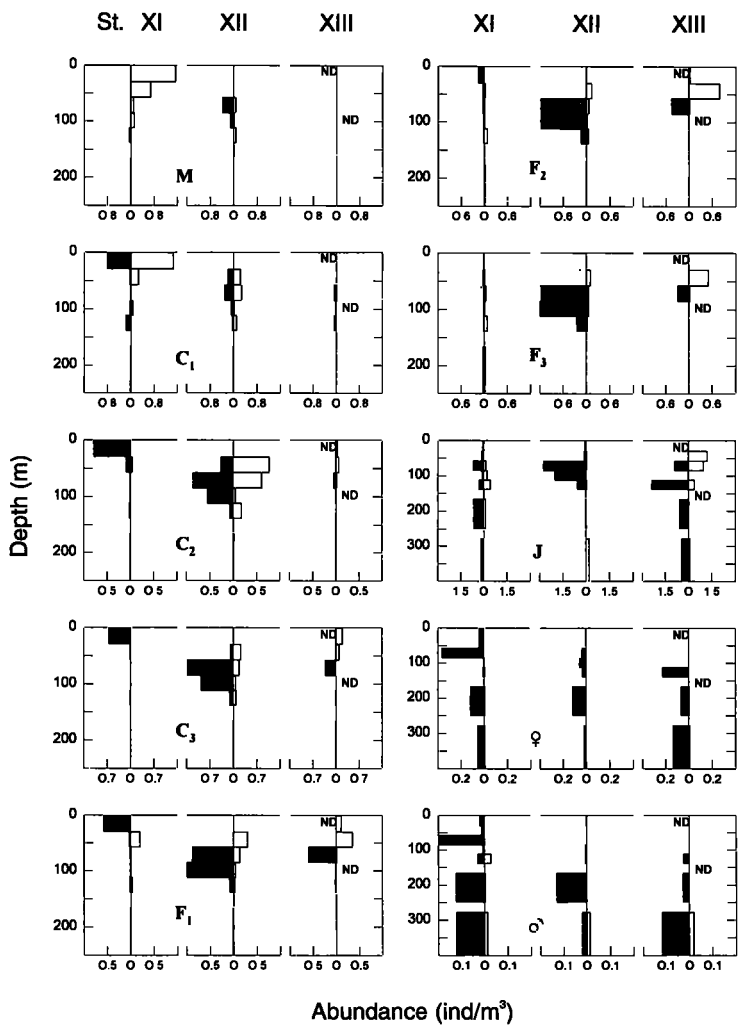

Figure 6

Vertical distribution of life stages of *Nematoscelis calyptopis* stages; M = metanauplii, C_1–C_2 = calyptopis stages; F_1–F_3 = furcilia stages; J = juveniles; ND = no data.

C_1 in the thermocline (*E. gibboides* and *N. difficilis*) and those with C_1 in the mixed layer (*N. simplex*, *E. eximia*, and *E. recurva*). These positions may be near the level of liberation of youngest larvae in species protecting eggs in maternal ovisacs such as done by *N. simplex* and *N. difficilis* (Brinton, 1966; Mauchline and Fisher, 1969). One day or even hours would have elapsed before moulting from metanauplius into C_1 stage. For *Nyctiphanes couchii* in the Celtic Sea, the liberation of mature metanauplii occurred within the euphotic zone, and moulting into calyptopis stage 1 (C_1) occurred in a matter of hours (Williams and Fragopoulu, 1985).

These authors observed in summer a stratified distribution of *N. couchii* during hours of light, with larger euphausiids at greater depths than smaller euphausiids. Similarly, in the northern Benguela Current, during winter, the larval calyptopes of *Nyctiphanes capensis* showed a shallower range of vertical distribution than furcilia (Barange and Pillar, 1992). In the present study the occurrence of older furcilias (F_4–F_6) of *N. simplex* at 200 m off Point Eugenia (Fig. 3) during daytime could indicate, as with *N. couchii* and *N. capensis*, an active daily migration. The restriction of early stages (C_1–F_3) of *N. simplex* to the nearshore station (32 km), exclusively in the surface layers, whereas late furciliar and postlarval stages extended to 64 km from the coast (from the surface into the layer below) may be explained by offshore flows, produced by coastal upwelling. As

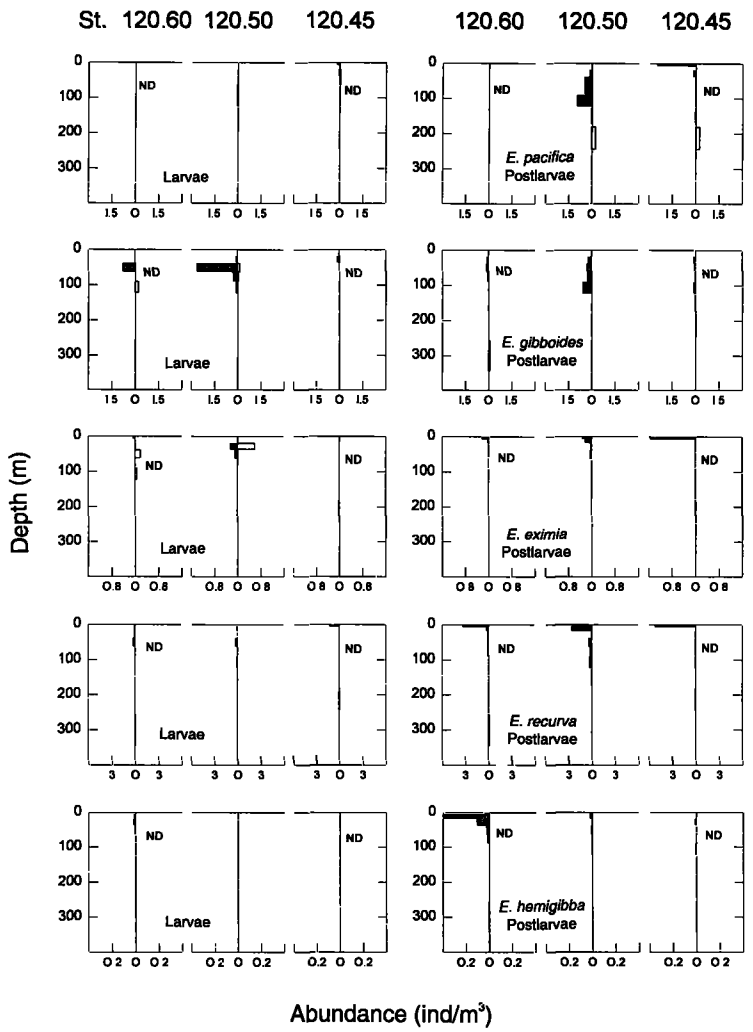

Figure 7

Vertical distribution of *Euphausia* species off Point Eugenia. Note the different scales used for abundance among species. ND = no data.

the larvae grow, they are carried offshore within the surface layers toward a convergence or frontal zone but eventually return to shore at depth by means of onshore flows. A cell of circulation of this kind conforms with the observations of a negative wind stress "curl" or Ekman convergence near the coast between Point Baja and Point Eugenia (Bakun and Nelson, 1977). Evidence for offshore flow in the surface, and onshore flow at 57 m, was found by Walsh et al. (1977) in the adjacent coastal shelf of Point San Hipolito (27°N). Similar conditions, within 28 km from the coast for early larval stages (nauplii and calyptopes) of *N. capensis*, and within 65 km for furcilias, were observed in Möwe Point (Benguela) (Barange and Pillar, 1992). These authors proposed a two-cell cross-shelf circulation to explain the maintenance of *N. capensis* near the coast.

From the same set of samples used in the present study, and from in situ observations in the Santa Barbara Basin (33°N), dense aggregations of stage-V copepodites of *Calanus pacificus californicus* were found (Alldredge et al., 1984). The presence of great abundances of resting copepodites of this species had been previously recorded along southern Baja California in oxygen-deficient water (Longhurst, 1967). Off Point Eugenia the species occupied a stratum near 300 m in offshore stations (120.60 and 120.50) but was found at 0–75 m in the nearshore station 120.45, both day and night. These differences were explained as population diapauses, at depth during

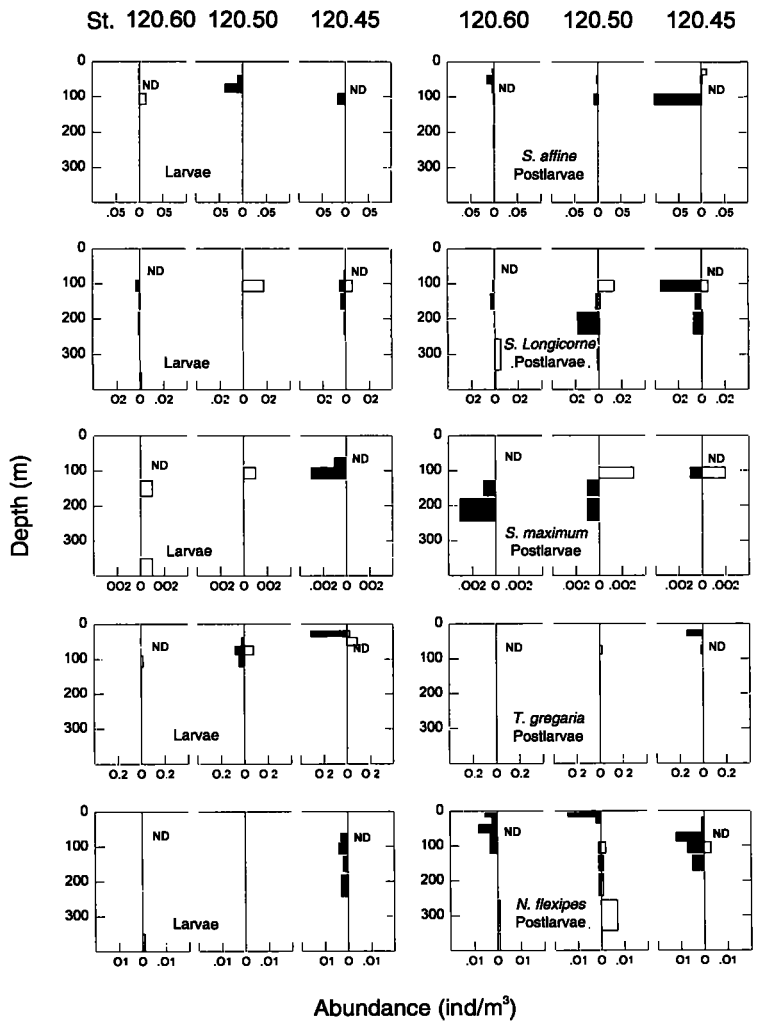

Figure 8

Vertical distribution of *Stylocheiron affine*, *S. longicorne*, *S. maximum*, *Thysanoessa gregaria*, and *Nematobrachion flexipes* off Point Eugenia. ND = no data.

periods of weak upwelling, with descent even to depths lacking oxygen (i.e. Santa Barbara Basin, Alldredge et al., 1984). In the present study, no aggregations of euphausiids analogous to copepods in diapause were found. For some euphausiid species, a low concentration of oxygen might limit migration at depth during daytime. This case apparently occurs in Saanich Inlet (British Columbia), where dense aggregations of *Euphausia pacifica* were observed directly above the anoxic layers (100–150 m) (Mackie and Mills, 1983). Near this site, in the temperate fjord of Dabbob Bay (Washington), a seasonal variation in the vertical migratory range of *E. pacifica* was recorded (Bollens et al., 1992). During the day, larvae of this species occurred deeper in the water column in late summer and fall than in spring. However, they were always above the depth levels of juveniles and adults (50–125 m) during the day, the entire population migrating to the surface at night (Bollens et al., 1992).

The relation between vertical distribution of euphausiids and low oxygen concentration has been discussed for the eastern tropical Pacific (ETP) (Brinton, 1979; Sameoto et al., 1987). In ETP the layer of strongly depleted oxygen (<0.1 mL/L) is present beneath the thermocline, to depths of 300–400 m. The vertically migrating species in the ETP group (*Euphausia lamelligera*, *E. distinguenda*, *E. diomedeae*, and *Nematoscelis gracilis*) tolerate intense O_2-deficiency at their daytime depths and enter the oxygenated mixed layer at night (Brinton,

Table 3

Depth (m) of maximal relative abundance of euphausiid postlarvae (juveniles and adults) of rare species off Point Eugenia, Baja California.

		St. 120.60		St. 120.50		St. 120.45	
Species		Depth	%	Depth	%	Depth	%
Nematoscelis gracilis	Night	200	75	—		—	
	Day	—		—		400	100
Euphausia mutica	Night	0	99	10	47	0	92
	Day	—		—		—	
Nematoscelis atlantica	Night	10	100	25	100	—	
	Day	—		—		—	
Stylocheiron suhmii	Night	—		—		—	
	Day	100	100	—		—	
Thysanopoda astylata	Night	10	100	500	100	—	
	Day	400	100	—		300	100
Nematobrachion boopis	Night	—		—		—	
	Day	400	100	—		—	
Nematoscelis tenella	Night	100	60	400	72	75	100
	Day	400	100	—		—	
Stylocheiron elongatum	Night	200	100	200	100	—	
	Day	—		200	100	—	
Thysanopoda orientalis	Night	—		—		—	
	Day	—		300	100	300	100

Table 4

Layer (m) of maximal relative abundance of euphausiid postlarvae (juveniles and adults) of tropical species in the Guaymas Basin, Gulf of California.

		St. XII		St. XIII	
Species		Layer	%	Layer	%
Euphausia ditinguenda	Night	0–30	50	—	
	Day	285–420	100	30–60	30
Euphausia eximia	Night	0–30	95	30–60	52
	Day	—		150–285	73
Euphausia lamelligera	Night	0–30	68	60–90	30
	Day	285–420	100	285–420	97
Nematobrachion flexipes	Night	285–420	100	—	
	Day	—		—	

1979). In one station in the Costa Rica Dome (9°N, 89.5°W), only *N. gracilis* and *Stylocheiron* spp. were found in water with oxygen below 0.1 mL/L (Sameoto et al., 1987). Off both coasts of central Baja California, the depletion of oxygen is not so strong as in the ETP and therefore it is not restrictive for vertical ranging of the dominant temperate species (*N. simplex* and *N. difficilis*). The relation between the thermocline and vertical migration was more important.

Acknowledgments

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Variability in the population structure of *Lutjanus adetii* (Castelnau, 1873) and *L. quinquelineatus* (Bloch, 1790) among reefs in the central Great Barrier Reef, Australia*

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Abstract.—The recent age validation of the tropical snappers *L. adetii* and *L. quinquelineatus* has facilitated the comparison of growth, mortality, and age structures for both these species at the spatial scale of individual reefs. The age structure of both species among reefs within the Great Barrier Reef Marine Park was based on counts of annuli from sectioned otoliths. There was significant variability in growth, mortality, and age structures. Significant differences in mean length, age, and weight (independent of the sex of the fish) were observed for both species among reefs. Peaks in abundance of year classes were variable from reef to reef. Comparisons of the von Bertalanffy growth curves indicated that the pattern of growth in individuals of *L. quinquelineatus* was significantly different among reefs, whereas the pattern of growth in *L. adetii* was not. However, there were no significant differences in the mean length of the early age classes of either species among reefs. The mortality rates and hence survivorship of both *L. adetii* and *L. quinquelineatus* among reefs were highly variable. It is hypothesized that the varying age structures and mortality rates of both of these species at the spatial scale of individual coral reefs are determined by the nonequilibrial balance of variable recruitment interacting with density-independent mortality. Hence the effect of good recruitment years may persist in the age structure of populations over time.

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Spatial comparisons of life history parameters of species of the family Lutjanidae have been undertaken only among broad geographic areas (e.g. Nelson and Manooch, 1982). Likewise, the majority of life history studies of species of the Lutjanidae have been based on widespread collections of individuals from broad geographic areas (e.g. Druzhinin and Filatova, 1980; Loubens, 1980; Liu and Yeh, 1991; Davis and West, 1992; Sanders et al.[1]; Mees[2]) and not on an individual reef scale. On the Great Barrier Reef in Australia, the fishing industry and other resource users (e.g. tourists, recreationalists, etc.) are managed under a system which protects marine areas of which individual coral reefs are the primary management unit.[3] To date, a comparison of age and growth parameters of lutjanids among individual reefs within a single geographic area has not been undertaken.

Comparisons of the age structure of lutjanids among a number of

* Contribution 757 of the Australian Institute of Marine Science, Townville, Queensland, Australia.

[1] Sanders, M. J., S. M. Kedidi, and M. R. Hegasy. 1984. Stock assessment for the bigeye snapper (*Lutjanus lineolatus*) caught by trawl in the Gulf of Suez. Food and Agriculture Organization of the United Nations Project for the Development of Fisheries in Areas of the Red Sea and Gulf of Aden, FAO/UNDP RAB/83/023/08, 40 p.

[2] Mees, C. C. 1992. Seychelles demersal fishery: an analysis of data relating to four key demersal species. Technical Report 019, Seychelles Fishing Authority, Victoria, Seychelles, 143 p.

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reefs within a single geographic area of the Great Barrier Reef have been published for only two species: the damselfishes *Pomacentrus moluccensis* and *P. wardi* (Doherty and Fowler, 1994, a and b). A number of studies have compared the abundance and size structure of the serranid *Plectropomus leopardus* between reefs open to fishing and those closed to fishing.[4,5,6] More recently, Ferreira and Russ (1995) have examined the size, age, and sex structure of populations of *P. leopardus* on closed and open reefs in the central Great Barrier Reef region.

The hussar, *Lutjanus adetii*, and the five-line snapper, *L. quinquelineatus*, are both widely distributed along the entire length of the Great Barrier Reef (10°S–24°S) and occur as far as 34°S (Kuiter, 1993). The habitats of both species vary, although they are most commonly associated with hard bottom areas. In the central Great Barrier Reef region, *L. adetii* is common at depths greater than 30 m within the midshelf group of reefs and is known to occur on the outershelf at depths up to at least 99 m, whereas *L. quinquelineatus* is common in both shallow and deep waters on both midshelf and outershelf reefs to a depth of at least 128 m (Newman, 1995). Loubens (1980) has demonstrated that both species are relatively long lived and slow growing in New Caledonia; similar conclusions have been obtained from the central Great Barrier Reef (Newman et al.[7]).

Neither of these lutjanids forms a significant portion of the commercial catch in the central Great Barrier Reef, and they form only a nominal contribution to the recreational catch in this region (Higgs, 1993; Newman, 1995). However, in the southern Great Barrier Reef, *L. adetii* contributes a significant proportion to the commercial lutjanid catch (Newman, 1995) and may become of increasing significance to the recreational line fishery in future years.[8] Relatively little information is available concerning the ecology of these species in Australian waters.

The recent validation (Newman et al.[7]) of age and growth for both *L. adetii* and *L. quinquelineatus* has facilitated the comparison of demographic parameters of both these species at the spatial scale of individual reefs. The aims of this study are to examine spatial variability in growth, mortality, and age structures of populations of *L. adetii* and *L. quinquelineatus* among reefs within the central Great Barrier Reef region (Fig. 1).

Materials and methods

Sampling procedures

Specimens of *L. adetii* (n=355) and *L. quinquelineatus* (n=573) were obtained between October 1991 and December 1993 from fish traps (O-trap design with 40-mm galvanized hexagonal wire mesh [Newman, 1995]) used during a research program investigating the distribution and abundance of lutjanids among reefs in the central Great Barrier Reef region (Newman, 1995; Newman and Williams, 1995). Samples of both species were obtained from four reefs (Rib [RI], John Brewer [JB], Lodestone [LO], and Kelso [KL]); additional samples of *L. quinquelineatus* were obtained from two other reefs (Davies [DV] and Myrmidon [MR]) (Fig. 1). Individual *L. adetii* <17 cm fork length (FL) and *L. quinquelineatus* <10 cm FL were usually not vulnerable to trap fishing and specimens in this size range were therefore not obtained for analysis.

Individuals of each species were measured (FL and standard length [SL]) and weighed (clean weight after removal of the gills and viscera), and sexes were determined by macroscopic examination of the gonads. The sagittal otoliths of individuals were removed and sectioned laterally through the focus with a Beuhler Isomet low-speed jewelry saw, and ages were determined according to the methods described in Newman et al.[7]

Analysis of data

Because a previous study (Newman et al.[7]) indicated significant differential growth between sexes in both species, two-way factorial analyses of variance were used to compare the mean length (FL, mm), age (years), and clean weight (g) of each species both among reefs and between sexes (in order to prevent

[4] Ayling, A. M., and A. L. Ayling. 1984. Distribution and abundance of coral trout species (*Plectropomus* spp.) in the Swain group of reefs. Capricorn section of the Great Barrier Reef Marine Park. Unpubl. report to the Great Barrier Reef Marine Park Authority (GBRMPA; Project 171), Australia.

[5] Ayling, A. M., and A. L. Ayling. 1986. A biological survey of selected reefs in the Capricornia section of the Great Barrier Reef Marine Park. Unpubl. report to the Great Barrier Reef Marine Park Authority (GBRMPA; Project 243 and 269), Australia.

[6] Ayling, A. M., and B. P. Mapstone. 1991. Unpublished data collected for GBRMPA from a biological survey of reefs in the Cairns section of the Great Barrier Reef Marine Park. Unpubl. report to the Great Barrier Reef Marine Park Authority (GBRMPA), Australia.

[7] Newman, S. J., D. McB. Williams, and G. R. Russ. Age validation, growth, and mortality rates of the tropical snappers (Pisces: Lutjanidae), *Lutjanus adetii* (Castelnau, 1873) and *L. quinquelineatus* (Bloch, 1790) from the central Great Barrier Reef, Australia. Submitted to Mar. Freshwater Res. (1996).

[8] Williams, D. McB., and G. R. Russ. 1994. Review of data on fishes of commercial and recreational fishing interest on the Great Barrier Reef, Vol. 1. Great Barrier Reef Marine Park Authority Research Publication 33, 106 p.

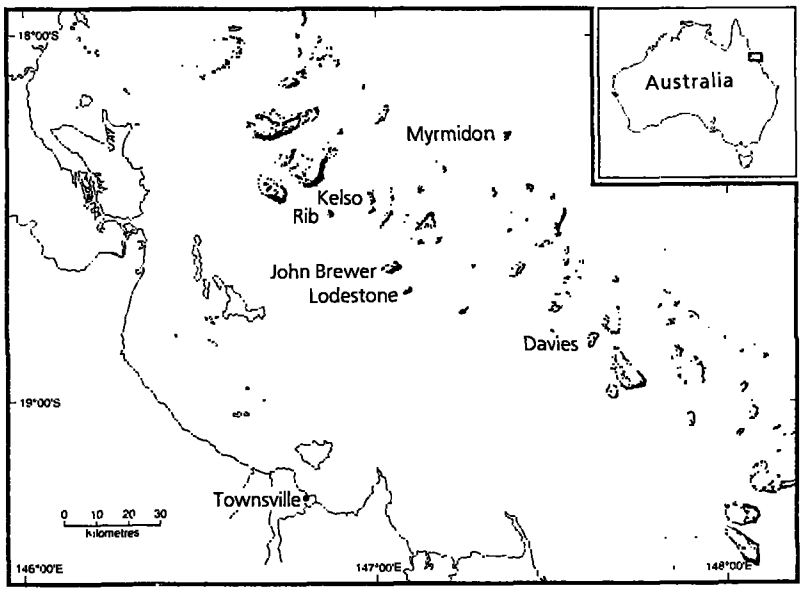

Figure 1

The locations of the reefs sampled for *Lutjanus adetii* and *L. quinquelineatus* from October 1991 to December 1993 in the central region of the Great Barrier Reef, Australia.

confounding differences among reefs with differences between sexes). Both reefs and sexes were treated as fixed and orthogonal factors in the analysis. Multiple comparisons were performed with Tukey's honestly significant difference (HSD) test (α=0.05).

The Kruskal-Wallis one-way analysis of variance by ranks was used to test for differences in the age structures of each species among reefs (Siegel and Castellan, 1988). Multiple pair-wise comparisons were performed, by using Kolmogorov-Smirnov (K-S) tests, to determine differences in the age structure of each species between individual reefs (Zar, 1984).

Growth rates for each species at each reef were also examined. The von Bertalanffy growth function (VBGF) was fitted to lengths at age for each species from each reef by using nonlinear least-squares estimation procedures.[9] The VBGF is defined as follows:

$$L_t = L_\infty (1 - e^{-K(t-t_0)})$$

where L_t = length at time t;
L_∞ = asymptotic length;
K = Brody growth coefficient;
t = age of the fish; and
t_0 = theoretical origin of the growth curve.

Von Bertalanffy growth curves were compared by using the likelihood-ratio test (Kimura, 1980), considered the most robust measure (Cerrato, 1990). A modified analysis of the residual sum of squares (ARSS) was also employed to compare VBGF's among reefs (Zar, 1984; Chen et al., 1992). Further, one-way analysis of variance was used to determine whether there were significant differences in the mean length (FL) of the early age classes of each species among reefs (α=0.05).

Analysis of covariance was used to determine whether there were significant differences in the clean weight at length (FL) relationships among reefs and between sexes for each species. Length and weight data were transformed to a natural logarithm function ($\log_e x$) to satisfy assumptions of normality and homogeneity as detected by Cochran's test (Winer, 1971). Both reefs and sexes were treated as fixed and orthogonal factors in the analysis. Again, multiple comparisons were performed by using Tukey's honestly significant difference (HSD) test.

Estimates of the annual instantaneous rate of total mortality (Z) for each species among individual reefs were obtained by using the age-based catch-curve method of Beverton and Holt (1957) and Ricker (1975). The natural logarithm of the number of fish

[9] Prager, M. H., S. B. Saila, and C. W. Recksiek. 1989. FISHPARM: a microcomputer program for parameter estimation of nonlinear models in fishery science, 2nd ed. Old Dominion University Oceanography Technical Report 87-10.

in each age class (N_t) was plotted against their corresponding age (t), and Z was estimated from the descending slope, b. Estimates of the survival rate of both species on different reefs were then calculated from the Z that was derived from catch curves, because $Z = -\log_e S$ (Ricker, 1975).

Results

There were significant differences in mean length, age, and weight of both species among reefs, and these differences were independent of the sex of the fish (Tables 1 and 2). Tukey (HSD) comparisons showed that, in general, mean length and weight were larger and mean age greater for both species at KL, although the multiple comparisons among reefs were not all definitive (Tables 1 and 2). Significant differences in mean length, age, and clean weight of both species between sexes were the same as those described in Newman et al.,[7] with males larger than females in species (Tables 1 and 2).

Age structures

Age structures of *L. adetii* differed significantly among reefs (Kruskal-Wallis statistic: H=13.85, P<0.01), with the greatest difference being that between RI and JB (Table 3). The relative abundance of older fish (year classes 10–22) at RI was greater than that at JB (Fig. 2). This pattern was seen also at LO and KL, although the overall age structures were not significantly different (Table 3). The pattern of peaks in abundance of year classes was not consistent across all reefs. The small sample size taken from KL may have biased results; however, the sample covered a range of 10 age classes and was similar to the age structure at RI. The age structure at KL was significantly different from that of both JB and LO, and the age structure at JB was significantly dif-

Table 1

Analyses of variance comparing mean length, age, and weight among reefs and between sexes for *Lutjanus adetii* (significant P values are in bold type) and a posteriori multiple comparison of means using Tukey (HSD) analysis (α=0.05; reefs are presented in order of decreasing magnitude). MS = mean square.

Source of variation	df	MS	F	P
Dependent variable: fork length (mm)				
Reefs	3	3106.15	12.912	**< 0.001**
Sex	1	462.23	1.92	> 0.15
Reefs × Sex	3	54.45	0.23	> 0.85
Residual	321	240.56		
Dependent variable: age (years)				
Reefs	3	128.85	8.57	**< 0.001**
Sex	1	43.67	2.90	> 0.05
Reefs × Sex	3	7.24	0.48	> 0.65
Residual	320	15.04		
Dependent variable: clean weight (g)				
Reefs	3	31684.62	14.70	**< 0.001**
Sex	1	23013.95	10.68	**< 0.01**
Reefs × Sex	3	799.39	0.37	> 0.75
Residual	288	2154.85		

Tukey HSD analysis among reefs

Fork length:	Kelso	Lodestone	Rib	John Brewer
Age:	Kelso	Rib	Lodestone	John Brewer
Clean weight:	Kelso	Lodestone	Rib	John Brewer

Tukey HSD analysis between sexes

Clean weight:	Males	Females

ferent from that of LO. JB and LO had strong modes in year class 7, whereas KL suggested a mode in year class 9 (Fig. 2). The abundance of year classes 10–22 at LO was greater than that at JB (Fig. 2).

Age structures of *L. quinquelineatus* also differed significantly among reefs (Kruskal-Wallis statistic: H=21.41, P<0.001). Kolmogorov-Smirnov tests (Table 4) showed that MR and LO were significantly differ-

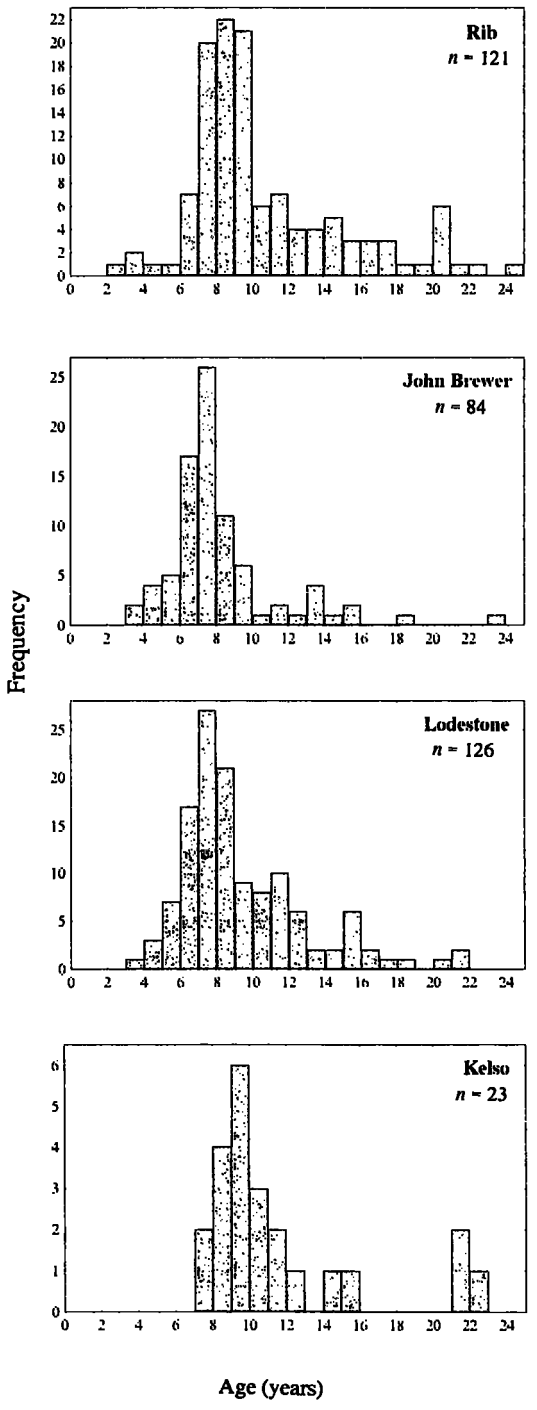

Figure 2

Age-frequency distributions for *L. adetii* among reefs in the central Great Barrier Reef.

Table 2

Analyses of variance comparing mean length, age, and weight among reefs and between sexes for *Lutjanus quinquelineatus* (significant *P* values are in bold type) and a posteriori multiple comparison of means using Tukey (HSD) analysis (α=0.05; reefs are presented in descending order). MS = mean square.

Source of variation	df	MS	*F*	*P*
Dependent variable: fork length (mm)				
Reefs	5	5944.89	25.70	**< 0.001**
Sex	1	19962.29	86.31	**< 0.001**
Reefs × Sex	5	166.94	0.72	> 0.60
Residual	551	231.29		
Dependent variable: age (years)				
Reefs	5	547.00	17.03	**< 0.001**
Sex	1	40.95	1.27	> 0.25
Reefs × Sex	5	41.13	1.28	> 0.25
Residual	550	32.11		
Dependent variable: clean weight (g)				
Reefs	5	28723.22	35.83	**< 0.001**
Sex	1	98157.42	122.45	**< 0.001**
Reefs × Sex	5	1524.81	1.90	> 0.05
Residual	551	801.60		

Tukey HSD analysis among reefs

Fork length:	Kelso	Davies	Rib	John Brewer	Myrmidon	Lodestone
Age:	Kelso	Rib	John Brewer	Davies	Myrmidon	Lodestone
Clean weight:	Kelso	Davies	Rib	John Brewer	Myrmidon	Lodestone

Tukey HSD analysis between sexes

Fork length:	Males	Females
Clean weight:	Males	Females

Table 3

Differences in the distribution of age structures of *Lutjanus adetii* between reefs were determined by using the Kolmogorov-Smirnov test (values of D_{max} are shown, significance level α=0.05, significant results are marked with an asterisk [*]).

	Reef		
Reef	John Brewer	Lodestone	Kelso
Rib	0.38*	0.17	0.19
John Brewer		0.21*	0.56*
Lodestone			0.35*

i.e. John Brewer Lodestone Rib Kelso

ent from all other reefs. KL was not significantly different from RI, but was significantly different from all other reefs. JB was not significantly different from either DV or RI, whereas DV was significantly different from RI. MR showed a peak in year class 5 and relatively strong year classes 6, 7, and 8 (Fig. 3). However, few fish older than 8 years were represented in catches. LO had relatively strong year classes 2, 3, 4, and 5, but abundance per age class declined rapidly to year 26, except for a strong mode in year class 14 (Fig. 3). DV was somewhat similar, with strong modes in year classes 5 and 6 but with the abundance of subsequent year classes declining approximately exponentially to year 22 (Fig. 3). Data were more limited for KL, which showed relatively even distribution from year classes 2–30 and peaks in year classes 5 and 14. Compared with those from

Table 4

Differences in the distribution of age structures of *Lutjanus quinquelineatus* between reefs were determined by using the Kolmogorov-Smirnov test (values of $D_{max.}$ are shown, significance level α=0.05, significant results are marked with an asterisk [*]).

	Reef				
	John Brewer	Lodestone	Davies	Myrmidon	Kelso
Rib	0.14	0.31*	0.23*	0.43*	0.14
John Brewer		0.27*	0.20	0.43*	0.27*
Lodestone			0.35*	0.30*	0.41*
Davies				0.28*	0.36*
Myrmidon					0.54*

i.e. Myrmidon Lodestone Davies John Brewer Rib Kelso

other reefs, older year classes were relatively dominant at KL. JB and RI had relatively flat age distributions for year classes 2–24 compared with those for LO, DV, and MR. The only pattern that was consistent across all reefs was the strong mode of 5-year-old individuals (Fig. 3), and this may have reflected the age at which these fish attained full recruitment to the sampling gear (fish traps).

Growth models

The von Bertalanffy models of the length-age relationship among reefs for *L. adetii* are shown in Figure 4; the coefficients of determination among reefs ranged from 0.177 to 0.462. The low coefficients of determination were attributable to the absence of younger and smaller fish in the samples. Therefore no point of inflexion was evident in the growth models among reefs. As a result, the parameters of the von Bertalanffy models for *L. adetii* among individual reefs were characterized by large asymptotic standard errors (Table 5), with LO having the best-fitting model. The von Bertalanffy model from LO was similar to that derived from all reefs pooled within the central Great Barrier Reef (Table 5). Despite the absence of small and younger fish caused by the bias in sampling, the von Bertalanffy growth function was the best empirically based assessment of growth in *L. adetii* (Fig. 4). The von Bertalanffy growth curves for *L. adetii* were not significantly different among reefs (likelihood-ratio test, P>>0.05; ARSS:F=1.13, P>>0.05), and the resulting growth curves (Fig. 4) appeared to be similar. Additionally, there were no significant differences in the mean length (FL) of the early age classes (6+, 7+, 8+, and 9+) of *L. adetii* among reefs (Table 6).

The von Bertalanffy model provided a better description of the length-age relationship among reefs for *L. quinquelineatus* (Fig. 5), with coefficients of determination among reefs ranging from 0.267 to 0.752. The younger and smaller fish were underrepresented in the catch samples from some reefs and this was reflected in the coefficients of determination (Table 5; Fig. 5). The parameters of the von Bertalanffy models for *L. quinquelineatus* among individual reefs were characterized by relatively small asymptotic standard errors (Table 5). The growth curves for *L. quinquelineatus* were significantly different among reefs (likelihood-ratio test, P<0.01; ARSS:F=8.401, P<0.001). Differences among reefs were observed in values of L_∞, K, and t_0 (Table 5). However, there were no significant differences in the mean length (FL) of the early age classes (2+, 3+, 4+, 5+, and 6+) of *L. quinquelineatus* among reefs (Table 7).

Analysis of covariance (ANCOVA) demonstrated that the relationship between weight and length in *L. adetii* was significantly different both among reefs and between sexes and that the among-reef differences were independent of the sex of the fish (Table 8). Similarly, ANCOVA demonstrated that the relationship between weight and length in *L. quinquelineatus* was also significantly different both among reefs and between sexes (Table 8). However, the significant among-reef differences were not independent of the sex of the fish (a significant interaction effect occurred between reefs and sex). The differences among reefs were different for each sex (Table 8).

Mortality

In general, individual *L. adetii* less than 7 years of age did not appear to be fully recruited in the sampled

population and were excluded from the mortality estimates derived from catch curves. For RI, JB, LO, and KL, the reef-specific total annual rate of mortality, Z, of *L. adetii*, was 0.179 (fish aged 8–24 years, r^2=0.729, SE=0.0292), 0.304 (fish aged 7–15 years, r^2=0.512, SE=0.1123), 0.225 (fish aged 7–21 years, r^2=0.781, SE=0.0344) and 0.286 (fish aged 9–15 years, r^2=0.795, SE=0.0726), representing an annual survivorship of approximately 83%, 74%, 80%, and 75%, respectively (Fig. 6). The mortality rates of *L. adetii* among reefs were significantly different (homogeneity of slopes test, P<0.01), and a multiple com-

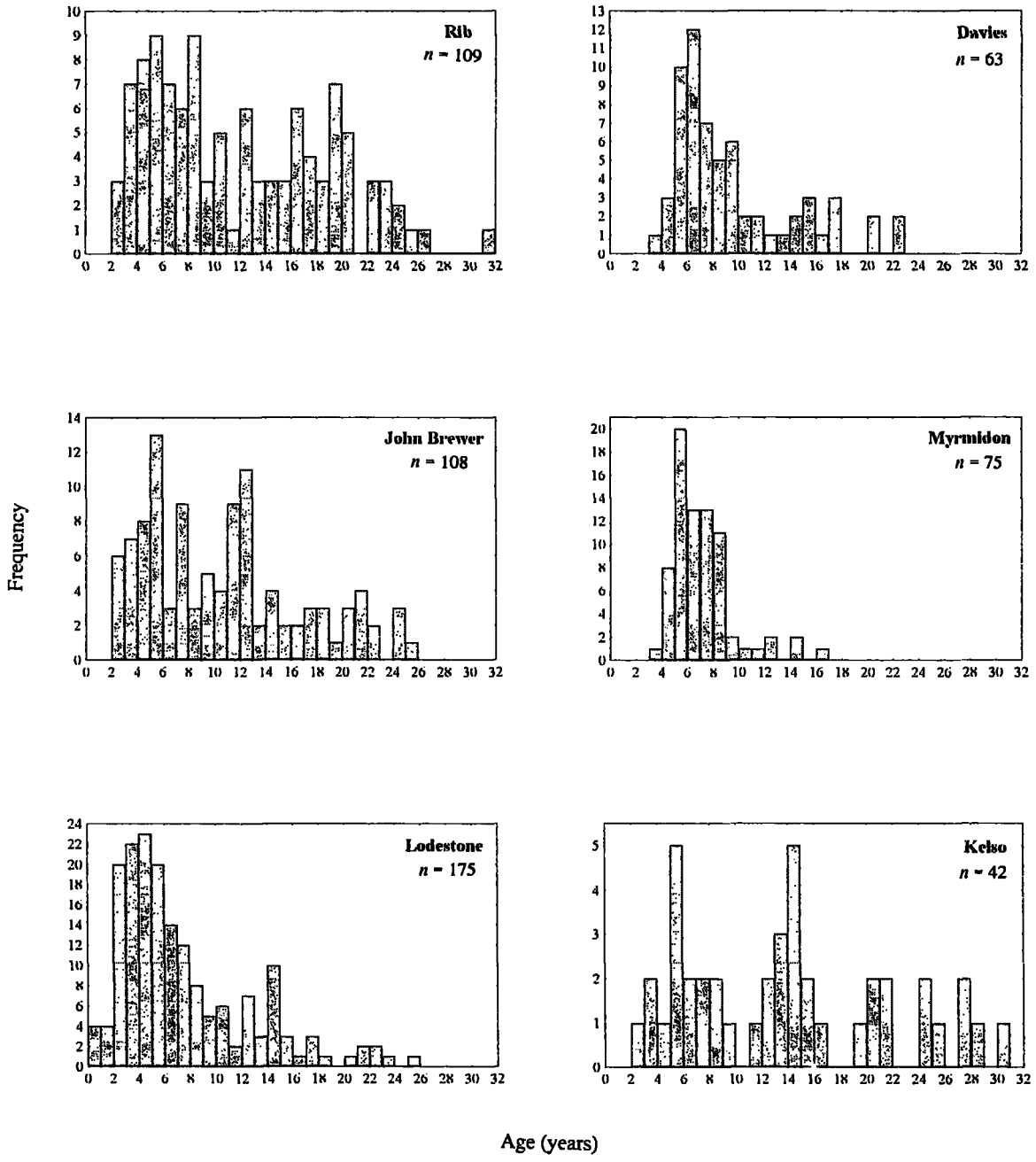

Figure 3

Age-frequency distributions for *L. quinquelineatus* among reefs in the central Great Barrier Reef.

parison of slopes indicated that the mortality rate at Rib Reef was significantly lower than that at all other reefs (RI<[JB=LO=KL]).

Individual *L. quinquelineatus* <5 years of age were usually not fully recruited in the sampled population and were excluded from the mortality estimates derived from catch curves. Estimates of mortality with high coefficients of determination were obtainable from only two reefs, LO and MR. The other reefs had a poor fit to the catch-curve regressions (Fig. 7), and hence mortality rates were not obtained either because there was a persistence of numerous strong

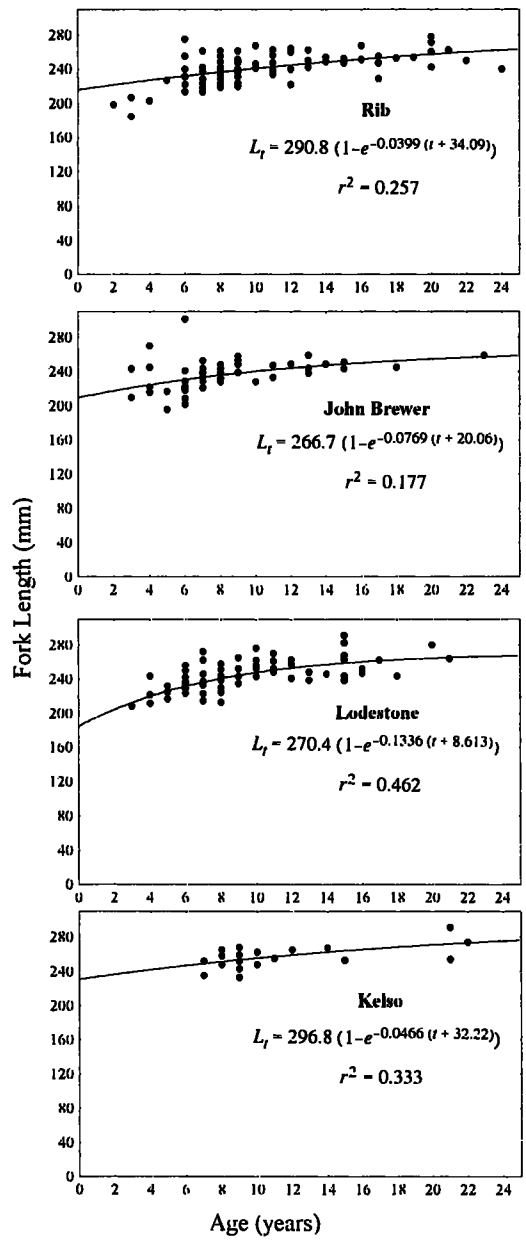

Figure 4

Von Bertalanffy growth curves and observed length at age for *L. adetii* among individual reefs in the central Great Barrier Reef.

Table 5

Growth parameters and asymptotic standard errors (ASE) calculated from the von Bertalanffy growth function, mean fork length (FL, mm), and age (years) for *Lutjanus adetii* and *L. quinquelineatus* among reefs in the central Great Barrier Reef (GBR).

Lutjanus adetii

Parameters	Reefs: Rib (n=122)	John Brewer (n=84)	Lodestone (n=126)	Kelso (n=23)	All reefs pooled central GBR (n=369)
L_∞ (FL)	290.8	266.7	270.4	296.8	265.2
ASE	59.95	34.27	8.93	119.4	4.229
K	0.0399	0.0769	0.1336	0.0466	0.1454
ASE	0.0511	0.0959	0.0484	0.1638	0.0285
t_0	−34.09	−20.06	−8.613	−32.22	−8.077
ASE	31.26	22.10	3.961	94.31	2.132
r^2	0.257	0.177	0.462	0.333	0.390
FL_{mean} (SE)	240.3 (1.48)	234.6 (1.67)	242.0 (1.39)	256.7 (2.59)	241.1 (0.88)
FL_{min}	185	196	209	233	185
FL_{max}	285	301	291	291	301
t_{mean} (SE)	10.24 (0.397)	7.79 (0.350)	8.93 (0.314)	11.17 (0.934)	9.27 (0.206)
t_{min}	2	3	3	7	2
t_{max}	24	23	21	22	24

Lutjanus quinquelineatus

Parameters	Reefs: Rib (n=110)	John Brewer (n=108)	Lodestone (n=175)	Davies (n=63)	Myrmidon (n=75)	Kelso (n=42)	All reefs pooled central GBR (n=577)
L_∞ (FL)	214.1	204.1	198.1	211.5	208.0	220.4	206.9
ASE	5.221	1.665	1.697	2.417	11.26	2.72	0.979
K	0.1125	0.3138	0.4665	0.3048	0.1711	0.2182	0.3064
ASE	0.0433	0.0506	0.0367	0.0694	0.1290	0.0474	0.0174
t_0	−14.12	−2.789	−1.108	−2.313	−8.238	−3.978	−2.587
ASE	5.774	0.8787	0.1942	1.456	7.443	1.588	0.2708
r^2	0.421	0.652	0.745	0.603	0.267	0.752	0.638
FL_{mean} (SE)	198.5 (1.5)	193.2 (1.5)	180.3 (1.9)	199.3 (1.6)	190.5 (1.3)	207.0 (2.8)	191.6 (0.8)
FL_{min}	148	146	60	163	170	155	60
FL_{max}	231	230	230	224	219	233	233
t_{mean} (SE)	11.6 (0.66)	10.2 (0.59)	6.9 (0.39)	9.06 (0.60)	6.65 (0.28)	13.43 (1.21)	9.12 (0.25)
t_{min}	2	2	< 1	3	3	2	< 1
t_{max}	31	25	25	22	16	30	31

year classes or because there were age-varying mortality rates (Fig. 7). The estimates of total mortality rate, Z, of *L. quinquelineatus* at LO and MR were 0.153 (fish aged 4–22 years, r^2=0.711, SE=0.0245) and 0.335 (fish aged 5–16 years, r^2=0.661, SE=0.0703), representing an annual survivorship of approximately 86% and 72%, respectively. Mortality rates of *L. quinquelineatus* between LO and MR reefs were significantly different (homogeneity of slopes test, P<0.01). Figure 7 shows that mortality rates and hence survivorship of *L. quinquelineatus* among reefs is highly variable.

A comparison of mortality rates among successive years (with a relatively large sample size) could be determined only for *L. quinquelineatus* at LO. The total rate of mortality, Z, of *L. quinquelineatus* at LO in 1992 was 0.176 (fish aged 4–17 years, r^2=0.615, SE=0.0402, n=109), representing an annual survivorship of approximately 84% (Fig. 8), whereas the total rate of mortality, Z, of *L. quinquelineatus* at LO in 1993 was 0.155 (fish aged 3–14 years, r^2=0.409, SE=0.0621, n=64), representing an annual survivorship of approximately 86% (Fig. 8). The mortality rates of *L. quinquelineatus* at LO were not significantly different between successive years (homogeneity of slopes test, P>0.05; Fig. 8). The natural mortality rate, M, of both species among reefs is considered equal to total mortality owing to the negligible amount of fishing mortality.

Table 6

Mean length (FL, mm) of early age classes of *Lutjanus adetii* among reefs and analyses of variance comparing the mean lengths of individual age classes among reefs. Number of samples per age class is in parentheses. ns = not significant.

	Reefs					
	Rib	John Brewer	Lodestone			
Age class	Mean FL	Mean FL	Mean FL	df	*F*	*P*
2+	199.0 (1)	— (0)	— (0)	—	—	—
3+	196.0 (2)	226.5 (2)	209.0 (1)	—	—	—
4+	203.0 (1)	238.3 (4)	226.0 (3)	—	—	—
5+	227.0 (1)	212.2 (5)	226.3 (7)	—	—	—
6+	237.1 (7)	228.5 (17)	234.1 (17)	2, 38	0.744	ns
7+	231.3 (20)	233.2 (26)	234.4 (27)	2, 70	0.507	ns
8+	235.3 (22)	239.6 (11)	238.9 (21)	2, 51	0.920	ns
9+	238.3 (21)	245.5 (6)	243.9 (9)	2, 33	1.825	ns

Table 7

Mean length (FL, mm) of early age classes of *Lutjanus quinquelineatus* among reefs and analyses of variance comparing the mean lengths of individual age classes among reefs. Number of samples per age class is in parentheses. ns = not significant.

	Reefs								
	Rib	John Brewer	Lodestone	Davies	Myrmidon	Kelso			
Age class	Mean FL	Mean FL	Mean FL	Mean FL	Mean FL	Mean FL	df	*F*	*P*
1+	—	—	113.0 (8)	—	—	—	—	—	—
2+	163.0 (3)	160.5 (6)	154.3 (20)	—	—	155.0 (1)	3,26	0.523	ns
3+	179.9 (7)	167.6 (7)	166.8 (22)	163.0 (1)	174.0 (1)	172.0 (2)	5,34	1.171	ns
4+	185.0 (8)	179.1 (8)	179.1 (23)	180.0 (3)	181.1 (8)	173.0 (1)	5,45	0.360	ns
5+	188.7 (9)	187.2 (13)	186.8 (20)	191.7 (10)	187.8 (20)	193.6 (5)	5,71	0.984	ns
6+	193.4 (7)	195.7 (3)	188.6 (14)	193.4 (12)	189.4 (13)	193.0 (2)	5,45	0.754	ns

Discussion

The significant differential growth in length and weight of both species among reefs and between sexes indicates that rates of growth in terms of weight at length of both species was variable at the spatial scale of individual reefs. However, statistical and visual comparisons of the VBGF for *L. adetii* indicate that the pattern of growth in individuals among reefs with increasing age was relatively similar. Because only one gear type was used and the distribution of juvenile *L. adetii* was not determined and is presently not known, it was not possible to obtain a sufficient range of sizes to describe the first few years of growth. The growth patterns of *L. quinquelineatus* described by the VBGF were significantly different among reefs. However, no significant differences were detected in the mean lengths of individuals in age classes 2–6 among reefs (Table 6). These results indicate that initial growth rates among reefs were not significantly different and that the significant differences in the overall growth rates among reefs probably reflected the number of young fish available for capture at each reef.

The necessary pooling of size-at-age data over two different years may have biased the resulting growth patterns, if growth was variable among years. There was, however, no evidence to suggest that growth of either species was variable among years. The pooling of data over a number of years was necessary in order to sample a wide cross section of age classes. The inclusion of size-at-age data over a number of years has the advantage of providing a general description of the growth patterns of each species at each reef. However, large sample sizes covering a

range of age classes from a number of consecutive years would be needed to determine if growth rates were variable between years.

The age structures for populations of *L. adetii* and *L. quinquelineatus* among reefs usually showed several strong year classes that were variable among reefs. The occurrence of strong year classes is well documented in the commercial catches of many temperate species (Hjort, 1914; Sissenwine, 1984; Rothschild, 1986) and has recently been observed in a number of tropical species (Doherty and Fowler, 1994b; Ferreira and Russ, 1995). Year-class strength in both temperate and tropical species has been linked to early life history processes (e.g. Hjort, 1914; Sissenwine, 1984;

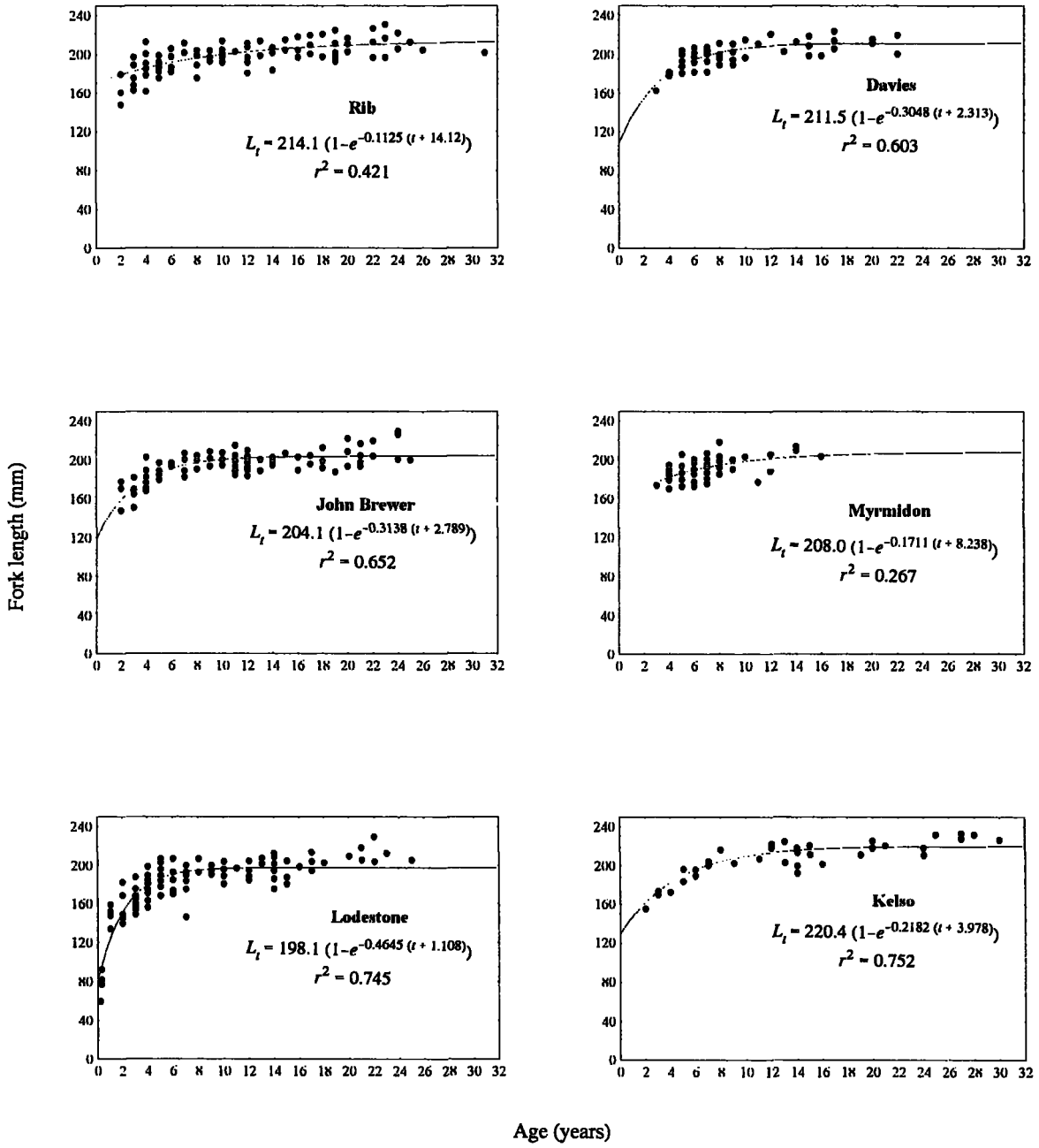

Figure 5

Von Bertalanffy growth curves and observed length at age for *L. quinquelineatus* among individual reefs in the central Great Barrier Reef.

Doherty and Fowler, 1994b). Further, the suggestion that recruitment variability is a major factor influencing both the distribution and local densities of coral reef fishes has been recognized for a number of years (Williams, 1980; Doherty, 1981, 1983, 1991; Victor, 1983; reviews of Doherty and Williams, 1988). Subsequently, Doherty and Fowler (1994b) have shown that for the common tropical damselfish *Pomacentrus moluccensis*, age structures from individual reefs have preserved major temporal variations in the recruitment patterns over at least 10 years, providing empirical evidence of a strong effect of recruitment history on subsequent year-class strength. It is therefore conceivable that the various age structures of both lutjanid species among reefs is a consequence both of variability in recruitment at the localized scale of individual reefs and of good recruitment years persisting in the age structure of populations over time.

Estimates of the rate of natural mortality in fish populations are essential to fishery management (see Ricker, 1975; Gulland, 1983; and Russ, 1991). The mortality rate for *L. adetii* was significantly different among reefs, although these differences were small. The mortality rates for this species in general were low and the rates of survivorship were correspondingly high. Mortality rates for *L. quinquelineatus* were not obtainable from all reefs owing to either the persistence of strong year-class modes, (possibly to nonconstant mortality rates at a number of reefs (although these were not detected among years at Lodestone Reef), or differential mortality of cohorts (as opposed to interannual variability in mean [cross-cohort] mortality rates). The results observed here suggest that interannual variation in recruitment may be retained in the age structure at each reef as found for *P. moluccensis* (Doherty and Fowler, 1994b). Mortality rates derived with the catch-curve method of Beverton and Holt (1957) and Ricker (1975) are based on the assumption that recruitment is constant in the population under con-

Table 8

Analyses of covariance comparing weight at length (transformed to $\log_e$, covariate = length) among reefs and between sexes for *Lutjanus adetii* and *L. quinquelineatus* (significant *P* values are in bold type; note Kelso Reef was not included in the analyses because of the small sample size) and a posteriori multiple comparison of means using Tukey (HSD) analysis (α=0.05).

Source of variation	df	MS	*F*	*P*
L. adetii				
Reefs	2	0.0328	11.917	**< 0.001**
Sex	1	0.0484	17.577	**< 0.001**
Reefs × Sex	2	0.0004	0.127	> 0.85
Residual	266	0.0028	—	—
Tukey HSD analysis among reefs	Lodestone	Rib	John Brewer	
Tukey HSD analysis between sexes	Males	Females		
L. quinquelineatus				
Reefs	4	0.0683	15.647	**< 0.001**
Sex	1	0.0258	5.907	**< 0.05**
Reefs × Sex	4	0.0129	2.948	**< 0.05**
Residual	510	0.0044	—	—
Tukey HSD analysis among reefs				
Male:	Rib	Davies	John Brewer	Myrmidon	Lodestone
Female:	Rib	Davies	John Brewer	Myrmidon	Lodestone
Tukey HSD analysis between sexes				
Rib:	Males	Females		
John Brewer:	Males	Females		
Lodestone:	Males	Females		
Davies:	Males	Females		
Myrmidon:	Males	Females		

sideration. Mortality estimates derived with the catch-curve regression method are least sensitive to minor violations of this assumption (Ricker, 1975) and this is particularly evident in *L. quinquelineatus*. Despite this, it is evident from Figure 7 that mortality rates of *L. quinquelineatus* are variable among reefs and are similar to those for populations of *L. adetii* in that they are characterized by low rates of total mortality and high rates of survivorship. However, mortality estimates cannot be derived with great confidence from populations where significant recruitment variability is retained in the age structure (e.g. Ferreira and Russ, 1995), and although Ricker (1975) has suggested that irregularities in catch curves caused by variable recruitment can be reduced by combining samples over successive years,

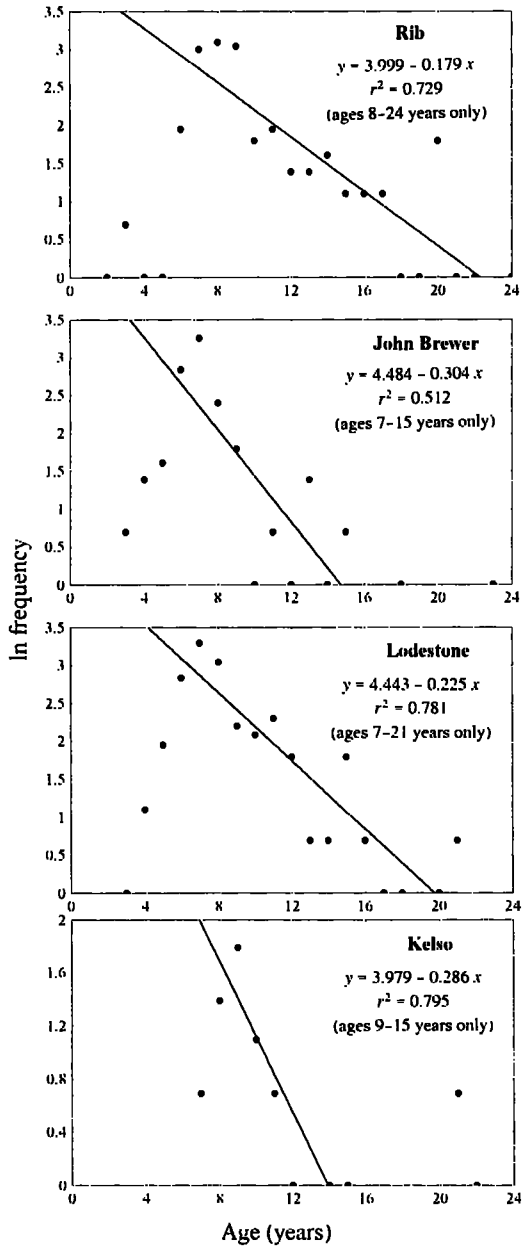

Figure 6

Catch curves for *L. adetii* among reefs, based on observed ages.

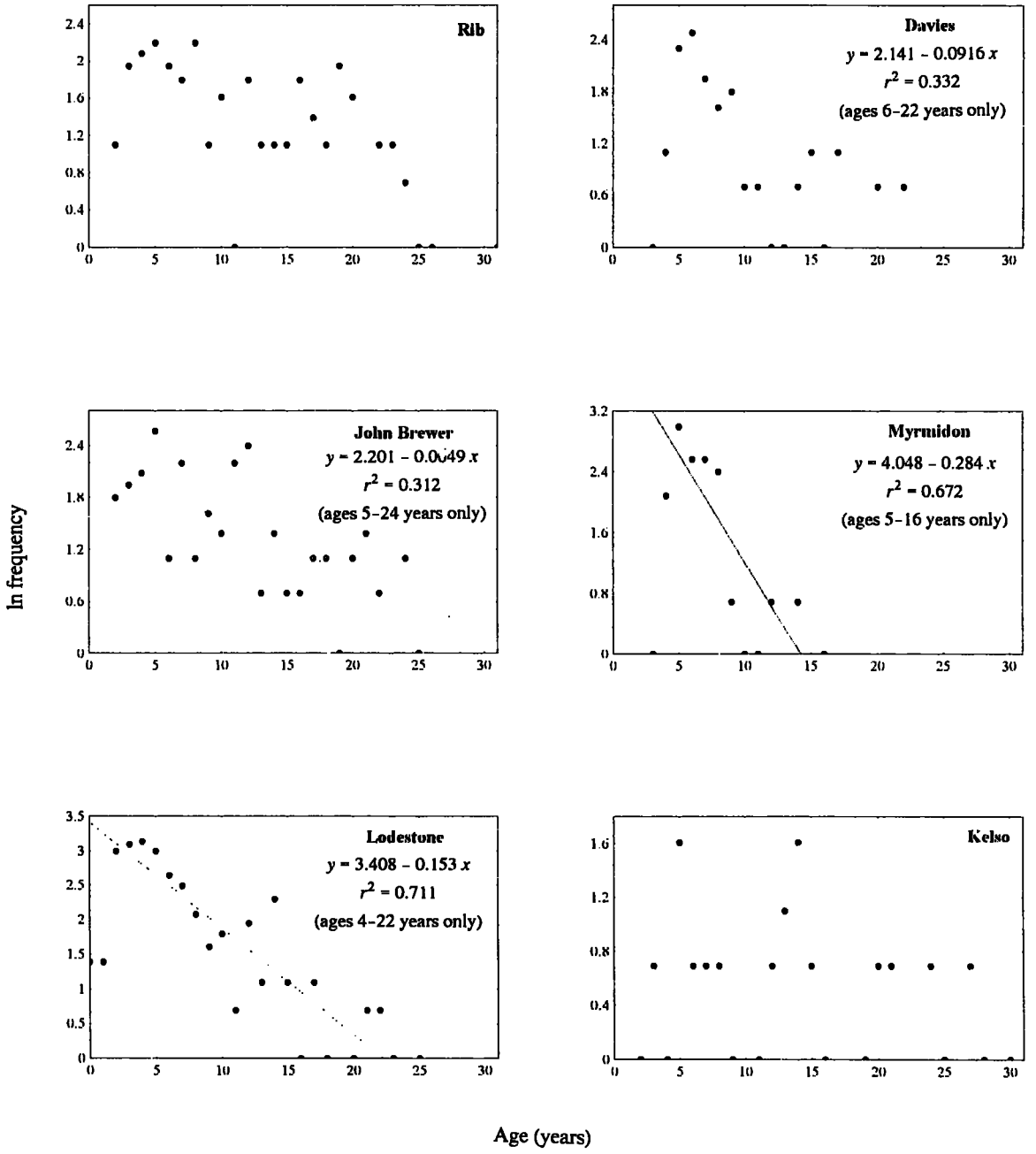

Figure 7

Catch curves, based on observed ages, for *L. quinquelineatus* among reefs.

this method was not expected to reduce variability among age classes in the present study.

However, the mortality rates of *L. quinquelineatus* at Lodestone Reef were not significantly different between successive years (Fig. 8). This result suggests that the variable mortality rates and hence survivorship of these species among reefs may be relatively consistent through time. Similarly, Doherty and Fowler (1994a) suggested that mortality schedules were consistent (not constant) across space and time for two damselfish species from the positive correlations that were present between spatial and temporal variation in recruitment and subsequent abundance. Therefore, the observed differences in mor-

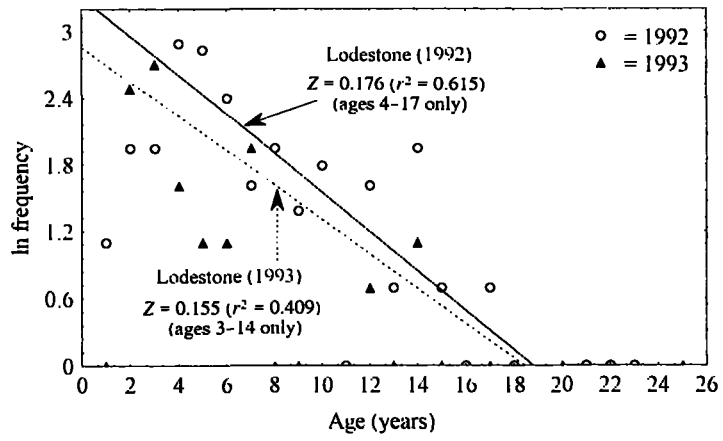

Figure 8

Catch curves for *L. quinquelineatus* from Lodestone Reef between successive years, based on observed ages.

tality rates among reefs for these species are likely to be authentic and not a product of the assumptions inherent in the use of catch curves.

In conclusion, this study demonstrated that significant variability exists in the mortality and age structures of *L. adetii* and *L. quinquelineatus* at the spatial scale of individual reefs. The demography of both these lutjanid species at the spatial scale of individual coral reefs is most likely to be a consequence of the nonequilibrial balance of variable recruitment interacting with density-independent mortality (Doherty and Fowler, 1994b). This spatial variability in demographic parameters among reefs should be considered in the development of management models. The significant differences in mortality rates and age structures for the populations of *L. adetii* and *L. quinquelineatus* among reefs would have more impact on management models than the small differences in growth for these species. Further, greater longevity conveys a selective advantage by increasing the cumulative lifetime fecundity (egg production) of the female parent (see Beverton, 1987). Therefore, in terms of the current management models of the Great Barrier Reef Marine Park, it would be advantageous to protect reefs that are characterized by species with extended longevity and low rates of natural mortality (in comparison with reefs of similar population size but which are characterized by fish with reduced longevity and high rates of natural mortality). The primary advantage of adopting this strategy would be that the spawning biomass of the longer lived fishes would be protected which has the capacity to act as a recruitment source for the surrounding areas that are fished.

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Abstract.—Fisheries discard data are often characterized by a smooth distribution of positive amounts of per-set discard but with an extremely large number of zero observations. This discontinuity is difficult to fit with a standard distribution. One approach is to model per-set discard with a mixture of two distributions, with one component representing the zero observations and the other representing the observations of positive discard. In this paper, we describe such a mixture model that is suitable when the discard observations have been rounded to integer amounts. In particular, when "rounded" zeros (representing small amounts of discard) and "true" zeros (representing no discard) are indistinguishable in the data, the mixture model can be used to estimate the proportion of either. We fit this model to tuna discard data collected by observers aboard the U.S. tuna purse-seine fleet in the eastern tropical Pacific Ocean during the years 1989–92. We use the model to estimate discard per set, allowing the model parameters to depend upon fishing strategy and geographic location, and we estimate mean discard per set fisherywide.

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A mixture model for estimating discarded bycatch from data with many zero observations: tuna discards in the eastern tropical Pacific Ocean

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Many fisheries catch unwanted individuals of nontarget species in addition to target species. This bycatch is generally discarded and in many fisheries few, if any, individuals survive capture and discard (e.g. Joseph, 1994). Estimating the extent of such discard is increasingly important as fisheries managers contend with situations where unwanted catch in a fishery is desirable in other contexts. For example, bycatch in one fishery may include juvenile members of the target species in the same or another fishery, or individuals from threatened, endangered, or protected species (e.g. Collins and Wenner, 1988; Caillouet et al., 1991).

Despite their increasing importance, bycatch and discard remain relatively unstudied. Few fisheries routinely measure discards so that the amount of discard usually must be estimated rather than reported directly (e.g. Berger et al., 1989). The U.S. tuna purse-seine fishery in the eastern tropical Pacific Ocean (ETP) provides an opportunity to examine this problem because quantitative information on discard of tuna (including both nontarget tuna species and juveniles of target species) has been collected from the fishery since 1988.

A flexible approach is required to model tuna discard from this fishery because the purse-seine vessels capture fish using three distinct fishing strategies. These strategies are defined by the different types of sets involved: "log fishing," "school fishing," and "dolphin fishing." Log fishing catches tuna by setting purse seines around fish associated with floating objects. Log sets usually capture schools of small (30–50 cm) yellowfin tuna, *Thunnus albacares*, or mixed schools of small yellowfin and like-size skipjack tuna, *Katsuwonus pelamis*. School fishing catches tuna by setting purse seines around schools composed purely of tuna (again, usually small fish and either pure schools of yellowfin or mixed schools of yellowfin and skipjack tuna), located by surface disturbances created by the schools. Dolphin fishing catches tuna by first locating surface disturbances created by closely associated dolphins (NRC, 1992) and by setting purse seines around both tuna and dolphins. Tuna associated with dolphins almost always consist of pure schools of large (80–120 cm) yellowfin tuna (IATTC, 1989).

Log fishing generates large amounts of tuna discard in almost every set, whereas school fishing generates

moderate amounts of tuna discard and in a smaller proportion of sets than does log fishing (Joseph, 1994). Dolphin fishing generates small amounts of tuna discard and only infrequently. Thus, tuna discard data from dolphin sets are almost all zero observations, whereas data from log sets are mostly nonzero observations, and school sets are an intermediate case.

In this paper we develop a method for using a single probability distribution to model discard per set for these three disparate types of data and show how to use the model to estimate mean discard per set for each set type. The focus of the present study is development and description of the model as a solution to a common problem in discard estimation. In general, the method presented is applicable to any situation involving analysis of data characterized by subsets with varying proportions of zero observations. Detailed results of applying the model and its implications for the U.S. tuna purse-seine fishery in the ETP are the subject of a future paper.

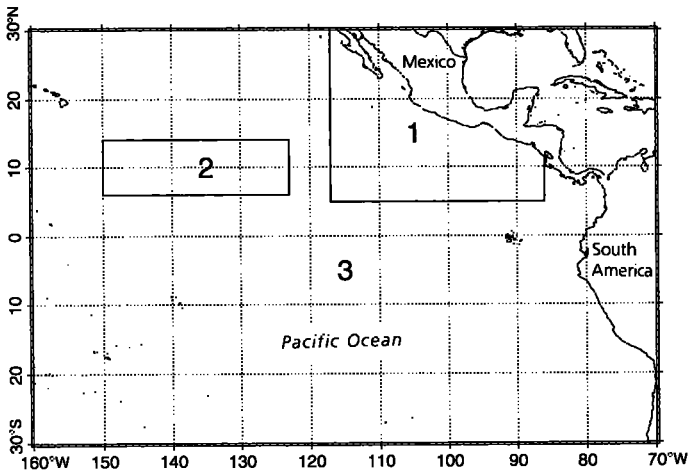

Figure 1

Geographic strata used in developing models to estimate mean discard per set for the U.S. tuna purse-seine fleet fishing in the eastern tropical Pacific Ocean, 1989–92 (Federal Register, 1989). Area 3 includes all ETP not explicitly included in areas 1 and 2.

Methods

Data

The data consisted of per-set estimates of total tons of tuna discarded by the U.S. fleet only. We did not have access to data on species or size composition of tuna discards nor to data on nontuna discards.

Data were collected by National Marine Fisheries Service (NMFS) or Inter-American Tropical Tuna Commission (IATTC) observers placed aboard U.S. tuna purse-seiners during routine fishing trips to the eastern tropical Pacific Ocean (Fig. 1) as part of a bycatch study initiated in 1989 by the IATTC. Observers recorded time and position of all sets made by U.S. vessels fishing in the ETP during the 31-month study period (from 1 September 1989 to 30 March 1992). Observer coverage was 100% during this period. However, during the first eleven months (from 1 September 1989 to 30 July 1990), discard information was recorded only for approximately half of the sets. Observers recorded discards for all sets during the remaining twenty months.

Because it was not feasible to weigh tuna discard directly, observers estimated the discard weight by counting the number of brailers (large fish baskets) used to empty the net after each set, multiplying by an estimated tonnage per brailer, and then multiplying by the estimated fraction of nontarget tuna in the catch. Observers estimated this fraction by observing the composition of brailers or by observing catch sorting on deck. Occasionally the majority of the catch was discarded before being brailed aboard. In these cases, observers estimated discard weight by first estimating the weight of the total catch and then subtracting an estimate of the tonnage loaded by brailer.

Observer estimates of discard tonnage were rounded to integer values, with rounding interval increasing with amount of discard (Fig. 2). There is a systematic tendency toward rounding to the nearest 5 or 10 metric tons (t) for small and medium estimates of discard and to the nearest 25 or 50 t for the largest estimates. For sets with moderately small amounts of discard, observer estimates tended to be more precise because the bycatch, as well as the target fish, were brailed aboard the vessel, then sorted on deck. This allowed the discard to be easily compared with the total catch. For sets with large amounts of discard, the fish may not have been brought on board, making precise estimates more difficult and rounding tendencies greater. For sets with very small amounts of discard, weights were rounded to the nearest ton so that it was not possible to distinguish observations with no discard from those with very small amounts of discard (less than one-half ton). Thus, "zero observations" may correspond to either case.

We did not attempt to account for the uncertainty introduced by these sources of measurement error and rounding. In the absence of data or studies for determining the ground truth of observer estimates

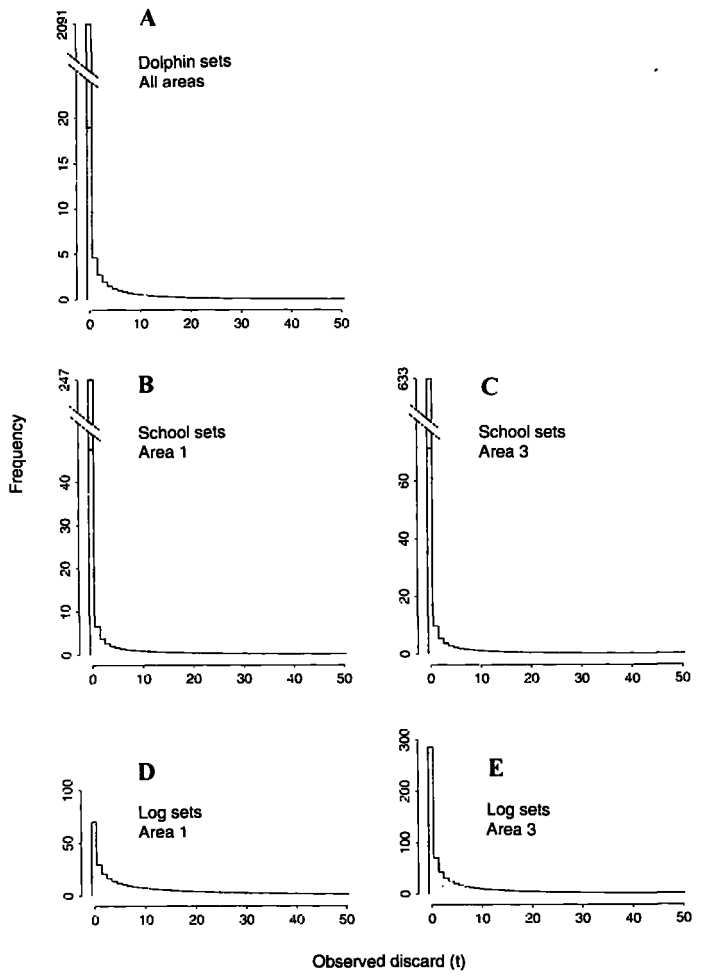

Figure 2

(**A–E**) Observed and fitted per-set tuna discards for school, dolphin, and log sets for the U.S. tuna purse-seine fleet fishing in the eastern tropical Pacific Ocean, 1989–92. Geographic areas are defined in Federal Register (1989) (Fig. 1). Bars indicate observed frequencies, lines indicate fitted frequencies from the negative binomial with added zeros model. Top portion (above horizontal division) of the fitted frequency for the zero bin of dolphin and school set data represents "true zeros," bottom portion represents "rounded" zeros from negative binomial (NB) component. Vertical axes have been cut and scaled to make NB components directly comparable. Not shown: (C) 3 observations >50 tons, (D) 16 observations >50 tons, (E) 12 observations >50 tons.

of discard or in the absence of a plausible model for the measurement errors, we treated the discard weight estimates as exact measurements.

Discard weight was recorded for 59% (2,110 of 3,590, Table 1) of observed dolphin sets, 76% (960 of 1,266) of observed school sets, and 75% (998 of 1,328) of observed log sets. These sets generated 134, 1,098, and 9,819 tons of reported discard, respectively. The relatively small discard totals for school and dolphin sets were due to the large numbers of those sets with zero discard reported. Positive amounts of tuna discard were reported in 65% (650 of 998, Table 1) of log sets for which discard was recorded, but in only 8% (80 of 960) of school sets and only 0.9% (19 of 2,110) of dolphin sets for which discard was recorded. We ignored log and school fishing in area 2 (see next sec-

Table 1

Fishing effort in numbers of sets for the U.S. tuna purse-seine fleet fishing in the eastern tropical Pacific Ocean, 1989–92. Geographic areas are defined according to Federal Register (1989) (Fig. 1). N is the total number of sets in a given area, n is the number of sets for which discard weight was recorded, and n^+ is the number of sets for which strictly positive discard was reported.

Set type	Area	N	n	n^+
Dolphin	1	2,496	1445	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]	1,328	998	650

[1] Totals for log sets do not include sets in geographic area 2 because these sets were not included in our analysis. See text for explanation.

tion) for this analysis, because 0 school sets and only 10 log sets (4 with estimated discard) occurred in this area (Table 1). We also omitted 7 sets in which the entire catch (target catch plus discard) was lost owing to equipment failure.

Modelling discard per set

We chose a modified negative binomial (NB) distribution known as the negative binomial with added zeros (NBAZ) (Johnson and Kotz, 1969) to model discard per set. This distribution can accommodate the wide range in the proportion of zero observations, as well as the relatively heavy tails in the observed distributions of discard for all three set types (Fig. 2). (See Discussion section for two other models considered but rejected.)

The NBAZ is a mixture of a NB distribution and a discrete probability mass at zero. Under this model, discard per set is either exactly zero with probability p or has a NB distribution with probability $1-p$. The NB portion of this distribution can be viewed as representing strictly positive amounts of discard rounded to integer values. Thus, zero values that are part of the NB can be interpreted as observations of small amounts of discard rounded down to zero. Zero values from the probability mass can be interpreted as exact zeros. The probability function for this modified NB distribution is

$$\Pr\{Y=y\} = \begin{cases} p+(1-p)\left(\frac{1}{1+a\mu}\right)^{1/a}, & y=0 \\ (1-p)\frac{\Gamma(y+1/a)}{y!\Gamma(1/a)}\left(\frac{1}{1+a\mu}\right)^{1/a}\left(\frac{a\mu}{1+a\mu}\right)^{y}, & y=1,2,\ldots \end{cases} \quad (1)$$

where Y is an individual observation (tons of discard per set), p is the probability of an observation coming from the "true zero" state, $1-p$ is the probability of an observation coming from the NB state, and μ and a are the mean and variance parameters, respectively, of the conditional NB.[1]

The parameter a determines the shape of the distribution. As a approaches zero, the conditional NB distribution in the mixture approaches a Poisson distribution. As a increases, the conditional NB becomes more skewed, with a heavier tail and higher probability of a zero observation. The parameter p is a mixing parameter which controls the relative importance of the NB and the probability mass at zero. When p is one, the distribution is a probability mass at zero. When p is zero, the probability distribution becomes strictly NB and expected discard per set is μ (the NB mean).

The expected value and variance for individual observations from this probability distribution are

$$E[Y] = (1-p)\mu \quad (2)$$

$$\mathrm{var}[Y] = (1-p)\left(\mu + (a+p)\mu^2\right). \quad (3)$$

We fit the NBAZ model using maximum likelihood and allowing the three model parameters to depend upon set type and geographic area. We also considered using tons of tuna loaded (i.e. commercial catch), time of day, and month as covariates, but rejected them as either unfeasible (due to sampling unbalance) or statistically unimportant. We did not attempt to account for any long-term (i.e. year to year) trend in discard rates because the data included too few years for such an analysis.

A priori, we used the same three geographic areas (Fig. 1) as those currently used to compare U.S. and non-U.S. dolphin mortality rates (Federal Register, 1989). These roughly define the major fishing areas in

[1] The NBAZ can be equivalently reparametized in terms of a "zero-truncated" NB and a probability mass at zero. The parameter corresponding to p would, in that case, denote the probability of a zero observation regardless of source. Thus, that form does not distinguish between "true" and "rounded" zeros.

the system. The total number of sets observed in each area, including sets for which discard was not recorded, represents the actual areal distribution of fishing effort during the study period. However, observation of discard was not proportional to this distribution of total effort (Table 1). In the analysis that follows, it is important to distinguish between the total number of sets, denoted by $N_{i,j}$, and the number of sets for which discard was recorded, denoted by $n_{i,j}$. The former define the actual distribution of fishing effort, whereas the latter simply reflect the sample taken. Because our sample of sets with discard recorded was not proportional to the total effort, ignoring area in the analysis could lead to biased estimates if the mean discard per set differs from area to area for a given set type.

Because there were clear differences between the the three set types in per-set discard, we included set type as a covariate for all three model parameters. Thus, with set type and geographic area as the only covariates, our analysis reduced to fitting the model (Eq. 1) independently for each set type, with p, μ, and α having possibly different values in each area. To determine an appropriate dependence upon area, we used stepwise likelihood-ratio tests to select the simplest model that could not be significantly improved by adding additional terms. We first made initial fits for each set type using no areal dependence, then progressively added dependence for more of the model parameters. At each step, we used a quasi-Newton numerical optimization algorithm to maximize the likelihood and estimate parameters. It should be noted that because this is not a linear model, significance levels (i.e. p-values) from these likelihood-ratio tests are approximate. We used the large-sample normal approximation for MLE's to compute standard errors for p, μ, and α. For comparison, we also computed bootstrap standard errors.

It can be shown from the likelihood equations for the NBAZ that estimates for the parameters α and μ depend solely on the positive observations in the data. The estimate for the parameter p depends on all the data, but most strongly upon the proportion of zero observations. Thus, the precision of the estimates for α and μ can be very poor if the data contain few positive observations, even though the precision of the estimate for p may still be very good.

Estimating mean discard per set

We used Equation 2 and the maximum likelihood estimates for p and μ from the best-fit models to estimate mean discard per set for each set type in each area. We also calculated a "pooled" estimate for each set type as the weighted average of the area-specific estimates, where weightings were proportional to total effort in each area. For example, mean discard per set of type i in area j is estimated as

$$\hat{E}[Y_{i,j}] = (1 - \hat{p}_{i,j})\hat{\mu}_{i,j}, \tag{4}$$

whereas the "pooled" estimate for all areas combined is estimated as

$$\hat{E}[Y_i]_{pooled} = \sum_j N_{i,j}\hat{E}[Y_{i,j}] \Big/ \sum_j N_{i,j}, \tag{5}$$

where $N_{i,j}$ is the total effort (in number of sets) of type i occurring in area j. Note that this "pooled" calculation is based on the proportion of total sets (including those for which discard was not recorded) observed in each area. This is an estimate of the mean discard per set over the entire fishery during the study period. However, it is also valid as a prediction of future discard if the proportion of effort (sets) in each area remains constant as the actual number of sets varies, assuming that other factors in the fishery, such as size and species composition of discard and style of fishing, remain the same.

While Equation 4 provides a straightforward way to compute the MLE for the product $(1-p)\mu$, the variance of that product can be difficult to estimate accurately. However, we were able to use the likelihood equations for the NBAZ to derive explicit forms for the MLE of mean discard per set. Specifically, only the product $(1-p)\mu$ need be estimated, and we derived, through algebraic manipulation of the likelihood equations, simple closed-form expressions that do not involve the individual parameter estimates. By the invariance properties of maximum likelihood estimates, these simpler forms give results that are identical to those from using Equation 4.

With no areal dependence, the MLE for the product $(1-p)\mu$ is simply the sample mean:

$$\hat{E}[Y] = \bar{y} = (1/n)\sum_k y_k, \tag{6}$$

where the set type subscript i is suppressed for clarity. Similarly, with complete areal dependence, the MLE for each area reduces to the sample mean in that area, and the "pooled" estimate is computed by using Equation 5. In both of these cases, the variance for the MLE of $(1-p)\mu$ can be estimated by using the sample variance of the data.

When only the mixing probability p depends on area, the MLE for mean discard per set in area j is slightly more complicated, and reduces to

$$\hat{E}[Y_j] = (n_j^+ / n_j) \sum_k y_k^+ / n^+ , \quad (7)$$

where n_j^+ and n_j are the number of positive observations and the total number of observations in area j, the y_k^+ are the positive observations in all areas, and n^+ is the total number of positive observations in all areas. Similarly, when only the NB mean μ depends on area, the MLE for mean discard per set in area j reduces to

$$\hat{E}[Y_j] = (n^+ / n) \sum_k y_{j,k}^+ / n_j^+ , \quad (8)$$

where n^+ and n are the number of positive observations and the total number of observations in all areas, the $y_{j,k}^+$ are the positive observations in area j, and n_j^+ is the total number of positive observations in area j. Again, Equation 5 is used to compute "pooled" estimates in these latter two cases. Note that the estimates for different areas are not independent, because both Equations 7 and 8 involve observations from all areas. In particular, the first term in Equation 7 is an area-specific estimate of the probability of a positive observation, whereas the second term is a "pooled" estimate of the mean for positive observations. This is consistent with the areal dependence on which Equation 7 is based, and provides more precise estimates of E[Y] than simply taking the sample mean in each area. A similar interpretation holds for Equation 8.

As a consequence of Equations 6, 7, and 8, the estimate of mean discard per set $(1-p)\mu$ can be much more precise than the estimates of the individual parameters involved in it, because it does not depend solely on either the positive observations or the proportion of zeros.

While variance estimators for Equation 6 are straightforward, there is no simple analytic result for estimating the variance of Equations 7 or 8 (see Discussion). Thus, for consistency, we used bootstrap methods in all cases. Our bootstrap resampling procedure varied slightly for each set type, depending on the particular areal dependence chosen for the model parameters. When no dependence was appropriate, data were resampled across all areas. When dependence was important, data were resampled by area in the same proportions as the original observations.

Results

Modelling discard per set

Based on the results of likelihood-ratio tests, geographic area was a statistically significant predictor of discard per set for only two of the three set types (log and school sets).

Nonzero observations of discard from the third set type (dolphin sets) were reported very infrequently (19 out of 2,110 sets, Table 1). The data provided little statistical information from which to distinguish patterns in discard between geographic areas, and area failed to produce a significant improvement in the fit when included as a covariate for dolphin sets. Therefore, we selected the model with no areal dependence for any of the parameters so that the estimates for p, a, and μ for dolphin sets are fisherywide values (Table 2). The standard error of the mixing parameter p for the dolphin model is small (CV=1.53%), reflecting the high estimate for p dictated by the extremely large number of zero observations of discard. The standard errors of the parameters for the NB portion of the probability distribution (a and μ) are quite large (CV's > 90%, Fig. 3), reflecting the few positive data available for their determination.

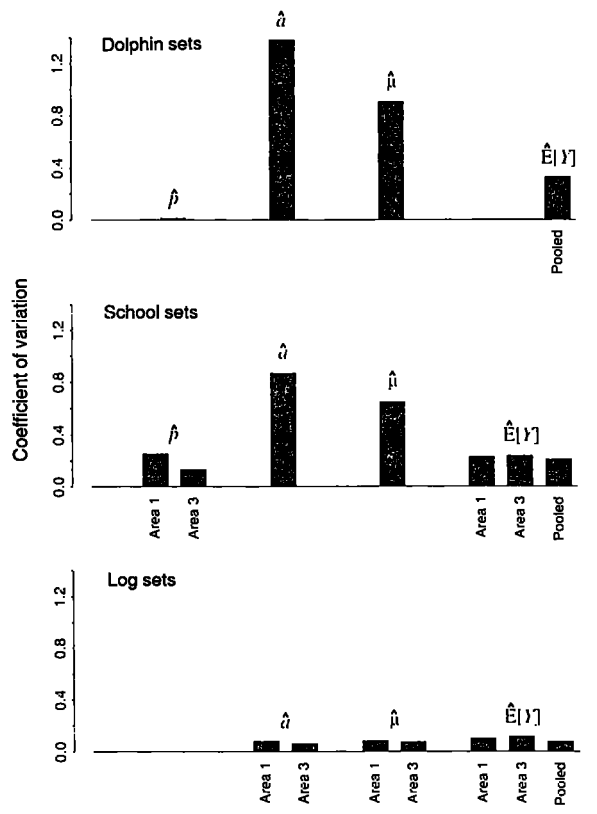

Figure 3

Coefficients of variation for estimates of the model parameters p, a, and μ, and for estimates of mean discard per set for the U.S. tuna purse-seine fleet fishing in the eastern tropical Pacific Ocean, 1989–92. Geographic areas are defined in Federal Register (1989) (Fig. 1). Pooled estimates are fisherywide, across all areas.

Table 2

Parameter estimates from a fit of the negative binomial with added zeros to tuna discard data from the U.S. tuna purse-seine fleet fishing in the eastern tropical Pacific Ocean, 1989–92. p is the mixing parameter, and μ and α are the mean and shape parameters of the conditional negative binomial. Standard errors are in parentheses. Geographic areas are defined according to Federal Register (1989) (Fig. 1).

		School sets		Log sets	
Parameters	Dolphin sets	Area 1	Area 3	Area 1	Area 3
p	0.982 (0.015)	0.715 (0.182)	0.825 (0.111)	0 (0)	0 (0)
μ	3.53 (3.21)	5.53 (3.60)		15.4 (1.3)	7.09 (0.55)
α	3.87 (5.36)	7.20 (6.28)		2.34 (0.19)	3.93 (0.25)

At the other extreme, nonzero discard observations were very frequent for log sets (650 out of 998 sets, Table 1). Using fishing area as a covariate for both the mean and shape parameters μ and α, we improved the fit significantly (p-value <0.001) over simpler models. However, the numerical optimization failed to converge to a positive value for p in either area, producing estimates of zero for p in both areas (Table 2). Thus, the estimated probability distributions effectively collapsed to unmodified NB's. Because positive observations were so abundant, estimated standard errors for the mean and shape parameters (Table 2) were small (CV's <8.5%, Fig. 3).

Discard from school sets presented an intermediate case in which we selected a model which included marginally different estimates for the mixing probability p in areas 1 and 3, but no geographic dependence for α or μ (Table 2). Because there were considerably fewer nonzero observations (80 out of 960 sets, Table 1) for school sets than for log sets, parameter estimates were much less precise. Likelihood-ratio tests indicated that fishing area should be included as a covariate for either the shape parameter α or the mixing probability p, but that including areal dependence for p and α simultaneously, or for μ, did not further improve the fit. Because the approximate p-values for adding areal dependence to the two parameters were fairly similar (0.04 for α, 0.12 for p) and the two parameters have similar effects in the model,[1] there was no clear basis for selecting one parameter over the other. We subsequently decided to include areal dependence only for p for two reasons. First, the small number of positive observations for school sets limits the precision of the shape estimate. Second, the difference in the estimated shape between areas was due mainly to two unusually large observations in area 3. Without these two observations, the difference in estimated shapes was reduced, and the significance levels of the two different models were nearly equal (approximate p-values of 0.09). As was the case for dolphin sets, the predominance of zeros in the school set discard data led to small estimated standard errors for the mixing probability p (CV's <13.5%, Fig. 3) but to large estimated standard errors for the mean and shape parameters (CV's > 65%, Fig. 3).

In our model, p may be interpreted as the probability of exactly zero discard, as opposed to small amounts of discard that have been rounded down to zero in the data. The estimates of p for the three set types imply that essentially all dolphin sets (98%) involve no discard, whereas log sets always involve at least some discard. Observer experience[2] indicates that this result is consistent with generally observed patterns for dolphin and log sets.

The estimated shape parameters varied widely between the three set types (Table 2), but the large standard error estimates for the school and dolphin shape parameters prevent us from making any strong statements about shape as a function of set type. As mentioned above, the estimated shape parameter for school sets was strongly affected by the presence of two unusually large observations (100 and 125 tons of discard) in area 3. Repeating the analysis without these two observations led to a shape estimate of 3.75 (SE=2.10), which is more similar to the shape estimates for log sets (2.94 for area 1, 3.93 for area 3).

We could not use bootstrap methods to compute standard errors for dolphin sets because there were so few sets observed with positive discard recorded (Table 1). In resampling for the bootstrap, approximately one-third of the samples contained too few positive observations for the maximum likelihood algorithm to converge. Therefore, Table 2 includes only the standard errors computed from the analytic approximation formulae.

[1] p and α are similar in the effect they have on the estimated distribution. Increasing either one increases the probability of a zero observation, although increasing α also increases the probability of a large observation.

[2] Jackson, A. 1994. Southwest Fisheries Science Center, Natl. Mar. Fish. Serv., P.O. Box 271, La Jolla, CA 92038. Personal commun.

Estimating mean discard per set

Because the model we fitted for discard from log fishing reduced to a simple NB distribution (with $\hat{p}=0$), the estimates of mean discard per log set in each fishing area are just the corresponding mean parameters μ_j. Mean discard per school or dolphin set was estimated with Equation 4.

Estimates of mean discard per log set were an order of magnitude larger than those for school sets and two orders of magnitude higher than those for dolphin sets (Fig. 4). Most of this difference is due to the wide range in the estimated proportion of sets with zero discard. By comparison (Table 2), estimated mean parameters for the NB component of the model differ by less than a factor of five. Thus, the model that we fitted indicates that, on average, there is a considerable difference among set types in per-set discard, although for sets in which discard actually occurs, there is comparatively less difference in the amount.

Mean discard for log sets was estimated at 10.5 t per set pooled over areas, ranging from 7.1 t per set in area 1 to more than double that value (15.4 t per set) in area 3 (Fig. 4). Mean discard for school sets was estimated at 1.16 t per set pooled over areas, ranging from 1.57 t in area 1 to 0.97 t in area 3. Mean discard per set for dolphin sets was estimated at 0.06 t per set fisherywide. Implications of these results for the fishery are discussed in another study (Edwards and Perkins, in prep.).

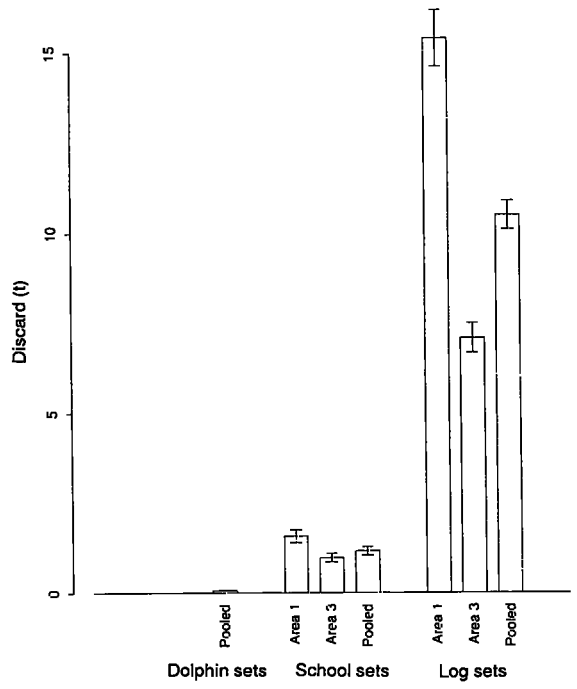

Figure 4

Estimated mean tuna discard per set for the U.S. tuna purse-seine fleet fishing in the eastern tropical Pacific Ocean, 1989–92. Geographic areas are defined in Federal Register (1989) (Fig. 1). Pooled estimates are fisherywide, across all areas. Standard errors are indicated by error bars.

The coefficients of variation (CV's) for the estimates of mean discard per school and dolphin sets (21% and 33%, respectively) are much smaller than those for the individual parameter estimates of a and μ (Fig. 3). As noted in Methods, this is because estimating mean discard per set (i.e. $(1-p)\mu$) is a more robust procedure than estimating the individual parameters. In the case of log sets, the CV's for the estimates of E[Y] and μ differ (Fig. 3), even though in this case the model reduced to a NB distribution where E[Y] = μ. The CV's differ because in estimating variances for the individual parameter estimates we used analytic approximations, while in estimating variances for mean discard, we used bootstrap methods (see Methods).

Where possible (i.e. log and dolphin sets), we estimated variances using the analytic expression in Equation 10 (see Discussion) and found that the results agreed with bootstrap estimates to within about 5%.

Note that the fisherywide estimates for log and school sets are not simply the average of the estimates in each fishing area. This is because the number of sets in each area for which discard was recorded was not proportional to the actual number of sets made in that area. This imbalance was an important reason for including geographic area in the analysis. Nonproportional sampling was not a factor for dolphin sets, because the estimated discard in that case was the same for all fishing areas.

Discussion

Estimating model parameters

Our approach differs somewhat from that of Mangel and Smith (1990), who used the NBAZ to estimate the total biomass of a fish stock. In their analysis, observations of catch from within a stock's geographic range were modelled with the NB component, while the probability mass at zero accounted for observations from outside the range. The sole parameter of interest was the mean μ of the NB component, and fixed values were assumed for the mixing and shape parameters p and a. They reduced the count data to "presence-absence" and derived a likelihood for μ in terms of that reduction. In contrast, we were inter-

ested in estimating the mean of all observations (including "true zeros") and in modelling per-set discard, which requires estimates of p and a. Therefore, we did not follow their approach because we did not have any a priori values for p and a. Reducing counts to simple presence-absence would have decreased the information in the sample such that estimation of the full set of parameters would not have been possible.

Estimating variances for model parameter estimates

The analytic approximation formulae that we used to estimate the variance of the individual parameter estimates are based on the asymptotic normality of MLE's. Since this method uses the estimates for p, a, and μ (rather than their unknown "true" values) in the information matrix, it suffers from the tendency for ML estimates of variance to be biased downwards (e.g. Efron, 1992). We did not attempt to "bias correct" these variance estimates.

When a variance estimate is based on a normal approximation to the sampling distribution of the parameter, the accuracy of the approximation should always be investigated. One way to help validate the normality assumption is to use results from bootstrapping to approximate the sampling distribution. Figure 5 illustrates some examples for the current data. Histograms of the bootstrap replicate parameter estimates for dolphin set data were very skewed. By implication, the normal-approximation variance estimates for the dolphin data, while convenient, are probably not satisfactory. For school set data, histograms of the replicates were slightly skewed because of a small number of unusually large observations. Bootstrap standard errors were consistently higher than the analytic approximations, indicating that the latter may be optimistic. For log set data, histograms were close to normality, and bootstrap standard errors were very similar to those from the analytic approximations. The analytic estimates in this case are probably appropriate.

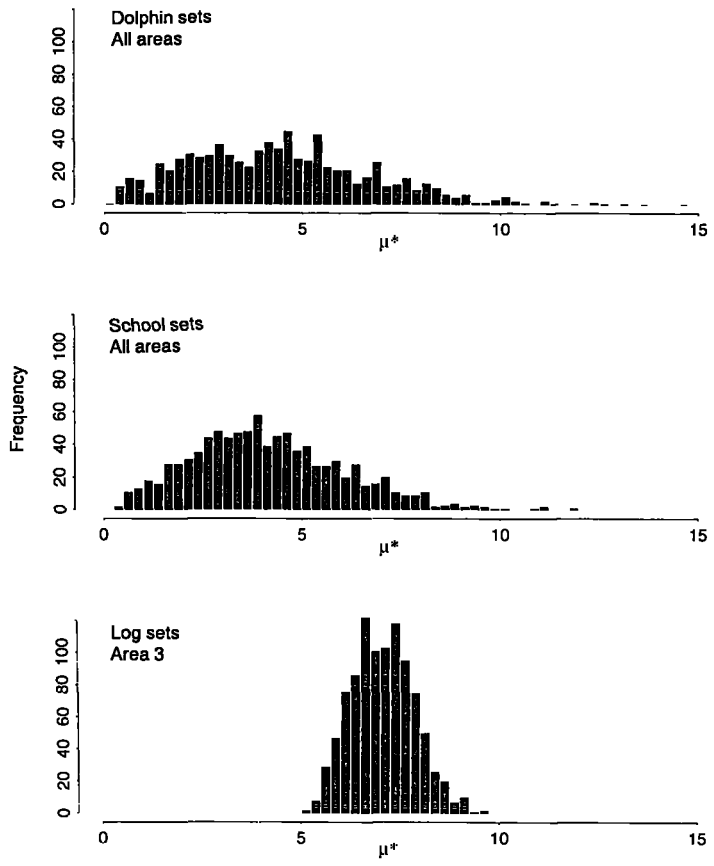

Figure 5

Sample histograms of 1,000 bootstrap replicates of estimates of the negative binomial mean parameter μ, for dolphin, school, and log sets. See text for a complete description of the parameter.

Estimating variances for mean discard per set estimates

In an attempt to derive analytic formulae for the variance of our estimates of E[Y], we manipulated the likelihood equations for the NBAZ and found simplified forms for the MLE of E[Y]. In some cases, the simplified form reduces to the sample mean, Equation 6, and the variance of that estimator is simply (suppressing area and set type subscripts for simplicity)

$$\begin{aligned}\operatorname{var}\left(\hat{\mathrm{E}}[Y]\right) &= (1/n)\operatorname{var}[Y] \\ &= (1/n)(1-p)\left(\mu+(a+p)\mu^2\right),\end{aligned} \tag{9}$$

which can be estimated by substituting MLE's for a, μ, and p. More simply, by using the fact that the estimator is just the sample mean, the minimum variance unbiased estimate of Equation 9 is the sample variance,

$$\widehat{\operatorname{var}}\left(\hat{\mathrm{E}}[Y]\right) = \left[\sum_i (y_i - \bar{y})^2\right] / (n-1), \tag{10}$$

where $\bar{y}$ is the sample mean. In other cases, the simplified forms for the MLE of E[Y] are slightly more complex (Eqs. 7 and 8), and Equations 9 and 10 no longer apply. We did derive expressions, analogous to Equation 9, for the variance of Equations 7 and 8 in terms of the three model parameters p, α, and μ. However, these formulae are so complex as to be of no practical use in estimation, and no expression analogous to Equation 10 seems possible.

Rounding errors in the observations

The NBAZ model used in this study comprises two components. As noted in the description of the model, zero values derived from the NB component can be interpreted as observations of small amounts of discard, rounded down to zero, whereas zero values from the probability mass component can be interpreted as exact zeros. This interpretation is based on the assumption of an underlying continuous distribution for positive discard amounts (e.g. a gamma distribution) upon which rounding errors have been superimposed.

One consequence of this interpretation is that the mean amount of discard that should be associated with "true zeros" is zero, and the mean amount that should be associated with "NB zeros" is nonzero. Thus, strict adherence to this interpretation of zeros leads to the conclusion that Equation 4 may be an underestimate of E[Y]. However, if we assume a strictly decreasing underlying distribution for positive discard, symmetric rounding of amounts larger than one-half ton would tend to increase the estimate. In the absence of a specific model for the rounding errors, we did not attempt to correct for any bias due to rounding.

The EM algorithm for maximizing likelihood

We used a quasi-Newton algorithm to maximize likelihood for the parameters p, α, and μ. A useful alternative for mixture models, including "added zero" distributions, uses the EM algorithm to maximize likelihood (e.g, McLachlan and Basford, 1988; Lambert, 1992). In situations with many covariates, it provides a well-behaved alternative to the high-dimensional gradient search required by general optimization algorithms. The algorithm can be implemented by using standard regression techniques for generalized linear models. We applied the EM algorithm to the NBAZ using a combination of logistic regression to maximize likelihood for p and quasi-likelihood NB regression for μ and α (Lawless, 1987). However, the logistic regression failed to converge for the current data because the ML estimate of p for log sets was zero.

Alternative models considered

We considered but rejected two alternatives to the NBAZ model: 1) the Δ-distribution (a mixture of a probability mass at zero with a lognormal [Aitchison, 1955; Pennington, 1983]); and 2) a Γ-distribution mixed with a probability mass at zero (Coe and Stern, 1982). Both have been used in similar cases where the data to be analyzed have contained large numbers of zeros. The Δ-distribution assumes that the natural logs of the positive observations are distributed normally, or can be so transformed, and this assumption was not plausible. The data in this analysis were rounded to the nearest ton and the mode of the positive observations was one ton. Thus, no transformation could bring these data to even approximate normality. The gamma mixture model was not appropriate for the current data because maximum likelihood estimation for a highly skewed gamma distribution depends heavily upon small (near zero) observations. In this study, all observations in that region were rounded to either zero or one, implying a large relative measurement error and therefore potentially poor accuracy. Another more fundamental reason why we rejected these two models was that both models mix a continuous distribution on the positive numbers with a probability mass at zero and assume that observations from each component remain distinguishable. In the current data set, small positive observations are grouped together with zero observations, and using an NB in the mixture allows the model to distinguish between "true zeros" (actual absence of discard) and "rounded zeros" (discard so small that it was ignored or missed).

Conclusions

The methods developed here were used to model fisheries discard data which were rounded to integer values and which included widely varying numbers of zero observations, depending on one or more covariates. The usual models for integer-valued data (e.g. the Poisson distribution) did not fit the data at all well because of the extreme skewness of some of the observed distributions. The NBAZ is more flexible than the standard models and provided a much better fit. In general, the model is applicable to any set of integer-valued data which exhibit a large proportion of zero observations combined with long positive tails. Both categorical and continuous covariates may be used.

Modelling these data with a parametric probability distribution allowed us to describe patterns in the discard in some detail, for example, in estimating the percentage of "true zeros" in the data. Addi-

tionally, we were able to examine whether differences in mean discard were due to different proportions of zero observations or to different distributions of positive observations. In contrast, computing sampling-based estimates of population mean and variance would not give any indication of the patterns in the individual observations. While average or total discard is of significant interest, it is also important to quantify the amount of discard possible for an individual set. Assuming that the parametric model is accepted as appropriate, one can estimate, for example, the probability that, owing to random chance alone, discard from a particular boat will exceed a certain limit in a fixed number of sets. One can also estimate the percentage of zero observations which actually represent small amounts of discard. Finally, a parametric model provides a natural framework for predicting future discard.

Acknowledgments

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Demographic analysis of the sandbar shark, *Carcharhinus plumbeus*, in the western North Atlantic*

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Abstract.—The sandbar shark, *Carcharhinus plumbeus*, is the most common large coastal shark in Virginia waters and is an important component of recreational and commercial fisheries along the east coast of the United States. Sandbar shark demographic analyses, using known and estimated life history parameters, including fishing mortality (F) at ages and levels estimated in a recent stock assessment, were used to estimate potential population growth and exploitation. Life history tables were constructed by using best estimates of natural mortality (M) of 0.11 or 0.07 for maximum ages of 30 or 60 yr, respectively. Natality was fixed at 2.1 female pups/yr. Fishing mortality (F=0.05, 0.10, 0.15, 0.20, or 0.25) was simulated to begin at age 8, 10, 15, 20, or 29. The annual population growth rate was highest under a "best-case" scenario of M=0.05 (½ best estimate) and maximum age of 30 yr, but was only 11.9%/yr. At M=0.11 for all ages, the population increase rate was 6.4%/yr, and the generation time was about 20 years. At higher juvenile mortality rates, the population growth rate decreased to 2.6%/yr. Adding fishing mortality at immature ages caused the population to decline unless F levels were <0.10 and 0.05 at maximum age = 30 and 60, respectively. It is apparent that sandbar shark populations will decline under any substantial fishing mortality on immature ages and that mature fish can be exploited only at very low levels.

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Fishery Bulletin 94:341–347 (1996).

The sandbar shark, *Carcharhinus plumbeus*, ranges from Cape Cod to Brazil in the western North Atlantic (Bigelow and Schroeder, 1948; Springer, 1960; Garrick, 1982) and is the most common large coastal shark in Virginia waters (Musick et al., 1993). It comprises 20% of the large-shark fauna of the U.S. east coast and is an important component of recreational and commercial fisheries (Hoff, 1990; Musick et al., 1993; Anonymous[1]). Age and growth (Casey et al., 1985; Casey and Natanson, 1992; Sminkey and Musick, 1995), seasonal distribution (Bigelow and Schroeder, 1948; Springer, 1960; Musick et al., 1993), and reproductive biology (Colvocoresses and Musick[2]) of the sandbar shark have been studied, but population studies have been limited to a time series of relative abundance in Virginia waters (Musick et al., 1993) and to a demographic analysis based on previously published life history parameters (Hoff, 1990).

The recent increase in fishing pressure on sandbar sharks and subsequent decline in abundance (Musick et al., 1993), revised age and growth studies (Casey and Natanson, 1992; Sminkey and Musick, 1995), and a reexamination of fecundity data presented in Colvocoresses and Musick[2] have provided updated parameters necessary for a demographic analysis of the sandbar shark. This analysis uses estimates of longevity, age-specific survival, and age-specific natality to construct a life history table which generates estimates of the net reproductive rate per generation, the generation time, and the intrinsic rate of increase of the population (Krebs, 1985). These parameters are useful for management purposes and for input into population models (Krebs, 1985; Hoenig and Gruber, 1990). The objective of this study is to provide an updated demographic analysis of the sandbar shark by estimating population parameters under varying conditions of natural mortality and fishing mortality (i.e. mortality caused by fishing).

* Contribution 1983 of the Virginia Institute of Marine Science, School of Marine Science, College of William and Mary, Gloucester Point, VA 23062.

[1] Anonymous. 1992. Fishery management plan for sharks of the Atlantic Ocean. U.S. Dep. Commer., NMFS, NOAA, 10 December 1992.

[2] Colvocoresses, J. A., and J. A. Musick. 1989. Reproductive biology of the sandbar shark, *Carcharhinus plumbeus*, in the Chesapeake Bight. Abstract, 69th annual meeting, Am. Soc. Ichthyology and Herp.; 17–23 June 1989, San Francisco, CA.

Materials and methods

Based on size at maturity (Springer, 1960; Sminkey, 1994) and von Bertalanffy growth equations for sandbar sharks determined by Sminkey and Musick (1995), age at 100% maturity was determined to be 15 years. Casey and Natanson (1992) determined age at maturity to be ca. 29 years on the basis of a von Bertalanffy growth equation derived from tag and recapture information and a similar size at maturity. For this demographic analysis, 15 and 29 years therefore were used in separate trials as conservative estimates of the age at which 100% of females were mature.

The age-specific natality was determined from a reexamination of the data from 50 pregnant sandbar sharks collected from 1974 to 1986 (Colvocoresses and Musick[2]) and from 3 additional females collected during 1990–92. Results similar to those reported by Colvocoresses and Musick[2] were obtained. The relationship between maternal size and number of pups was very weak (Fig. 1; r^2=0.25), with the average number of pups per litter equal to 8.4 (n=53, SD=2.3). Sandbar sharks produce a litter once every 2 years (Branstetter[3]; Musick, unpubl. data) with a sex ratio not significantly different from 1:1. Thus, age-specific natality was fixed at 2.1 female pups per year beginning with age of maturity.

[3] Branstetter. S. 1994. Gulf and South Atlantic Fisheries Development Foundation, Tampa, FL 33609. Personal commun.

The probable maximum age for sandbar sharks differs between the von Bertalanffy growth equation derived from vertebral data (Sminkey and Musick, 1995) and the growth equation from tag and recapture data (Casey and Natanson, 1992). The latter study reported tagged sandbars estimated to be 22 (155 cm fork length, FL), 32 (157 cm FL), and over 40 years old (185 cm FL) at recapture; the 22-year-old was determined to be immature. The first 2 of these ages were estimated on the basis of length at release, a vertebrally derived growth equation (sexes combined) of Casey and Natanson (1992), and on time at liberty. Regarding the 40+ year old shark, Casey and Natanson (1992) stated "since length at first maturity is 150 cm FL, it is reasonable to assume that this individual was over 30 yr old at tagging and over 40 yr at recapture." Casey and Natanson (1992) then suggested that sandbar sharks may live in excess of 50 years. Sminkey and Musick (1995) reported that the oldest individual examined (175 cm FL) was 24 years old (determined by vertebral counts). On the basis of vertebral data of Sminkey and Musick (1995), it seems reasonable to consider the maximum age for sandbar sharks to be about 30 years. For the life history tables, 30 and 60 years were considered as maximum ages in separate trials.

To examine the effects of fishing mortality (F) on the demography of the sandbar shark, the survivorship function was modified in several trials to include fishing mortality. Values of F included 0.25,

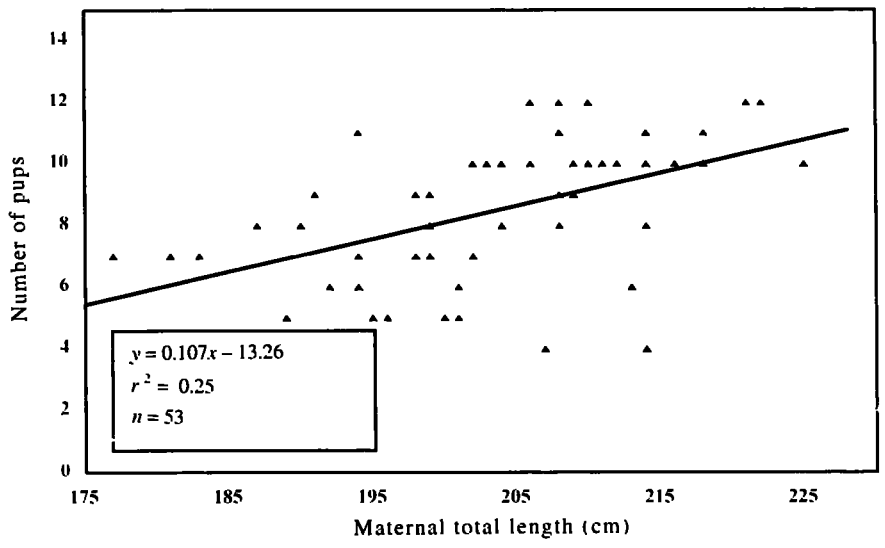

Figure 1

Maternal size (total length) of sandbar shark, *Carcharhinus plumbeus*, versus number of pups produced per litter.

0.20, 0.15, 0.10, and 0.05. F = 0.25 was the approximate level of mortality on large coastal sharks in the fishery from 1986 to 1991 and is the recommended F for maximum sustainable yield (Anonymous[1]). The mean carcass size of all large coastal sharks in the 1986–91 fishery was approximately 24 lb (Anonymous[1]), but the mean carcass size landed for sandbar sharks only was approximately 40 lb (Branstetter[3]). Based on two sandbar shark growth models, 24 and 40 lb correspond to ages 8 and 12 years, respectively (Sminkey and Musick, 1995; Musick, unpubl. data) or 15 and 24 years, respectively (Casey and Natanson, 1992). Considering that a mean is a measure of central tendency, then nearly 50% of the catch was younger than these ages. Therefore, fishing mortality was simulated to begin at 8, 10, 15, 20, and 29 years, which are conservative estimates based on mean carcass sizes.

Annual survival including natural mortality was estimated to be only 0.90 (max. age=30) and 0.93 (max. age=60) following the method of Hoenig (1983), which related maximum age attained to instantaneous total mortality rate (Z). If the maximum age attained was estimated from unexploited or lightly exploited stocks, Z approximates the instantaneous natural mortality rate (M). However, it has been suggested that survival of young-of-year sandbar sharks may be lower (Hoff, 1990). Increased mortality on neonate and age-1 sharks would primarily result from predation by larger sharks (Springer, 1960; Branstetter, 1990). Therefore, natural mortality during the first two years of life was varied in the life history tables. But, the population of large predatory sharks in coastal Virginia waters has been severely depleted (Musick et al., 1993), potentially reducing the mortality rate on juvenile sandbar sharks. Following Hoff (1990), a best-case life history table was constructed with survival equal to 0.95 (one-half of estimated mortality rate).

The net reproductive rate (R_0), the generation time (G), and the intrinsic rate of increase of the population (r) were calculated (Krebs, 1985) for each trial.

The effects of exploitation can be assessed from the value and sign of the intrinsic rate of increase. Based upon the outcome, an appropriate minimum size (age) and fishing mortality level (F) for sandbar sharks may be recommended to maintain a viable, reproducing population.

Results

Using the growth model for sandbar sharks calculated by Sminkey and Musick (1995) and the best estimate of annual survival rate (0.90) with no increased juvenile mortality, the population will increase at 6.4% per year (Table 1). If natural mortality were lower ("best-case" scenario, survival=0.95), the population could increase at a rate of nearly 12%/yr (Table 2). If there was increased mortality of neonates and age-1 sharks, the population increase rate would range from 2.1%/yr to 7.2%/yr (Table 2). These rates all suggest healthy and increasing populations without fishing. Population replacement (r=0.0) was attained with annual survival rates of 0.70 for neonates and 0.85 for age 0+ fish, and 0.50, 0.70, and 0.88 for ages 0, 1, and 1+, respectively (Table 2). Any greater mortality would lead to population declines.

If age at maturity and maximum age are set at 29 and 60 years, respectively, and annual survival is 0.93, the population increase rate will be 3.5%/yr (Table 2). If natural mortality is 0.1 for all ages (annual survival=0.9), the population will decrease at 0.1%/yr (Table 2). With decreased juvenile survival (0.70 for age 0, and 0.50 and 0.70 for ages 0 and 1), the population increase rates are only 2.7% and 1.1%/yr, respectively (Table 2). With similar juvenile mortality rates, population equilibrium is obtained when postjuvenile survival is 0.91 and 0.92 (Table 2).

When fishing mortality is added at the recommended level for maximum sustainable yield [MSY] (F=0.25; Anonymous[1]), age of maturity is fixed at 15 years, and age at first capture is set at 8 years, the population would decrease by >7%/yr (Table 3). Assuming these ages of first maturity and first capture, we conclude that fishing mortality would have to be reduced to F=0.10 to maintain a growing population (Table 3). If a minimum-size limit equivalent to a 15-year-old sandbar shark (135 cm precaudal length, 148 cm fork length, or 178 cm total length) were imposed, fishing mortality could remain at F=0.25 and still support an increasing population (Table 3). However, population doubling time (= ln(2)/r) would be about 33 years.

Under an age of maturity of 29 years and a maximum age of 60 years, the population increases at all levels of F up to 0.25, if fishing does not begin until age 29. Population doubling time, however, would increase dramatically as F increased, ranging from 27.7 years if F=0.05 to 693 years if F=0.25. If fishing begins before age 29, the population could increase only at very low fishing mortality rates (Table 3). The generation time (G) is the period between the birth of the parents and the birth of the offspring. When offspring are produced over a period of time, G is the mean period between the parent's birth and the birth of each offspring. As fishing mortality increases, survival of parents decreases, leading to fewer offspring later in life, therefore G decreases. This result does not suggest more rapid population replacement.

Table 1

Life history table for sandbar shark, *Carcharhinus plumbeus*, using best estimate of natural mortality only, no increased juvenile natural mortality, age at maturity = 15, and maximum age = 30. Column symbols are as follows: X = age in years; l_x = survivorship (annual survival = 90%); m_x = natality (no. of female pups/yr); $X \times l_x \times m_x$ = age-specific reproductive rate; R_0, net = reproductive rate per generation; G = generation time (yr); r = intrinsic rate of population increase; and % = population increase rate (%/yr).

X	l_x	m_x	$l_x \times m_x$	$X \times l_x \times m_x$	R_0	G	r	%
0	1.00				3.54	20.37	0.062	6.4
1	0.90							
2	0.81							
3	0.73							
4	0.66							
5	0.59							
6	0.53							
7	0.48							
8	0.43							
9	0.39							
10	0.35							
11	0.31							
12	0.28							
13	0.25							
14	0.23							
15	0.21	2.1	0.43	6.51				
16	0.19	2.1	0.39	6.25				
17	0.17	2.1	0.35	5.98				
18	0.15	2.1	0.32	5.70				
19	0.14	2.1	0.28	5.41				
20	0.12	2.1	0.26	5.13				
21	0.11	2.1	0.23	4.85				
22	0.10	2.1	0.21	4.57				
23	0.09	2.1	0.19	4.30				
24	0.08	2.1	0.17	4.04				
25	0.07	2.1	0.15	3.79				
26	0.07	2.1	0.14	3.55				
27	0.06	2.1	0.12	3.32				
28	0.05	2.1	0.11	3.10				
29	0.05	2.1	0.10	2.89				
30	0.04	2.1	0.09	2.69				

Discussion

Demographic analysis using life history tables is a useful tool for fishery managers to evaluate potential population changes under various conditions of fishing mortality (Hoenig and Gruber, 1990). In this study, the demographic analyses indicate that if fishing mortality continues to target small sandbar sharks, beginning with 8-year-old sharks, at the level of fishing estimated for 1986–91 (F=0.25; Anonymous[1]), the population will decrease by >7% per year. The population of sandbar sharks along the mid-Atlantic coast declined to about 15% of its previous level over a 13-year span (Musick et al., 1993; Musick et al.[4]), suggesting that this demographic study may be an accurate estimate of potential population changes as a result of excessive fishing mortality. The potential population increase rates reflect an evolutionary strategy not well adapted to sudden and severe population depletions, particularly if applied to many age classes simultaneously or persisting over several years.

Natural mortality is difficult to estimate directly for any fish population; therefore we chose to use the longevity relationship of Hoenig (1983) to estimate this parameter. Additionally, following the example of Hoff (1990), we reduced the natural mortality by half to examine the "best-case" population under the conditions of the vertebrally derived growth model. This simulation may indicate the maximum poten-

[4] Musick, J. A., S. Branstetter, and T. R. Sminkey. 1994. Trends in shark abundance from 1974 to 1993 for the Chesapeake Bight region of the U.S. mid-Atlantic coast. Contrib. SB-19, Shark evaluation workshop, 14–18 March 1994, Southeast Fisheries Science Center, Natl. Mar. Fish. Serv., Miami, FL 33149, 16 p.

Table 2

Life history parameters for sandbar shark, *Carcharhinus plumbeus*, under two growth models (Sminkey and Musick [1995]: age at maturity = 15, max. age = 30; and Casey and Natanson [1992]: age at maturity = 29, max. age = 60) with varying natural mortality only. Natality is 2.1 female pups/yr. R_0 = net reproductive rate per generation; G = generation time (yr); and r = intrinsic rate of population increase. Negative values are in bold.

Annual survival (%/yr)						
Age 0	Age 1	Age 2+	R_0	G	r	Population increase rate
Age at maturity = 15						
0.70	0.90	0.90	2.76	20.37	0.050	5.1
0.50	0.70	0.90	1.53	20.37	0.021	2.1
0.70	0.85	0.85	1.00	19.44	0.000	0.0
0.50	0.70	0.88	1.00	19.95	0.000	0.0
0.95	0.95	0.95	11.20	21.45	0.113	11.9
0.50	0.70	0.95	5.01	23.16	0.070	7.2
Age at maturity = 29						
0.93	0.93	0.93	3.79	39.05	0.034	3.5
0.90	0.90	0.90	0.97	36.88	**–0.001**	**–0.1**
0.70	0.93	0.93	2.84	39.05	0.027	2.7
0.50	0.70	0.93	1.52	39.05	0.011	1.1
0.50	0.70	0.92	1.00	38.28	0.000	0.0
0.75	0.91	0.91	1.00	37.20	0.000	0.0

Table 3

Life history parameters for sandbar shark, *Carcharhinus plumbeus*, under varying rates of fishing mortality and two growth models (Sminkey and Musick [1995]: age at maturity = 15, max. age = 30; and Casey and Natanson [1992]: age at maturity = 29, max. age = 60). Natality is 2.1 female pups/yr in both models. Age_i = age at which F starts; R_0 = net reproductive rate per generation; G = generation time (yr); r = intrinsic rate of population increase. Negative values are in bold.

Instantaneous fishing mortality					
Age_i	F	R_0	G	r	Population increase rate (%/yr)
Age at maturity = 15					
Annual survival = 0.90					
8	0.25	0.25	17.29	**–0.080**	**–7.7**
8	0.20	0.40	17.68	**–0.051**	**–5.0**
8	0.15	0.66	18.17	**–0.023**	**–2.2**
8	0.10	1.12	18.77	0.006	0.6
8	0.05	1.95	19.50	0.034	3.5
10	0.25	0.42	17.29	**–0.051**	**–5.0**
10	0.20	0.60	17.68	**–0.029**	**–2.8**
10	0.15	0.90	18.17	**–0.006**	**–0.6**
10	0.10	1.37	18.77	0.017	1.7
10	0.05	2.16	19.50	0.039	4.0
15	0.25	1.45	17.29	0.021	2.2
15	0.20	1.64	17.68	0.028	2.8
15	0.15	1.90	18.17	0.035	3.6
15	0.10	2.26	18.77	0.043	4.4
15	0.05	2.77	19.50	0.052	5.4
Age of maturity = 29					
Annual survival = 0.93					
15	0.25	0.03	31.66	**–0.109**	**–10.4**
15	0.20	0.07	32.23	**–0.081**	**–7.8**
15	0.15	0.18	33.06	**–0.052**	**–5.1**
15	0.10	0.45	34.29	**–0.023**	**–2.3**
15	0.05	1.23	36.19	0.006	0.6
20	0.25	0.11	31.66	**–0.070**	**–6.8**
20	0.20	0.20	32.23	**–0.050**	**–4.9**
20	0.15	0.37	33.06	**–0.030**	**–2.9**
20	0.10	0.74	34.29	**–0.009**	**–0.9**
20	0.05	1.58	36.19	0.013	1.3
29	0.25	1.04	31.66	0.001	0.1
29	0.20	1.20	32.23	0.006	0.6
29	0.15	1.44	33.06	0.011	1.1
29	0.10	1.82	34.29	0.017	1.8
29	0.05	2.47	36.19	0.025	2.5

tial for population growth in the absence of fishing mortality. The annual population increase rate of nearly 12% is modest when compared with teleost reproductive potential (Hoff, 1990) and probably is not actually attainable in sandbar shark populations.

The Casey and Natanson (1992) growth model assumes the maximum age attained is 60 years, resulting in an estimate of M = 0.07. However, if natural mortality was 0.10, the life history table predicts a population decrease rate of 0.1% in the absence of any increased neonate mortality or fishing mortality (Table 2). This indicates a nonviable population under natural mortality levels, particularly if neonate and juvenile mortality were higher. Therefore, if sandbar sharks are assumed to grow according to this model, it seems reasonable to accept the lower estimate of natural mortality.

There is great uncertainty regarding age-specific natural mortality during the first two years of life when juvenile sandbar sharks are vulnerable to predation by large coastal sharks. The trials with increased mortality during these years demonstrate the sensitivity to natural mortality estimates in the life history table. If age at maturity is 15 years and mortality is >0.10, the population increase rate is considerably reduced (2.1%–5.1%/yr), suggesting that the population may be near equilibrium (r=0.0) under these conditions (Table 2). However, Musick et al. (1993) and Musick et al.[4] suggest that the apparent stable abundance of juvenile sandbar sharks in

the Chesapeake Bay is the result of a marked decrease in the large coastal shark population. In this case juvenile survival is probably less dependent upon predation and may be age-independent (M=0.10 for all ages). Assuming this natural mortality level, the population increases at 6.4%/yr (Table 1).

The life history parameters generated by the two growth models with the best estimates for natural mortality, suggest similar population increase potential but on two different time scales. The intrinsic rates of population increase are 0.062 and 0.034 for the growth models of Sminkey and Musick (1995) and Casey and Natanson (1992), but the generation times are 20.37 and 39.05 years, respectively, and population doubling times are 11.2 and 20.4 years, respectively. The life history tables with the vertebral growth model agree well with the results of Hoff (1990), although he used an age-fecundity relationship.

The effects of fishing mortality on the intrinsic rate of increase with both growth models demonstrate the detrimental effect of exploitation on immature fish (Table 3). At fishing mortality levels >0.10, the population will decline. The ages used for these estimates (8 and 15) correspond to the mean carcass size in the 1986–91 large coastal shark fishery and are based upon the most recent data available. At the currently estimated fishing mortality level (0.25) these populations are not viable and will eventually collapse. The recent analyses of Musick et al. (1993) and Musick et al.[4] report that the adult coastal stock has already been reduced to only 15% of its abundance in 1980–81. Clearly the sandbar shark, with a slow growth and low net reproductive rate typical of most elasmobranchs, cannot withstand even a low rate of fishing mortality on immature individuals.

Cailliet (1992) used demographic analyses to examine population growth in the leopard shark, *Triakis semifasciata*, including fishing mortality to begin at several ages. The population would replace itself (r=0) if fishing began at age 4 at the estimated rate (F=0.084) and would slowly increase (0.4–6.4%/yr) if fishing did not begin until later ages (5, 10, 15, 21 years). However, it was demonstrated that if fishing mortality doubled (F=0.168), the age at which F starts must be >12 to produce a growing population. Although females first mature at age 17, Cailliet (1992) concluded that a size limit of 110 cm TL (approximately 13 years) would ensure population replacement at this moderately low fishing level.

A demographic analysis of the Pacific angel shark, *Squatina californica*, examined the effects of low fishing mortality rates (F=0.05, 0.10, 0.20, 0.22) simulated to begin at age 10 yr (Cailliet et al., 1992). This age was the estimated age of entry into the fishery as well as the approximate age of first maturity. Cailliet et al. (1992) concluded that the population would grow very slowly (0.4%/yr) at F=0.20, would decrease at higher F, and that a size limit above the size of first maturity should be imposed in the absence of better estimates of natural and fishing mortality.

Demographic analyses of the Atlantic sharpnose shark, *Rhizoprionodon terranovae*, classified as a "small coastal" species in the Fishery Management Plan (FMP) for sharks of the Atlantic Ocean, indicated that, in the absence of fishing mortality, the population would increase by only about 4.5%/yr (Cortés, 1995). This best estimate is considerably below the rate derived for "small coastal" sharks of the Atlantic Ocean (e^r=1.91; 91%/yr) (Parrack[5]). Furthermore, if fishing mortality continues at the estimated rate for 1986–90 (F=0.43) (Anonymous[1]), a size limit of about 97 cm TL (nearly 6 years old) would have to be imposed just to allow population replacement (Cortés, 1995). Cortés (1995) demonstrates that extreme modification of the reproductive and survival parameters was required to attain the population increase rate derived by Parrack[5] and concluded that management of the Atlantic sharpnose under the FMP was based on unrealistic biological parameters.

This demographic analysis of sandbar sharks provides additional life history information on acceptable levels of exploitation. If the current FMP recommendation of F=0.25 for MSY (Anonymous[1]) is implemented in an unrestricted fishery, the sandbar shark population will not recover. This level of fishing would be acceptable for a healthy population if a minimum size limit of 135 cm precaudal length or about 23 kg carcass weight (size at first maturity) were imposed and juvenile survival remained high. But, with the current severe depletion of the sandbar shark population of the western North Atlantic, far more restrictive fishing mortality levels must be implemented to allow the population to rebuild itself. Such a conservative approach would also provide a buffer against natural perturbations during the crucial recovery phase.

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[5] Parrack, M. L. 1990. A preliminary study of shark exploitation during 1986–1989 in the U.S. FCZ. Contrib. MIA-90-493, Southeast Fisheries Science Center, Natl. Mar. Fish. Serv., Miami, FL 33149, 23 p.

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Contribution to the biology of the grooved and triangle Tanner crabs, *Chionoecetes tanneri* and *C. angulatus*, in the eastern Bering Sea

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Abstract.—Populations of the grooved Tanner crab, *Chionoecetes tanneri*, and the triangle Tanner crab, *C. angulatus*, were surveyed along the continental slope of the eastern Bering Sea with a bottom trawl. Over the depth range sampled (100–1,000 m), the relative abundance of the two species was about equal. Mature male and female *C. tanneri* occurred at the same depths, but for *C. angulatus*, males were found at significantly shallower depths than were females. Carapace widths at 50% maturity for males and females were 118.7 mm and 79.2 mm for *C. tanneri* and 91.4 mm and 57.8 mm for *C. angulatus*. Fecundity of *C. tanneri* did not increase with carapace width (CW, mm) and averaged 86,500 eggs over the sizes sampled. Fecundity of *C. angulatus* increased with carapace width according to the following formula: eggs = $-65{,}600 + 1660 \times CW$. Mean egg diameter was 0.75 mm for *C. tanneri* and 0.74 mm for *C. angulatus*. The relationship between body weight (gm) and carapace width did not differ between species: weight = $1.219/10^4 \times CW^{3.183}$.

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The continental slope of the North Pacific Ocean is inhabited by several species of crabs in the genus *Chionoecetes* that are similar in size to their shallower, commercially harvested relatives *C. bairdi* and *C. opilio* but are immediately distinguishable by their brilliant orange or red color and slender legs. In the eastern North Pacific Ocean there are two species: the grooved Tanner crab, *C. tanneri*, ranging from northern Mexico to Kamchatka, and the triangle Tanner crab, *C. angulatus*, ranging from Oregon to the Sea of Okhotsk (Hart, 1982). In the western North Pacific there is a single species, *C. japonicus*, which occurs in the Sea of Japan (Sinoda, 1982). Although the potential for commercial fisheries for *C. tanneri* has been recognized for quite some time (Pereyra, 1967), commercially successful fishing ventures have occurred only recently (Jamieson, 1990). In contrast, *C. japonicus* has been commercially fished since the mid-1960's (Sinoda, 1982). The primary impediment to the development of commercial fisheries for *C. tanneri* and *C. angulatus* has been that the large supply of other *Chionoecetes* species on the world market has kept the price too low to offset the high costs of fishing in deep water. Fisheries for other slope-dwelling species, however, have developed when the catches of shallower, related species have declined. For example, in Japan the fishery for *C. japonicus* developed after the local stocks of *C. opilio* declined (Sinoda, 1982). In Alaska, the fishery for the slope-dwelling king crab *Lithodes aequispina* developed after the decline in abundance of the shelf-dwelling king crabs *Paralithodes camtschaticus* and *P. platypus* (Somerton and Otto, 1986). This pattern may be reflected in Alaskan *Chionoecetes* because as *C. bairdi* and *C. opilio* populations in the Bering Sea have declined, landings of *C. tanneri* have increased from a negligible amount in 1992 to 360 metric tons in 1993, and to 414 metric tons in 1994.[1]

Although aspects of the biology of *C. tanneri* have been documented in areas off Oregon (Pereyra, 1966, 1968; Tester and Carey, 1986) and British Columbia (Jamieson et al., 1990), only information on size dis-

[1] 1995. Alaska Department of Fish and Game, 211 Mission Road, Kodiak, AK 99615. Unpubl. data.

tribution (Hughes, 1981; Alton, 1986) has been reported for Alaskan waters. Furthermore, nothing about the biology of *C. angulatus* has ever been reported. We collected information on both species on a 1982 Japan-U.S. cooperative trawl survey of the continental slope of the eastern Bering Sea. Here we summarize these data, focusing on the depth and size distributions, sizes at maturity, weight-size relationships, and various aspects of the reproductive biology of both species.

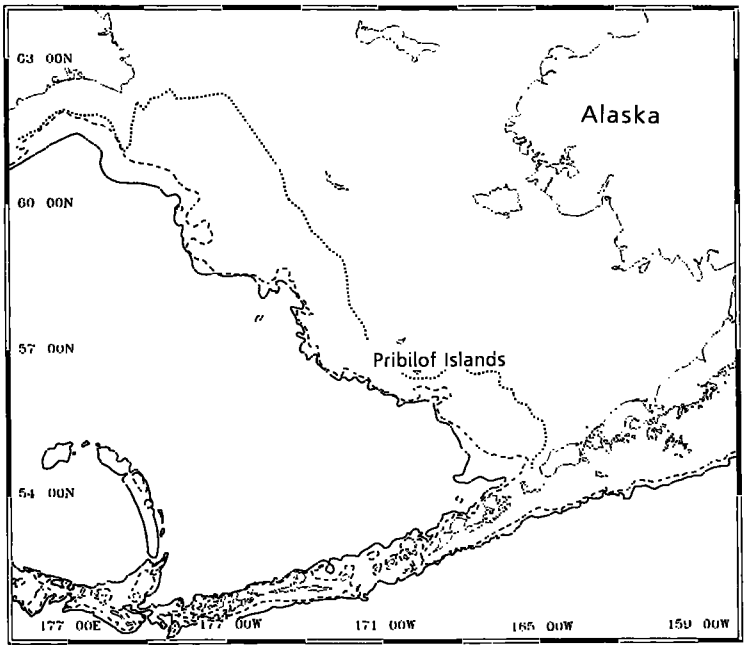

Figure 1

Area surveyed during the Japan-U.S. cooperative survey of the slope of the eastern Bering Sea. The 100-m (dotted line), 200-m (dashed line), and the 1,000-m (solid line) isobaths are shown for the eastern Bering Sea.

Materials and methods

Sampling of *C. tanneri* and *C. angulatus* was conducted from the Japanese stern-trawler, *Ryujin Maru No. 8*, on the continental slope of the eastern Bering Sea between 58.3°N and 60.9°N latitude (Fig. 1). Crabs were captured with a bottom trawl that measured 23 m between the wings, had a codend consisting of three layers of 90-mm mesh, and had a footrope equipped with 55-cm diameter steel bobbins. The study was divided into two parts: from 11 July to 4 August 1982, scientists from the Alaska Fisheries Science Center collected data on all of the biological parameters described below; from 8 August to 25 August, Japanese scientists collected only carapace width data. For both parts, species identification was based on characteristics provided in Garth (1958).

Maximum carapace width of all crabs was measured with vernier calipers to the nearest 1.0 mm, excluding lateral spines. In the first part of the study, both sexes were evaluated for shell condition and females were additionally evaluated for reproductive condition. Shell condition was rated on a 4-point scale, based on hardness, color, and wear of the exoskeleton (see Somerton, 1982), which represents the approximate time interval since the last molt. Briefly, the characteristics of each shell-condition category and its assumed postmolt interval (PMI) are as follows:

1 carapace pliable (PMI <2 wk);
2 carapace hard, little wear on tips of dactyli, few scratches (2 wk <PMI <1 yr);
3 carapace hard, conspicuous wear on tips of dactyli, abundant scratches (1 yr <PMI <2 yr);
4 same as condition 3, except that wear on dactyli is more pronounced (PMI >2 yr).

Reproductive condition was rated on a 5-point scale. Characteristics of each reproductive condition category are as follows:

1 immature—narrow flattened abdomen;
2 nonovigerous—no embryos or empty egg cases attached to the pleopod setae;
3 uneyed embryos—embryos without conspicuous dark eyes;
4 eyed embryos—embryos with clearly visible dark eyes;
5 empty egg cases—empty egg cases and funiculi attached to the pleopod setae.

Whenever possible, one or more of the following types of data were also collected:

- height of the right chela of males (excluding males with partially regenerated right-hand chela) measured to the nearest 0.1 mm according to the definition in Jamieson et al. (1990);
- total wet body weight of intact males measured to the nearest gram on a triple-beam balance;
- uneyed egg masses from ovigerous females (stored in formalin diluted to 10% with seawater).

Egg masses were processed as follows: mean egg diameter was estimated by randomly selecting 10 eggs from each of 10 randomly selected egg masses and measuring the diameters to the nearest 0.1 mm with an ocular micrometer. Fecundity was estimated

by first air drying the egg masses and, after separating the eggs from the pleopods and setae, weighing them to the nearest 0.1 mg. Two subsamples of about 200 eggs from each dried egg mass were randomly selected, weighed, and counted. Fecundity was then estimated by dividing the total weight of an egg mass by the average of the two estimates of individual egg weight.

Male functional maturity (Conan and Comeau, 1986) was determined from chela allometry. The procedure used is based on the observation that, for *Chionoecetes,* when chela measurements are plotted against carapace measurements on log-log axes, the data conform to two, nearly parallel, straight lines, one representing immature individuals and the other representing individuals that have undergone a puberty molt and have acquired the secondary sexual characteristic of enlarged chelae (Hartnoll, 1978; Somerton, 1980; Conan and Comeau, 1986). We determined with which line an individual observation was associated by using the computer algorithm described in Somerton (1980) to reassign observations iteratively to the two lines until the residual sum of squares was minimized. The carapace width at 50% maturity (W_{50}) for both males and females was estimated by fitting a logistic regression model to the maturity and carapace width data by using generalized linear modeling (Chambers and Hastie, 1992). W_{50} and the variance of W_{50} were then estimated from the parameters of the fitted model with formulas provided in Somerton (1980). In addition to W_{50}, we also calculated the mean carapace width of mature individuals (W_m) as an alternative measure of the size at maturity for comparative purposes.

Weight and carapace width relationships for males of each species were estimated by nonlinear regression (Chambers and Hastie, 1992) to fit a power function to weight and carapace width data. A between-species difference in these relationships was tested by making the relationships linear with a log transformation of the data, and by using analysis of covariance to test whether species-specific relationships fit the data significantly better than a single, combined relationship.

Results and discussion

The 205 trawl hauls that were successfully completed were distributed evenly over the latitudinal range of the survey area (Fig. 2), but fewer hauls were made at greater depths. Over the survey area, both species displayed patchy distributions; much of the catch came from relatively few sampling sites (Fig. 2). *Chionoecetes tanneri* occurred at 47 sites and had a mean CPUE (catch in numbers per kilometer of towed distance) at these sites of 1.9; *Chionoecetes angulatus* occurred at 50 sites and had a mean CPUE of 2.6. The difference in CPUE was not significant (t-test, P=0.418).

Size distribution

Chionoecetes tanneri males ranged 42–170 mm in carapace width (CW); females ranged 38–126 mm CW (Fig. 3). The maximum size of females was similar to maximum sizes reported off Oregon (126 mm, Pereyra, 1966; 122 mm, Tester and Carey, 1986), whereas the maximum size of males fell between the maximum sizes reported for Oregon (181 mm, Pereyra, 1966; 162 mm, Tester and Carey, 1986). *Chionoecetes angulatus* males ranged 25–160 mm CW; females ranged 35–104 mm CW. The maximum sizes of both sexes were slightly larger than the reported maximum sizes of *C. japonicus* in the Sea of Japan (males 150 mm, females 90 mm, Watanabe and Suzuuchi, 1983).

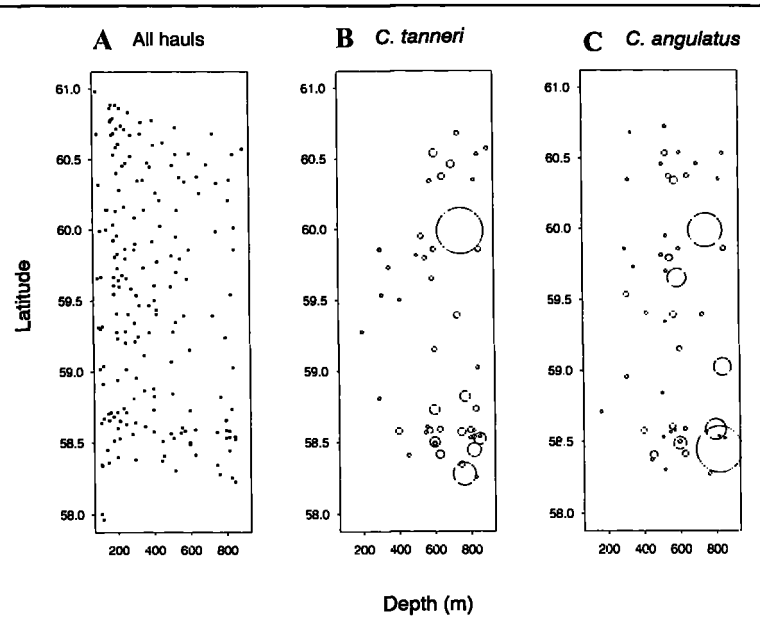

Figure 2

Distribution of all successful trawl hauls (**A**), positive *Chionoecetes tanneri* hauls (**B**), and positive *C. angulatus* hauls (**C**), with respect to latitude and depth in meters. For both species, the size of the circle is proportional to the total catch in numbers per kilometers of towed distance.

Depth distribution

Both species occurred in the deeper portion of the survey area; few individuals of either species were encountered shallower than 300 m (Fig. 4). For *C. tanneri*, the mean depth of mature males (752 m) was not significantly different from the mean depth of mature females (709 m; *t*-test, P=0.38). This is in contrast to the summertime depth distributions of *C. tanneri* reported off British Columbia (males 580–670 m, females 670–720 m, Jamieson et al., 1990) and off Oregon (males 640–686 m, females 503–549 m, Pereyra, 1966) where mature males were found at distinctly shallower depths than those for mature females. Thus in the eastern Bering Sea, *C. tanneri* does not show a clear depth segregation of males and females as is seen in more southerly latitudes, and the depths occupied by both sexes are greater.

For *C. angulatus*, the mean depth for mature males (647 m) was significantly less than the mean depth for mature females (748 m; *t*-test, P<0.001), indicating that this species does appear to have the same pattern of sexual segregation by depth as that displayed by *C. tanneri* in more southerly latitudes (Pereyra, 1966). The depth distribution reported for *C. japonicus* (Yosho and Hayashi, 1994) indicates that the greatest abundance of both sexes occurs at about 1,000 m. Although this finding suggests that *C. japonicus* may occur deeper than *C. angulatus*, it is clear (Fig. 4) that the distribution of *C. angulatus* extends into deeper water than was covered in our survey and that our estimates of mean depth are low (*C. angulatus* has been reported as deep as 2,974 m [Hart, 1982]; in fact, the type specimen of *C. angulatus* was taken quite near our sampling site in 2,549 m [Rathbun, 1932]).

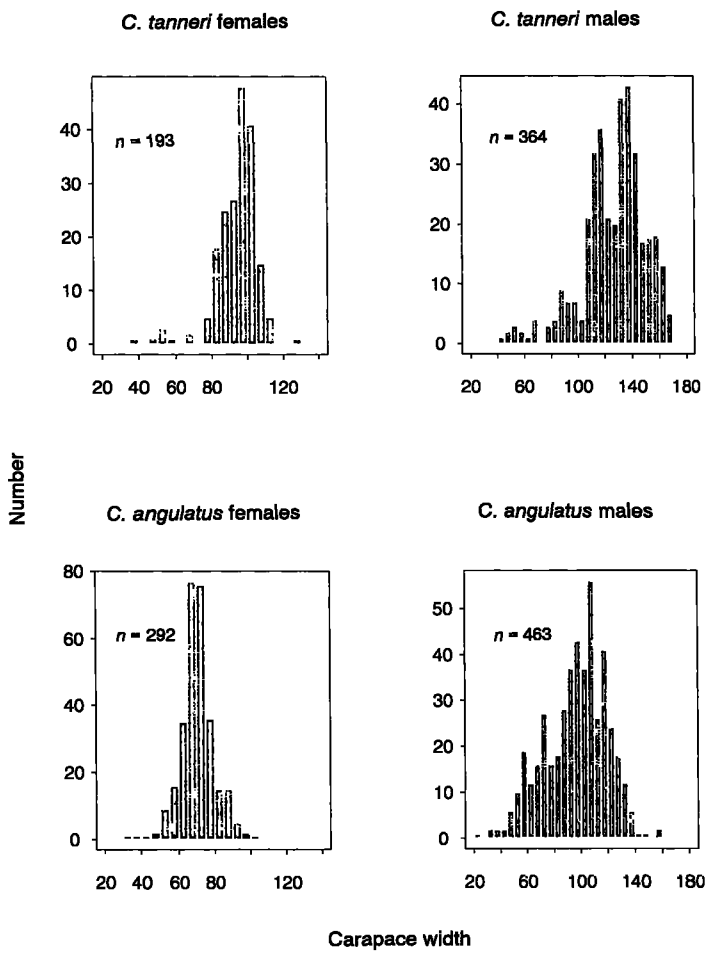

Figure 3

Carapace width distribution for male and female *Chionoecetes tanneri* and *C. angulatus*. The total number of individuals measured (n) in each category is indicated for each sex and species.

Juvenile male *C. tanneri* were found in significantly shallower waters than were mature males (*t*-test, P<0.001), whereas juvenile male *C. angulatus* were not significantly different (P=0.30) in mean depth from mature males. This is in contrast to the depth distribution reported for *C. tanneri* from British Columbia to Oregon where there is a strong depth segregation by size, where juveniles are found in deeper water than are adults (Pereyra, 1968; Jamieson et al., 1990). The observed between-area difference in vertical distribution indicates that the factors producing the size variation with depth at more southerly latitudes do not function similarly in the Bering Sea. Pereyra (1968) hypothesized that *C. tanneri* larvae are advected offshore by Ekman transport and settle to the bottom in deep water. The strong variation in size with depth then results from a shoreward ontogenetic migration of the young crabs. In the region where we surveyed, however, advection of the near-surface water is either quite weak or onshore,[2] rather than strongly offshore. Thus the difference in the observed size variation with depth between the Bering Sea and Oregon may be due to differences in the local oceanographic conditions.

[2] Pease, C. 1995. Pacific Marine Environmental Laboratory, Seattle, Washington. Personal commun.

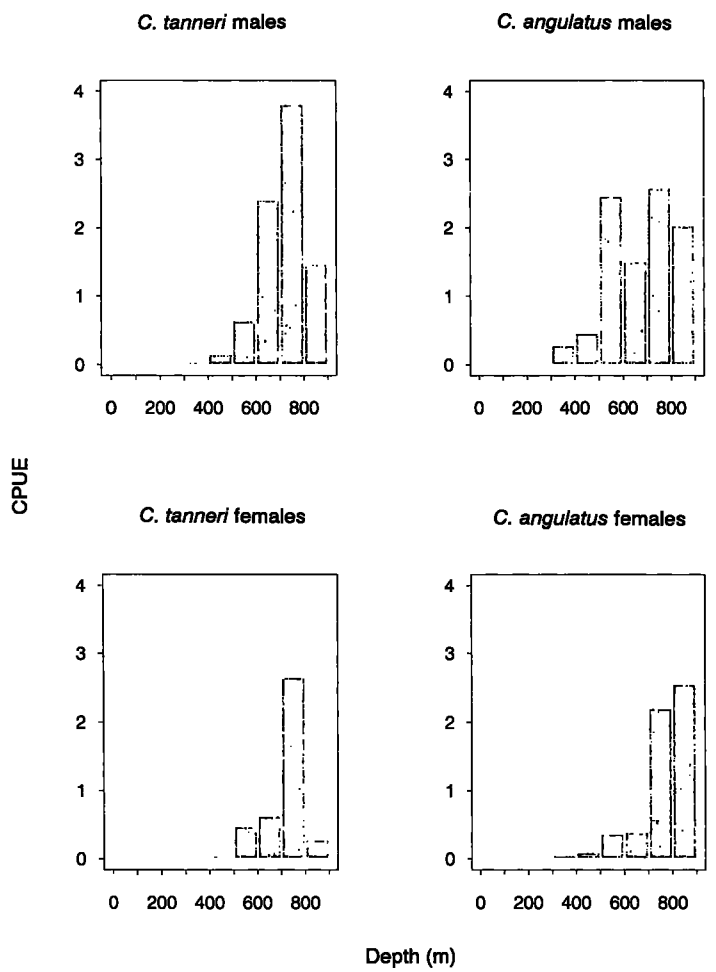

Figure 4

Depth distribution is shown for *Chionoecetes tanneri* and *C. angulatus*, by sex, expressed as mean catch in numbers per kilometer of towed distance (CPUE) within 100-m depth intervals.

Size at maturity

Estimates of the carapace width at 50% maturity, W_{50}, for both male and female *C. tanneri* (Figs. 5 and 6) were not significantly different from reported values of W_{50} off Oregon (Table 1). Likewise, the estimate of the mean carapace width of mature individuals, W_m, for females was not significantly different from the estimate of W_m for Oregon, but the estimate of male W_m was significantly smaller than the estimate for Oregon (Table 1). Although there may be a slight change in size at maturity from Oregon to the Bering Sea, compared with the large spatial variation in size at maturity observed for the shallow-water species *C. bairdi* and *C. opilio* on the Bering Sea shelf (W_m changes by up to 17% over distances of 200 km, Somerton, 1981a), the constancy of size at maturity over the latitudinal range of *C. tanneri* is remarkable. Such constancy has been documented before (Tester and Carey, 1986) and has been attributed to the uniformity of water temperature over great distance at the depths inhabited by this species. For *C. angulatus*, the observed estimates of W_{50} (Figs. 5 and 6; Table 1) were similar to values of W_{50} for *C. japonicus* in the Sea of Japan.

Reproduction

Fecundity of *C. tanneri* did not increase significantly with carapace width (P=0.89, n=29; Fig. 7), primarily because of the large variability in fecundity at size. Over the carapace widths sampled (83–113 mm), mean fecundity was 86,500 eggs. Fecundity of *C. angulatus* displayed much less variability and increased significantly with carapace width (fecundity = –65,608 + 1,664 × CW, P<0.001, R^2=0.55, n=24). For *C. japonicus*, Ito (1976) reported that 70-mm females have about 40,000–50,000 eggs, approximately the same as the fecundity predicted for *C. angulatus* at the same size (Fig. 7). Mean egg diameter was 0.75 mm (SE=0.04) for *C. tanneri* and 0.74 mm (SE=0.04) for *C. angulatus*. Although these estimates are not significantly different from the estimates reported for *C. japonicus* (0.68 mm, Ito, 1976; 0.74 mm, Fukutake, 1965), they are significantly larger than the estimates reported for both of the shallow-water species *C. bairdi* (0.56 mm) and *C. opilio* (0.66 mm, Haynes et al., 1976).

Most mature females of both species carried eggs in the same stage of development (Table 2); therefore it appears that both species have synchronous and seasonal reproduction, in other words, all reproductively active females mate and extrude eggs at about the same time of year. Seasonal reproduction has been previously reported for *C. tanneri* (Pereyra, 1966; Jamieson et al., 1990) and *C. japonicus* (Ito, 1976). However, it has also been reported that *C. japonicus* has a 2-year reproductive cycle (Ito, 1976) and therefore does not have synchronous spawning. If this is true for either *C. tanneri* or *C. angulatus*, one would expect to find more heterogeneity in the observed stages of egg development, unless our macroscopic evaluation of reproductive condition failed to detect differences in embryonic development between the first and second year of a 2-year cycle.

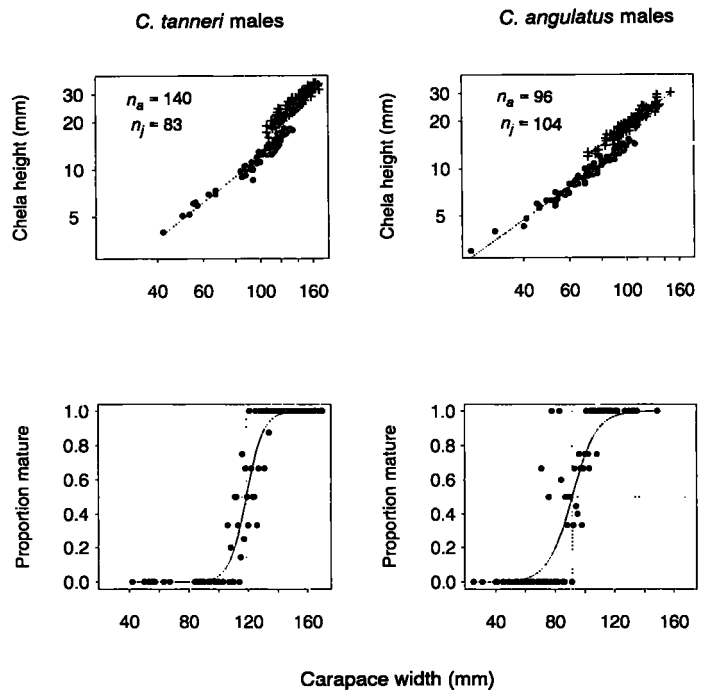

Figure 5

Size at 50% maturity (W_{50}) for male *Chionoecetes tanneri* and *C. angulatus*. Upper graphs show the assignment of chela height and carapace width data to juvenile (dot) and adult (plus) categories. The number of observations in each category (n_a for adults, n_j for juveniles) is indicated in the appropriate graph. Lower graphs show the fit of a logistic model (solid line) to the proportion mature within 1-mm size categories. Dotted lines show the carapace width associated with a 0.50 proportion mature.

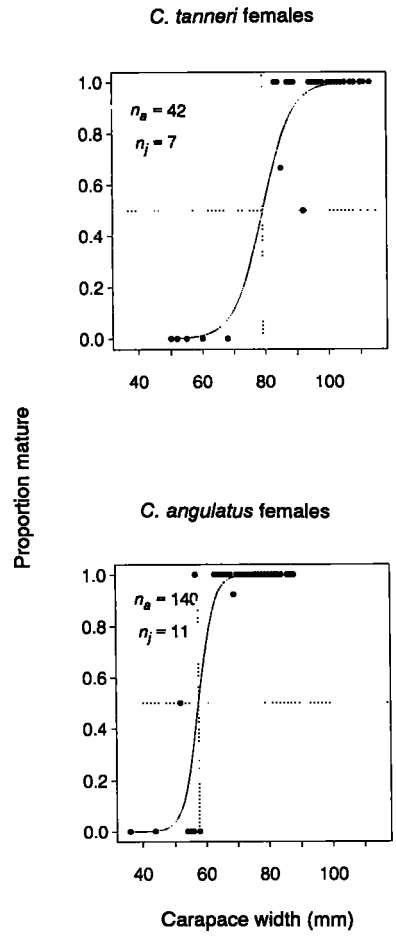

Figure 6

Size at 50% maturity (W_{50}) for female *Chionoecetes tanneri* and *C. angulatus*. For each species is shown the fit of a logistic model (solid line) to the proportion mature within 1-mm size categories. Dotted lines show the carapace width associated with a 0.50 proportion mature. Number of adults and juveniles sampled are indicated in each graph.

Synchronous seasonal reproduction is not necessarily the norm for slope-dwelling crabs. For example, the two species of king crabs that also inhabit the eastern Bering sea slope, *Lithodes aequispina* and *L. couesi*, have asynchronous and nonseasonal reproduction (Somerton, 1981b; Somerton and Otto, 1986) as evidenced by a wide variation among adult females in the developmental stages of their embryos. These king crab species also have eggs that are more than twice the diameter of eggs from shallow-water king crabs, such as *Paralithodes camtschaticus*, and have exceptionally large larvae provisioned with a greater amount of yolk (Somerton, 1981b). Such larvae may be lecithotrophic (i.e. nonfeeding) and therefore remain at depth throughout their development. This larval strategy could, in turn, reduce or eliminate larval dependency on the seasonal production of food and thus obviate the need for seasonal reproduction (Somerton, 1981b). For *C. tanneri* and *C. angulatus*, however, the mean egg diameter is only slightly larger than that for the shallow-water species *C. bairdi* and *C. opilio*, indicating that *C. tanneri* and *C. angulatus* probably have planktotrophic larvae which must migrate to feed in surface waters where prey concentrations are greater. Although such ontogenetic vertical migrations by the larvae of deep-sea fauna were once considered improbable, it is now known that a variety of taxa, from depths even greater than those for *C. tanneri* or *C. angulatus*, possess vertically migratory planktotrophic larvae (Young, 1994).

Molting

For mature female *C. tanneri* and *C. angulatus*, relative abundance of the four shell-condition categories

Table 1

Carapace width at 50% maturity (W_{50}) and mean carapace width of mature individuals (W_m), in millimeters, by species, sex, and area. Standard errors are shown in parentheses. Estimates for W_{50} for *C. japonicus* were interpolated from a figure in the noted source and are therefore approximate.

Species	Sex	W_{50}	W_m	Area	Source
C. tanneri	male	118.7 (1.26)	137.9 (1.25)	Bering Sea	This study
	female	79.2 (4.82)	99.5 (1.25)	Bering Sea	This study
	male	118.0	142.7	Oregon	Tester and Carey (1986)
	female	85.0	102.0	Oregon	Tester and Carey (1986)
	male		148.9	Oregon	Pereyra (1966)
	female		102.5	Oregon	Pereyra (1966)
C. angulatus	male	91.4 (1.64)	105.2 (1.58)	Bering Sea	This study
	female	57.8 (1.46)	72.2 (0.52)	Bering Sea	This study
C. japonicus	male	~95		Japan	Watanabe and Suzuuchi (1983)
	female	~55		Japan	Watanabe and Suzuuchi (1983)

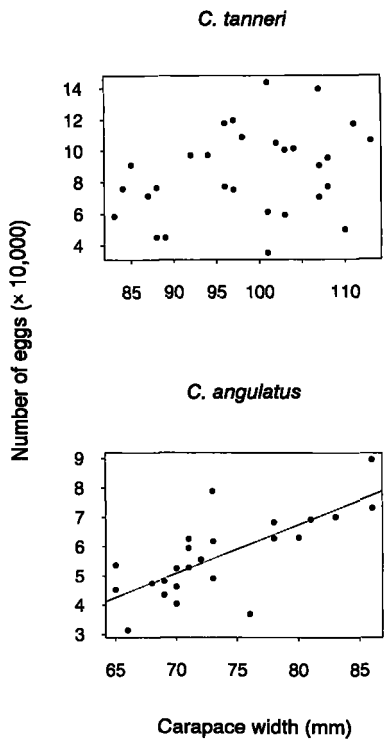

Figure 7

Fecundity is shown as a function of carapace width for female *Chionoecetes tanneri* (upper graph) and *C. angulatus* (lower graph). The number of eggs was not significantly related to size for *C. tanneri*, but it was significant for *C. angulatus* and the regression line is shown.

Table 2

Number and percentage of individuals examined in each of three reproductive conditions for mature female *C. tanneri* and *C. angulatus*.

Reproductive condition	*C. tanneri*	*C. angulatus*
3 (uneyed eggs)	33 (79%)	121 (86%)
4 (eyed eggs)	0	2 (1%)
2, 5 (no eggs)	9 (21%)	17 (12%)

did not differ significantly between species (Table 3; χ^2=0.27, P=0.53). Most mature females were scored as having shell condition 3 (Table 3), indicating that they probably had not molted for at least 1 year and likely have a terminal molt similar to that of the shallower water species *C. bairdi* and *C. opilio*. Some individuals of both species had molted so recently that their exoskeletons were still pliable. Because the puberty molt is usually associated with mating, some mating must have occurred as late as July. However, the primiparous (shell conditions 1 and 2) females also had a surprisingly high percentage of barrenness (*C. tanneri*—60%; *C. angulatus*—76%) compared with multiparous (shell condition 3) females (*C. tanneri*—16%; *C. angulatus*—3%). For *C. bairdi* and *C. opilio*, primiparous females are rarely barren because mating and egg extrusion quickly follow the puberty molt (Watson, 1970). Perhaps for *C. tanneri* and *C. angulatus*, egg extrusion does not follow a molt as closely as it does for shallower species, and

Table 3

Number and percentage of individuals examined in each shell condition category for adult female and male *C. tanneri* and *C. angulatus*.

Shell condition	*C. tanneri*	*C. angulatus*
Females		
1	1 (2%)	4 (3%)
2	4 (10%)	11 (8%)
3	37 (88%)	121 (88%)
4	0	2 (1%)
Males		
1	5 (5%)	20 (21%)
2	123 (88%)	63 (65%)
3	12 (9%)	14 (14%)
4	0	0

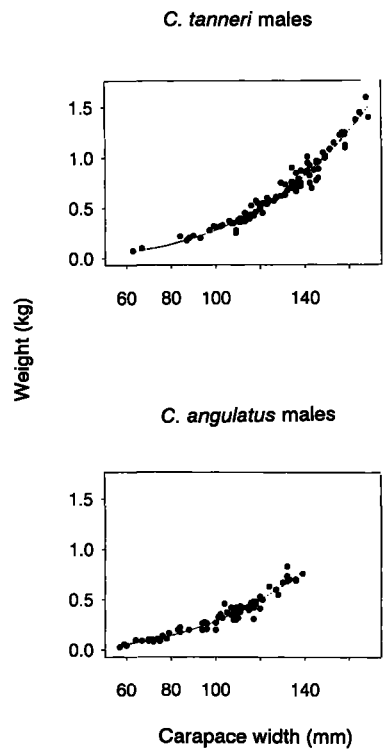

Figure 8

Weight-length relationships for *Chionoecetes tanneri* and *C. angulatus* and the fitted power curves.

the high incidence of barrenness was due simply to our sampling between times of molting and egg extrusion.

For mature male *C. tanneri* and *C. angulatus*, the relative abundance of the four shell condition categories differed significantly between species (χ^2=21.4, P<0.001), primarily because there were considerably more *C. angulatus* males in a recently molted condition (Table 3). The high incidence of recently molted *C. angulatus* males was not due to the chance capture of a large molting aggregation, because recently molted individuals were found at many of the sampling sites. Therefore, it is likely that the timing of the male molting season differs between species.

For both species, however, the relative abundance of the four shell conditions differed between sexes (*C. tanneri*, χ^2=104.1, P<0.001; *C. angulatus*, χ^2=130.0, P<0.001) primarily because males had lower shell-condition scores than did females. Such between-sex differences in shell condition scores could reflect differences in the timing of the molt relative to sampling, differences in preferred habitat, or differences in adult mortality rate. Alternatively, such differences in shell condition could indicate that mature males have molted more recently, on average, than adult females, raising the question of whether males cease molting at maturity. Jamieson et al. (1990) believed that male *C. tanneri* undergo a terminal puberty molt and are therefore similar to *C. opilio*, for which a male terminal molt has been clearly established (Conan and Comeau, 1986). However, Tester and Carey (1986) also found a between-sex difference, similar to our study, in the index of postmolt age for *C. tanneri* off Oregon; mature males exhibited considerably lower incidence of exoskeleton damage from chitonoclastic bacteria than did mature females. This sexual difference in exoskeleton damage was interpreted as an indication that male *C. tanneri* continue to molt after maturity. Although our shell-condition data were consistent with the observations of Tester and Carey (1986), we are not convinced that this indicates that males contintue to molt.

Weight–carapace-width relationship

The increase in male body weight with carapace width (Fig. 8) was not significantly different between the two species (ANCOVA, P=0.92; Table 4), therefore a single function was fitted to the combined data. This similarity in the weight-width relationship reflects a remarkable similarity in the shape of *C. tanneri* and *C. angulatus* compared with shallow-water species of *Chionoecetes*. For example, the predicted weight at 120 mm CW is 505 gm for both *C. tanneri* and *C. angulatus* males. The weight of a similar-size *C. japonicus*, another slope-dwelling species, is 588 gm (Watanabe and Suzuuchi, 1983), fairly close to *C. tanneri* and *C. angulatus*. However, the

Table 4

Parameter estimates for the fitted equation weight (gm) = a (carapace width in mm)^b, number of data (n), and goodness of fit (R^2) for male *C. tanneri* and *C. angulatus*, and for both species combined.

	a	b	n	R^2
C. tanneri	1.186×10^{-4}	3.189	101	0.96
C.angulatus	2.244×10^{-4}	3.054	76	0.94
Combined	1.219×10^{-4}	3.183	177	0.97

weight of a similar-size *C. opilio* from the shelf of the eastern Bering Sea is 739 gm (Somerton, 1981c), considerably heavier than the slope species. The likely explanation for this is that slope species of *Chionoecetes*, like slope species of king crabs, have proportionately thinner legs than shelf species (Somerton, 1981b). The evolutionary significance of such depth-related changes in shape is unclear, but for other deep-water crustacea, reduced musculature is assumed to be an adaptation for energy efficiency in a habitat where food is scarce (Childress, 1971).

Similarity of *C. angulatus* and *C. japonicus*

Repeatedly throughout the foregoing discussion, we have compared various distributional or life history characteristics reported from other studies of *C. japonicus* with those determined for *C. angulatus* from our samples because we suspect that the two species actually are either taxonomically identical or that *C. japonicus* is a subspecies of *C. angulatus* (3 years after Rathbun [1932] described *C. japonicus*, Derjugin and Kobjakowa [1935] described *C. angulatus bathyalis* on the basis of specimens that were also collected near Japan). We base our question not only on the similarity of the various biological features that we examined (e.g. size and depth distribution, size at maturity) but also on the high degree of similarity in shape between the two species. We recommend that the validity of the separation of *C. angulatus* and *C. japonicus* be re-examined by qualified systematists.

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Biology and distribution of arrowtooth, *Atheresthes stomias*, and Kamchatka, *A. evermanni*, flounders in Alaskan waters

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Abstract.—The biology and distribution of arrowtooth, *Atheresthes stomias*, and Kamchatka, *A. evermanni*, flounder were examined in Alaskan waters to determine whether there were sufficient differences to justify treating them as separate species in resource assessment surveys conducted by the National Marine Fisheries Service. Geographic ranges of the two flounder species overlap in Alaska waters; both occur in the eastern Bering Sea and western Aleutian Islands region. However, only arrowtooth flounder occur throughout the eastern Aleutian Islands region and the Gulf of Alaska. Arrowtooth flounder were abundant over a wide range of depths (76–450 m) and were more abundant than Kamchatka flounder in catches shallower than 325 m. Kamchatka flounder were abundant only in deep trawl hauls (226–500 m) and were more abundant than arrowtooth flounder in catches at depths greater than 375 m. Arrowtooth flounder were also abundant over a wide range of bottom-water temperatures (2.1°–4.6°C), whereas Kamchatka flounder were abundant in a much narrower range of bottom temperatures (3.8°–4.2°C). By percentage, females dominated the arrowtooth flounder population in the eastern Bering Sea (68.6%) and Aleutian Islands region (59.6%), whereas the Kamchatka flounder population was 55.9% and 47.5% female, respectively. The females of both species attained greater length at age than did the males. The difference in growth between the sexes was greater among arrowtooth flounder and may account for the preponderance of females in the arrowtooth flounder population.

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Arrowtooth flounder, *Atheresthes stomias*, and Kamchatka flounder, *A. evermanni*, were not always treated as separate species in resource assessment bottom trawl surveys of the Alaska Fisheries Science Center (AFSC) prior to 1991 because of their similarity in appearance, lack of commercial importance, and the limited abundance of Kamchatka flounder in comparison with arrowtooth flounder. They were both grouped as arrowtooth flounder and possible differences between them were not thoroughly documented. Most of the previous research conducted on *Atheresthes* spp. has treated them as a species complex. The few comparative studies of *Atheresthes* spp., based on morphometrics (Norman, 1934; Wilimovsky et al., 1967; Yang, 1988), genetics (Ranck et al., 1986), diet (Yang and Livingston, 1986), and geographic distribution (Shuntov, 1965; Wilimovsky et al., 1967; Allen and Smith, 1988), have documented few differences between the two species.

Arrowtooth flounder accounts for 55% of the flatfish biomass in the western Gulf of Alaska (Brown[1]); it is the dominant flatfish of that area, and yet it has not supported a large fishery. Arrowtooth flounder have been caught commercially in small fisheries off the Pacific coast of Canada and off the Washington and Oregon coasts for use in animal feeds as well as for human consumption (Kabata and Forrester, 1974). Softening of the flesh, probably caused by an enzyme released from a myxosporean parasite (Greene and Babbitt, 1990), has limited the marketability of arrowtooth flounder as food. Recent work, however, has shown promise in producing marketable flounder products, such as arrowtooth flounder fillets (Greene and Babbitt, 1990), arrowtooth flounder surimi (Wasson et al., 1992; Porter et al., 1993; Reppond et al., 1993), and Kamchatka flounder surimi (Haga et al.[2]). Potentially, a fishery targeting arrowtooth flounder in Alaskan waters could have an effect on the Alaskan population of Kamchatka flounder. Knowledge of the biology of the two species may provide crucial information needed for their proper management and conservation. Therefore, since 1991, these species have been considered as two separate

[1] Brown, E. S. 1994. Alaska Fisheries Science Center, Resource Assessment and Conservation Engineering Division, 7600 Sand Point Way NE, Seattle, WA 98115. Personal commun.

[2] Haga, H., R. Shigeoka, and T. Yamauchi. 1980. Method for processing fish contaminated with sporozoa. U.S. Patent 4,207,354, Jun. 10.

species during resource assessment surveys conducted by the AFSC.

The purpose of the present work was to document the geographical overlap of the two flounder species in Alaskan waters and to describe the ecological differences, such as length at age, sex-ratios, and depth and temperature preferences that allow such externally similar species to coexist. Incorporation of this information into future AFSC surveys may prove essential for the management of the two species.

Materials and methods

Data were obtained from bottom trawl surveys conducted from research vessels over the continental shelf (<200 m) and slope (200–800 m) of the eastern Bering Sea and off the Aleutian Islands (<500 m). The surveys were conducted from June through September 1991. Sample design, fishing gear and methods, catch sampling procedures, and data analyses are described by Goddard and Zimmermann[3] for the eastern Bering Sea shelf and slope and by Harrison (1993) for the Aleutian Islands. The bottom trawl used in the Bering Sea shelf survey was different from that used in the Bering Sea slope and Aleutian Islands region. The bottom trawl used on the Bering Sea shelf had smaller meshes in the net wings and body and was used without roller gear; therefore it fished heavily on the bottom. The bottom trawl used on the Bering Sea slope and in Aleutian Islands region was used with bobbin roller gear and had larger meshes in the net wings and body. Additional data were incorporated from the western Gulf of Alaska bottom trawl survey (<500 m) conducted in 1993 but were used only for defining geographic ranges. Nets were towed at approximately 5.5 km/hr (3 knots) for 30 minutes, covering a distance of 2.8 km (1.5 nmi). Mean net width, as measured with SCANMAR net mensuration gear, was multiplied by the distance traveled to calculate the area swept by the net. Catch per unit of effort (CPUE) was calculated for each species for each tow in kilograms per hectare (kg/ha). Either micro-bathythermograph probes fixed to the net or expendable bathythermograph probes dropped at the haul sites recorded bottom temperatures (±0.1°C).

Arrowtooth and Kamchatka flounders were distinguished by the position of their upper eyes. The upper eye of arrowtooth flounder interrupts the profile of the head and can be seen from the blind side. The upper eye of the Kamchatka flounder does not interrupt the head profile. Fish whose upper eye was not located with any certainty or which had a damaged upper eye were distinguished by number of gill rakers (Yang, 1988). After sorting, each species was weighed separately. Fish size was recorded as fork length, and the sex of each fish was determined by making an incision posterior to the abdomen on the blind side and by visually inspecting the gonadal tissue.

Comparisons were made between the abundance of the two species in CPUE (kg/ha) by depth interval and water temperature interval. When there were a sufficient number of hauls, depth was divided into 25-m intervals and temperature into 0.1°C intervals. When there were few hauls, catches were grouped into 100-m depth intervals and 1.0°C intervals. For trawl hauls in which both species were caught, a logistic model was developed to show the relationship between the proportion of arrowtooth flounder in the total *Atheresthes* catch and depth;

$$(\ln(p/1-p) = \alpha + \beta x),$$

where p is the proportion of arrowtooth flounder in the total *Atheresthes* catch rate, $1-p$ is the proportion of Kamchatka flounder in the total *Atheresthes* catch rate, α and β are constants, and x is the depth in meters.

The geographic distributions of both species were described from our thorough but depth-limited bottom trawl survey data, supplemented by data supplied by the Fishery Observer Program of the AFSC, which also supplied species composition data on catches from deep waters in the Gulf of Alaska. Nonlinear regressions related mean length of arrowtooth and Kamchatka flounder by haul to depth;

$$L = L_{\infty} - Ae^{BM},$$

where L is estimated length, L_{∞} is theoretical maximum length, M is depth in meters, and A and B are constants.

Initial observations indicated an unusually high percentage of females in the arrowtooth flounder population. Juvenile fish from which the sex could not be determined, generally less than 20 cm in length, were not included in the analysis. The percentage of females in the arrowtooth flounder population was compared against the percentage of females in the Kamchatka flounder population for both the Aleutian Islands and the eastern Bering Sea. Comparisons were also made against the other major flatfish species in the eastern Bering Sea to de-

[3] 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. AFSC Processed Rep. 93-15, 342 p. Alaska Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA 98115-0070.

termine whether the unusually high percentage of females in the arrowtooth flounder population, seemingly an odd occurrence, was also typical of the other species from the same area caught in the same survey. Additional comparisons could not be made from data gathered in the Aleutian Islands because of the limited number of sex determinations of other flatfish species.

The unusually high percentage of females in the arrowtooth flounder population prompted us to analyze the data in different ways to look for trends in percentages of females. The percentage of females was calculated from individual trawl hauls in which the sex was determined from a minimum of 10 fish. Percent-female values for arrowtooth flounder were examined geographically to determine whether there were regions where male arrowtooth flounder were abundant. Percent-female values were also regressed against bottom temperature and depth. By searching for trends in percent-female values, we hoped to identify areas where high proportions of arrowtooth flounder males may have occurred but were not sampled or were underrepresented in our survey.

For fish from the eastern Bering Sea slope, sagittal otoliths were collected from up to three fish per sex per centimeter interval for ageing and were stored in a glycerol-thymol solution. Because previous methods for preparing the otoliths for ageing did not clearly reveal the annular rings, researchers at the AFSC developed a new technique (Scott[4]). Otoliths were cut along their dorsal-ventral axis through the nucleus and evenly heated in a muffle furnace at 270°C for 5 to 10 min. If the annular rings were not sufficiently darkened, the otoliths were burned in an alcohol flame. When cool, oil was applied to the otolith surface and the cut surface read with a binocular dissecting scope.

Von Bertalanffy growth curves were calculated for the age and length data by using nonlinear regression to provide estimates of L_∞, K, and t_0. To determine whether growth differed significantly between sexes or between species, the residual sum of squares (RSS) from a combined model was compared by using an approximate F-test (Draper and Smith, 1981):

$$F = \frac{(RSS_{TOTAL} - (RSS_1 + RSS_2))/3}{(RSS_1 + RSS_2)/N - 6},$$

where N is equal to the number of otoliths aged, and 1 and 2 are either male and female arrowtooth or male and female Kamchatka flounder. Kimura (1990) showed that this approximation of the test statistic, which tests for differences between all growth curve parameters simultaneously, can be useful for testing von Bertalanffy growth parameters. The test statistic was compared against values from the F-distribution at the α=0.05 level of significance. The von Bertalanffy parameters were then used to provide estimates of length at age for the range of ages found for each species and sex group.

Results

Atheresthes spp. were caught in 492 of the 779 trawl hauls. Neither species was caught in the shallowest trawl hauls (<25 m), whereas catch rates for both species were low in the deepest trawl hauls (700 m to 800 m). Arrowtooth flounder were abundant from 76 m to 450 m, with mean CPUE ranging from 3.3 to 13.6 kg/ha (Fig. 1). Kamchatka flounder were abundant from 226 m through 500 m, with mean CPUE ranging from 3.8 to 12.8 kg/ha. Arrowtooth flounder catch rates showed a bimodal distribution in relation to depth, with high catch rates in both shallow (76 m to 225 m) and deep (226 m to 450 m) trawl hauls. Kamchatka flounder catch rates were weakly bimodal, with only low catch rates in shallow waters and all the highest catch rates in deeper waters.

A comparison of the percent of the total *Atheresthes* CPUE by species for each depth interval shows that arrowtooth flounder were more abundant in the shallower depth intervals (≤250 m) (Fig. 2). There was a zone of transition between the two species from 251 m to 425 m. Finally, Kamchatka flounder were more abundant than arrowtooth flounder from 426 m to 800 m. For trawl hauls in which both species were caught, a logistic regression relating percentage of arrowtooth flounder of the total *Atheresthes* CPUE against depth (Fig. 3) showed a significant, negative relationship (df=277, F=98.8, P<0.001, R^2=0.26). The model was

$$3.47 - 0.009(Depth) = \ln(p/1-p),$$

where p = Arrowtooth flounder CPUE/*Atheresthes* CPUE.

Data on the water temperature distribution of *Atheresthes* spp. were recorded from 252 of the 492 trawl hauls in which *Atheresthes* spp. were caught. *Atheresthes* spp. were caught only in temperatures between 0.3° and 5.9°C (Fig. 4), whereas the survey temperatures ranged from −1.5° to 11.7°C. Arrowtooth flounder were abundant at a wide range of bottom temperatures, but they were most abundant at temperatures of 2.1° to 4.6°C. While the total range

[4] Scott, K. 1994. Alaska Fisheries Science Center, Resource Ecology and Fisheries Management Division, 7600 Sand Point Way NE, Seattle, WA 98115. Personal commun.

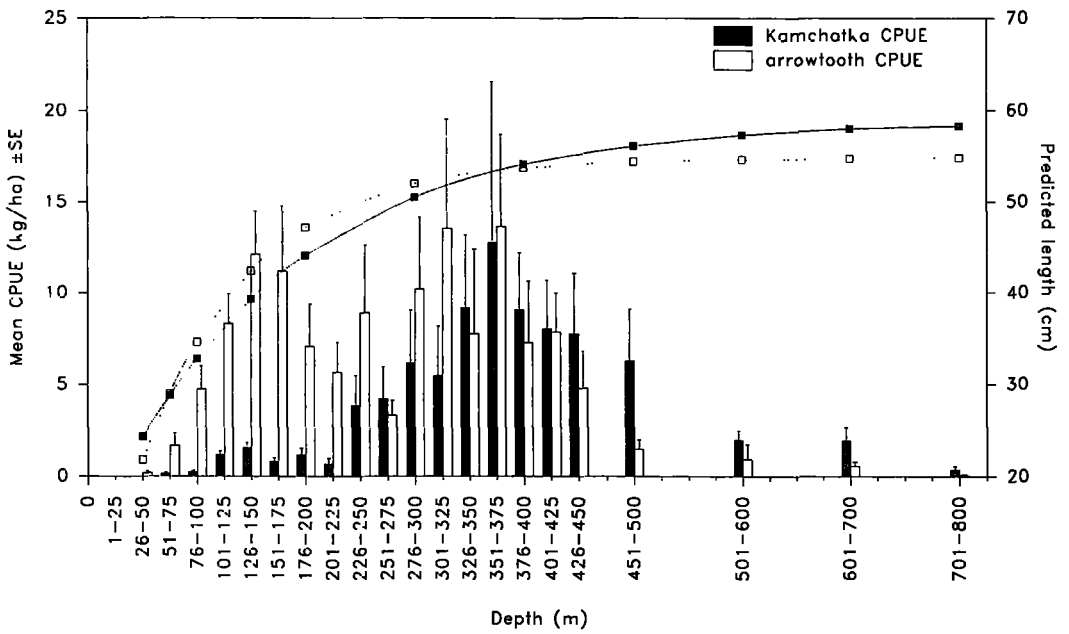

Figure 1

Mean catch per unit of effort (CPUE) in kg/ha (±1 SE) in relation to depth interval for the *Atheresthes* species. Length-at-depth curves are superimposed over the bar graph.

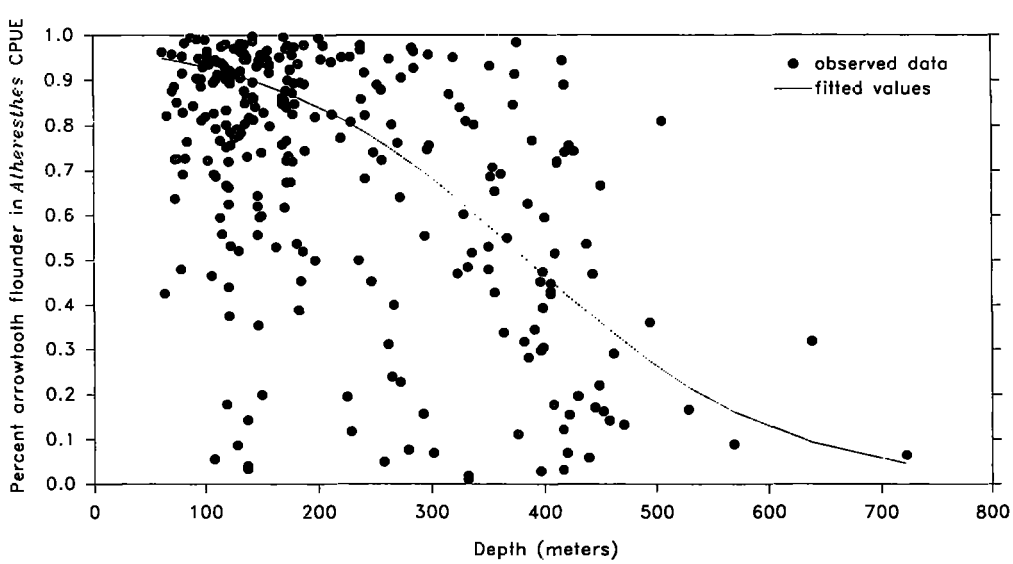

Figure 2

Percent by species of the total *Atheresthes* catch per unit of effort (CPUE) in relation to depth interval.

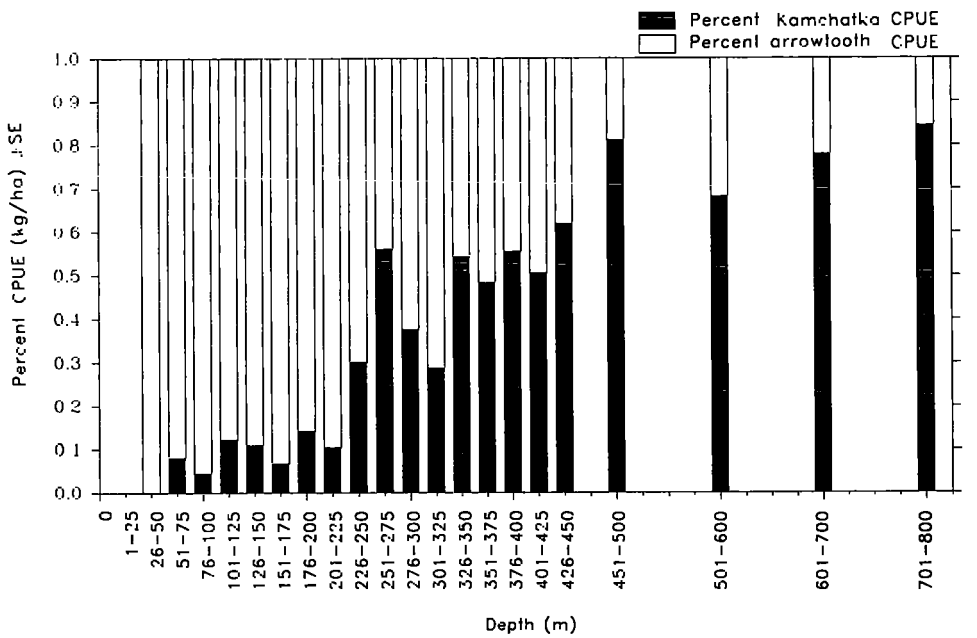

Figure 3

Logistic model relating percentage of arrowtooth flounder of the total *Atheresthes* catch rate to depth.

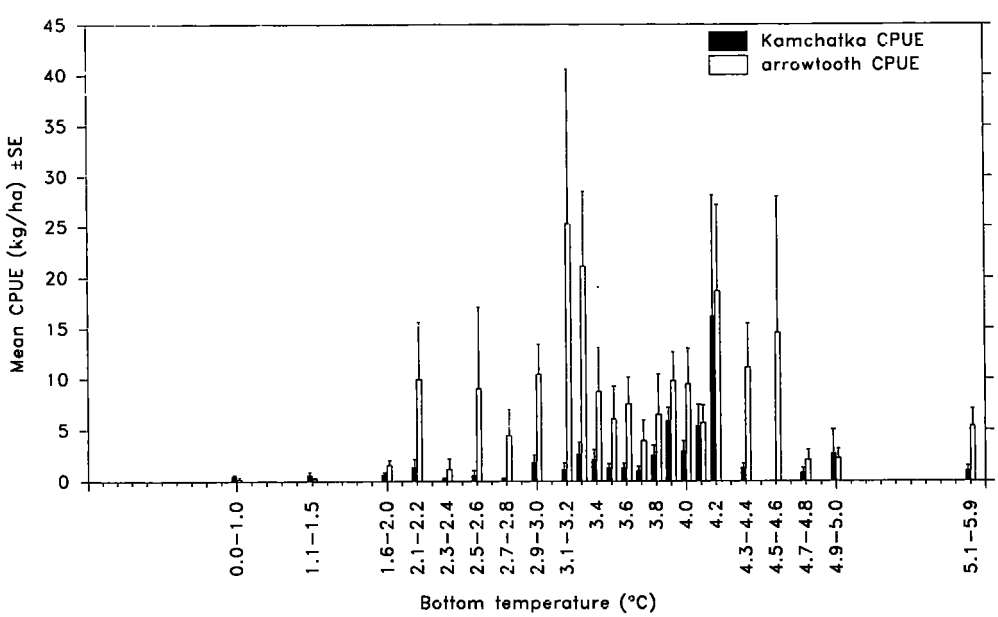

Figure 4

Mean catch per unit of effort (CPUE) in kg/ha for the *Atheresthes* species in relation to bottom temperature.

of water temperatures for Kamchatka flounder (0.7° to 5.9°C) was similar to the range for arrowtooth flounder (0.3° to 5.9°C), the highest catch rates of Kamchatka flounder were distributed over a narrower temperature range (3.8° to 4.2°C).

Arrowtooth flounder catch rates were high on the eastern Bering Sea continental shelf (7.3 kg/ha), especially in waters between 100 m and 200 m (17.7 kg/ha), on the eastern Bering Sea continental slope (8.8 kg/ha), and the fish occurred throughout the Aleutian Islands (Fig. 5). The Kamchatka flounder geographic distribution was similar to that of arrowtooth flounder (Fig. 6), except that Kamchatka flounder were not caught along the Alaska Peninsula, nor in the Gulf of Alaska. Kamchatka flounder were much less abundant than arrowtooth flounder in the eastern Bering Sea, especially on the shelf (1.2 kg/ha), and about half as abundant as arrowtooth flounder on the slope area (4.6 kg/ha). However, in the deepest half of the slope area (500 m to 800 m), the catch rate of Kamchatka flounder (1.5 kg/ha) was about twice that of arrowtooth flounder (0.7 kg/ha). Kamchatka flounder occurred on the northwest tip of the eastern Bering Sea shelf, whereas arrowtooth flounder were absent from that area. Arrowtooth flounder catch rate was high along the north side of the easternmost Aleutian Islands bordering the southern Bering Sea (16.4 kg/ha), where more than half of the total biomass for the entire Aleutian Islands occurred (Harrison, 1993). Kamchatka flounder generally decreased in abundance from west to east along the Aleutian Islands (Harrison, 1993). The easternmost Aleutian Islands were the southeastern border of their distribution, where the catch rate was low (0.7 kg/ha). In the rest of the Aleutian Islands area, Kamchatka flounder had a slightly higher catch rate (3.1 kg/ha) than arrowtooth flounder (2.9 kg/ha), particularly in the 300 m to 500 m depth interval (10.8 vs. 2.0 kg/ha, Harrison, 1993).

Data provided from the Fishery Observer Program of the AFSC indicated the presence of Kamchatka flounder in the Gulf of Alaska as far east as 154°26'W, but in limited numbers and at great depths (Conrad[5]). The identification of Kamchatka flounder oc-

[5] Conrad, M. 1994. Alaska Fisheries Science Center, Fishery Observer Program, 7600 Sand Point Way NE, Seattle, WA 98115. Personal commun.

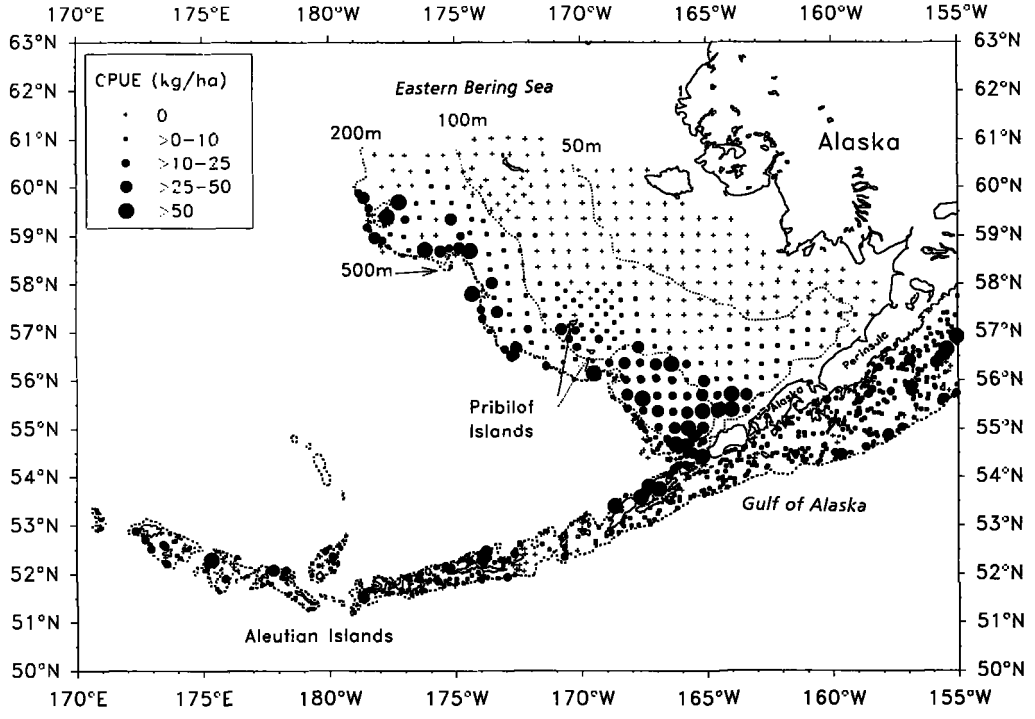

Figure 5

Map of arrowtooth flounder, *Atheresthes stomias*, CPUE (kg/ha) over the eastern Bering Sea shelf and slope, in waters off the Aleutian Islands, and in Gulf of Alaska areas. The 50-, 100-, and 200-m bathymetric contours are not included in the Aleutian Islands and Gulf of Alaska areas owing to complicated bottom topography.

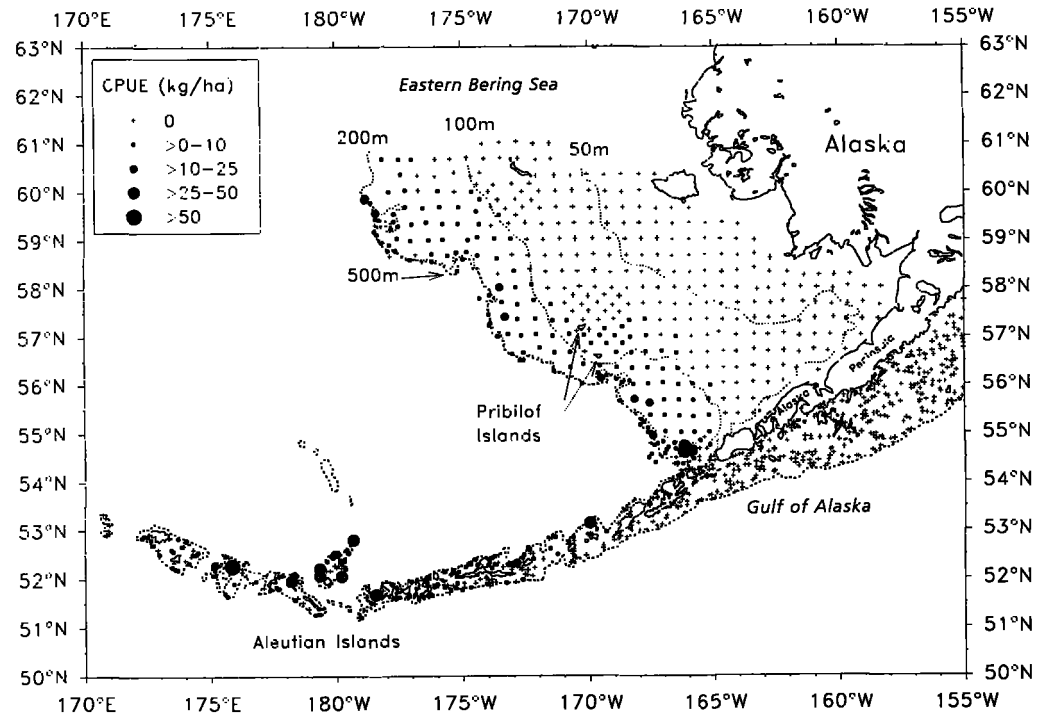

Figure 6

Map of Kamchatka flounder, *Atheresthes evermanni*, CPUE (kg/ha) over the eastern Bering Sea shelf and slope, in waters off the Aleutian Islands, and in Gulf of Alaska areas. The 50-, 100-, and 200-m bathymetric contours are not included in the Aleutian Islands and Gulf of Alaska areas owing to complicated bottom topography.

curring in the Gulf of Alaska was confirmed by meristic data recorded from three specimens. These rare occurrences of Kamchatka flounder in the Gulf of Alaska (length range 56–65 cm) were in depths (549–686 m) outside the depth range covered during the Gulf of Alaska bottom trawl survey.

The mean length of both *Atheresthes* flounders increased with depth, and asymptotic, curvilinear models were fitted to the data

$$\textit{arrowtooth flounder length} = 54.8 - 53.8e^{-0.0098 depth},$$

(df=131, F=3618.8, P<0.001, R^2=0.80);

$$\textit{Kamchatka flounder length} = 58.8 - 45.9e^{-0.0057 depth},$$

(df=64, F=2123.3, P<0.001, R^2=0.75).

The models show that for much of the size range (~30 cm to ~50 cm) for both species, Kamchatka flounder of the same length as arrowtooth flounder occur at a greater depth (superimposed on Fig. 1). Kamchatka flounder attain a greater length at depth than do arrowtooth flounder in depths greater than 400 m.

The relationship between length and water temperature was more complex and could be adequately described only in combination with geographic and depth relationships. The combined results from the eastern Bering Sea and Aleutian Island regions are presented in Table 1. A comparison of the depth and temperature differences between size groups and between species by statistical analyses was difficult because of lack of independence of the samples (both species were often taken together). Although the differences could not be tested, different size groups appeared to be associated with different depth zones and temperatures.

Catches of small arrowtooth flounder (<30 cm FL) were associated with shallow areas near the Pribilof Islands, the Alaska Peninsula, and the region north of the eastern Aleutian Islands. Medium-size arrowtooth flounder (from ≤30 to <40 cm FL) were grouped mostly between the 100 m and 200 m isobaths on the eastern Bering Sea shelf and around the central Aleutian Islands. The largest arrowtooth flounder

Table 1

Mean depth and mean temperature of trawl hauls from the eastern Bering Sea and Aleutian Islands region for small (<30 cm), medium (≥30 to <40 cm), and large (≥40 cm) arrowtooth, *Atheresthes stomias*, and Kamchatka, *A. evermanni*, flounder. Standard errors (±1) are in parentheses.

	Length group					
	Small	*n*	Medium	*n*	Large	*n*
Arrowtooth flounder						
Mean depth (m)	74.1 (3.11)	26	121.4 (2.64)	109	255.0 (10.41)	110
Mean temperature (°C)	4.5 (0.30)	16	3.4 (0.12)	48	3.7 (0.09)	70
Kamchatka flounder						
Mean depth (m)	—		135.1 (3.96)	37	351.4 (13.36)	66
Mean temperature (°C)	—		3.7 (0.19)	15	3.8 (0.09)	50

(≥40 cm FL) were caught near the edge of the Bering Sea shelf, in the Bering Sea slope area, and throughout the Aleutian Islands regions.

There was a difference in the temperature regimes of the Aleutian Islands and eastern Bering Sea regions. In waters off the Aleutian Islands, where collection of length data combined with bottom temperature data was scant (n=18), there was a significant, negative relationship between length and bottom temperature (df=16, F=13.5, P=0.002, R^2=0.46): smaller fish were present in the shallowest and warmest water (~5° to 6°C) whereas larger fish were found in deeper, cooler water, approaching 4°C. On the Bering Sea shelf and slope, there was a more complex relationship between fish size and bottom temperature, described by a large number (n=116) of observations. As fish size increased with depth, the bottom temperature dropped from 4.1°C (<30 cm FL, n=10) to 3.3°C (from ≤30 to <40 cm FL, n=43), and to 2.4°C (≥40 cm FL, n=12) near the shelf edge, though the largest fish were located where the bottom temperature increased (3.9°C, n=51) in the slope area.

For Kamchatka flounder, the group of smaller size fish was eliminated from analysis because it was represented by only five hauls, and for only two of those hauls had bottom temperatures been recorded. The groups of medium- and large-size Kamchatka flounder had geographic distributions similar to groups of comparable-size arrowtooth flounder. The medium-size (from ≤30 to <40 cm FL) Kamchatka flounder were found on the Bering Sea shelf generally between the 100 m and 200 m isobaths; however, they did not extend along the Alaska Peninsula nor near the eastern Aleutian Islands as did arrowtooth flounder. The group of large-size Kamchatka flounder (≥40 cm FL) was found along the edge of the Bering Sea shelf, the Bering Sea slope, and throughout waters off the Aleutian Island chain, similar in geographic range to arrowtooth flounder. However, they were absent from the eastern islands. The bottom temperature data for the Kamchatka flounder was similar to that of the arrowtooth flounder, except that there were fewer data.

Arrowtooth flounder catches typically had a high percentage of females, whereas the Kamchatka flounder catches taken from the same trawl hauls generally had an equal sex ratio (our observations). In the eastern Bering Sea, the arrowtooth flounder population had a greater percentage of females (68.6%) than did the Kamchatka flounder population (55.9% female) (Table 2). Arrowtooth flounder also had a greater percentage of females than did *Hippoglossoides* spp. (51.7% female), Alaska plaice (*Pleuronectes quadrituberculatus*, 42.3% female), rock sole (*P. bilineatus*, 48.9% female) and yellowfin sole (*P. asper*, 54.2% female).

In the Aleutian Islands, arrowtooth flounder also had a higher percentage of females (59.6% female) than did Kamchatka flounder (47.5% female) and rock sole (52.6% female), the only species encountered in sufficient numbers in trawl hauls for comparison.

Plotting female percentage values of arrowtooth flounder geographically did not indicate any large areas where the percentage of females was low. Nor did it indicate areas where the population had a low percentage of females but was either undersampled or outside of the sampled area. The percentage of females was not significantly related to depth

(P>0.05). The percentage of females was, however, significantly related to mean bottom-water temperature (df=121, F=9.3, P=0.003), but the relationship was very poor (R^2=0.07).

Otoliths were read from 187 arrowtooth and 120 Kamchatka flounder (Table 3). Computer generated estimates of L_∞, K, and t_0 were accepted except for the L_∞ estimates for arrowtooth flounder females. Our length measurement data indicated that the computer estimate was about 40 cm too long, therefore the relationship was forced, with L_∞ set to 85 cm. The von Bertalanffy growth curve was significantly different (F=42.8, P<0.001) between arrowtooth flounder males (n=53, range 3 to 9 years old) and females (n=134, range 4 to 12 years old, Fig. 7A). The growth curve was also significantly different (F=10.6, P<0.001) between Kamchatka flounder males (n=57, range 3 to 10 years old) and females (n=63, range 4 to 33 years old, Fig. 7B). Most of the Kamchatka flounder females were between the ages of 4 and 13 years, and just two fish were aged as 30 and 33 years old (not shown in Fig. 7B). All analyses were performed with and without the 30- and 33-year-old Kamchatka flounder females, with no change in results. The females of both species attained a longer length at age than did the males. For example, at age 9, female Kamchatka flounder were estimated to be 5 cm longer than male Kamchatka flounder and at age 9, female arrowtooth flounder were estimated to be 13 cm longer than the males.

The growth curves of arrowtooth flounder females and Kamchatka flounder females were significantly different (F=25.0, P<0.001), indicating that female arrowtooth flounder attain a greater length at age than Kamchatka flounder females (Fig. 7). For example, at age 9, female arrowtooth flounder were 7 cm longer than female Kamchatka flounder. The growth curve parameters of arrowtooth flounder males and Kamchatka flounder males were not significantly different (P>0.05).

Table 2

Percentage of females in the populations of the major flatfish species surveyed in the eastern Bering Sea in 1991.

Species	Percent female	Fish sampled	Trawl hauls
Arrowtooth flounder (*Atheresthes stomias*)	68.6	14,437	142
Kamchatka flounder (*A. evermanni*)	55.9	3,443	71
Yellowfin sole (*Pleuronectes asper*)	54.2	33,387	289
Flathead sole and Bering flounder (*Hippoglossoides* spp.)	51.7	25,872	342
Rock sole (*P. bilineatus*)	48.9	29,677	281
Alaska plaice (*P. quadrituberculatus*)	42.3	10,283	205

Discussion

In areas where the two species are found together, Kamchatka flounder occupy deeper water than arrowtooth flounder. The percent of arrowtooth flounder in the total *Atheresthes* catch was negatively related to depth. Even though the biomass of Kamchatka flounder was much smaller than that of arrowtooth flounder in the study area, their catch rates were actually higher than those for arrowtooth flounder in deep waters. For fish of similar size, Kamchatka flounder occurred at greater depths than arrowtooth flounder. The rare catches of small-size

Table 3

Parameters of the von Bertalanffy growth curves for arrowtooth, *Atheresthes stomias*, and Kamchatka, *A. evermanni*, flounder by sex, based on age readings from otoliths and length data from the 1991 AFSC bottom trawl survey of the eastern Bering Sea slope.

Group	Number of age readings	Age range (yr)	Length range (cm)	Parameters L_∞	K	t_0	Forced parameters
Arrowtooth flounder							
Male	53	3–9	33–51	57.932	0.172	–2.172	none
Female	134	4–12	36–75	85.000	0.161	0.812	L_∞
Kamchatka flounder							
Male	57	3–10	33–55	62.344	0.157	–1.411	none
Female	63	4–33	38–91	93.880	0.085	–1.519	none

and infrequent catches of medium-size Kamchatka flounder in the study area made it impossible to compare the catch rates of both species across the shallow end of the depth distribution. Whether this situation was a sampling artifact, year-class artifact, or an accurate representation of the Kamchatka flounder depth distribution, it increased the Kamchatka flounder's apparent preference for greater depths.

Comparison of the water temperature distribution of both species may also have been confounded by the limited catches of small- and medium-size Kamchatka flounder in the study area. For arrowtooth flounder, the more common catches on the Bering Sea shelf of small-size (warmest bottom temperature) and medium-size (coldest bottom temperature) arrowtooth flounder broadened the temperature range for the species. Thus the few trawl catches of small- and medium-size Kamchatka flounder on the Bering Sea shelf might have narrowed the temperature distribution of Kamchatka flounder.

The peculiar relationship of bottom-water temperature with mean fish size (i.e. medium-size fish at moderate depths but coldest water) may be explained by the unusual bottom-water temperature distribution of the eastern Bering Sea. The coldest bottom temperatures in the eastern Bering Sea in 1991 were on the mid-shelf area (Goddard and Zimmermann[3]), as is typically the case (Kinder and Schumacher, 1981). These mid-shelf waters are a cold-water remnant of the previous winter's ice cover (Takenouti and Ohtani, 1974). In contrast to the coastal waters, the mid-shelf waters do not increase in temperature with the spring and summer increase in solar radiation (Kinder and Schumacher, 1981). The depths of the mid-shelf waters are too great to permit wind- or tidal-driven mixing, and a thermocline develops that increases the stability of the water column. No strong currents bring warmer waters from the Gulf of Alaska into this area, and the relatively warm slope waters, which are not as affected by the winter ice cover, are fortified with warm waters from the deep (Schumacher[6]).

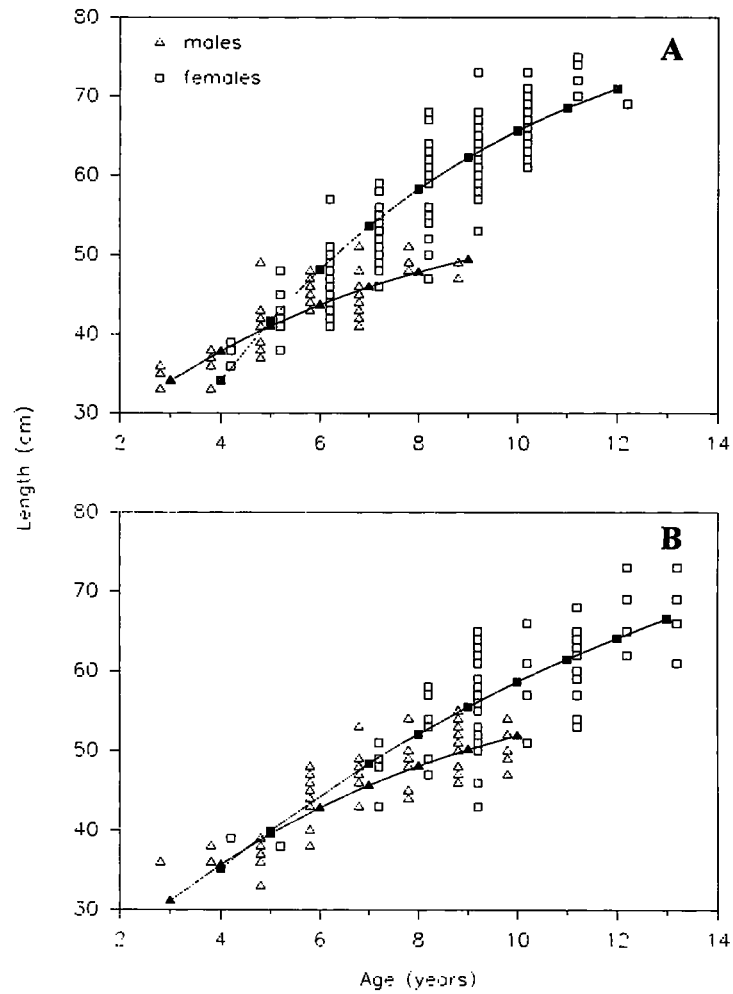

Figure 7

Individual length-at-age data (empty symbols) and von Bertalanffy estimates of mean length at age (filled symbols) for arrowtooth flounder, *Atheresthes stomias* (**A**), and Kamchatka flounder, *A. evermanni* (**B**).

The temperature data collected off the Aleutian Islands show a more typical relationship with depth; shallow bottom temperatures were warm and bottom temperature decreased, approaching 4°C, as depth increased. Most of the temperature data collected, however, came from the eastern Bering Sea shelf and slope.

Studies have shown that the geographic ranges of *Atheresthes* species do overlap in the north Pacific Ocean (Shuntov, 1965; Wilimovsky et al., 1967; Allen and Smith, 1988). The extent of the overlap and the southeastern boundary of the Kamchatka flounder distribution, however, had not been clearly defined. Kamchatka flounder has been reported to be the

[6] Schumacher, J. D. 1994. Pacific Marine Environmental Laboratory, 7600 Sand Point Way NE, Seattle, WA 98115. Personal commun.

dominant species on the northwestern side of the Pacific Ocean, and arrowtooth flounder the dominant species on the northeastern side of the Pacific Ocean (Wilimovsky et al., 1967).

Kamchatka flounder occurs along the eastern shores of Japan from as far south as 38°N (Moiseev, 1953), in the Sea of Japan (Allen and Smith, 1988), along the eastern and western shores of the Kamchatka Peninsula, and along the eastern coast of Siberia north to Cape Navarin (Shuntov, 1965). Shuntov (1965) also reported that Kamchatka flounder occurs in the eastern Bering Sea, Commander Islands region, throughout the Aleutian Islands, and into the Gulf of Alaska as far east as Shelikof Strait.

On the western side of the Pacific Ocean, arrowtooth flounder occurs along the eastern shore of the Kamchatka Peninsula north to Cape Navarin (Shuntov, 1965). It occurs in the Commander Islands region (Shuntov, 1965), the eastern Bering Sea, throughout waters off the Aleutian Islands chain, in the Gulf of Alaska, and down the West Coast of North America to San Simeon, California, 40°N (Allen and Smith, 1988).

The geographic distribution and overlap of *Atheresthes* species in Alaskan waters were more clearly defined than had been previously reported (Shuntov, 1965; Wilimovsky et al., 1967; Allen and Smith, 1988). The arrowtooth flounder population was less abundant in the Aleutian Islands than in the southern Bering Sea area. The absence of arrowtooth flounder from the northwest tip of the eastern Bering Sea shelf perhaps also indicates the decreasing abundance of arrowtooth flounder from east to west in the eastern Bering Sea. The waters around the easternmost Aleutian Islands marked the general southeastern border of the Kamchatka flounder population. Our bottom trawl survey data show a smaller geographic range for Kamchatka flounder than that reported by Shuntov (1965). Data collected by the Fishery Observer Program of the AFSC were supported by the findings of Shuntov (1965), indicating that the Kamchatka flounder distribution also extends into the Gulf of Alaska, but only in limited numbers and in deep water. Future bottom trawl hauls in deeper waters (>500 m) during AFSC Gulf of Alaska surveys may extend the Kamchatka flounder's known range farther east.

Although large-size Kamchatka flounder were reported from deep waters in the Gulf of Alaska (Conrad[5]), the lack of any Kamchatka flounder in our Gulf of Alaska survey may indicate that this is not a self-sustaining population. These large-size Kamchatka flounder may have ventured into the Gulf of Alaska from the Aleutian Islands or eastern Bering Sea areas. The westerly flowing currents in the Gulf of Alaska do not foster retention of larvae in this area (Schumacher[6]), which might make it more difficult for larval Kamchatka flounder spawned in the Gulf to remain there.

The observed high percentage of females in the arrowtooth flounder population clearly distinguishes this species from Kamchatka flounder. The overabundance of females in the arrowtooth flounder population is an unusual occurrence among the major flatfish species in the eastern Bering Sea. The possibility that the sampling gear undersampled males, either by not catching them or by not retaining them as well as it did females, remains a possible explanation that was not examined. Many other possible sources of error were explored to determine whether the number of arrowtooth flounder females was overestimated. There was no indication that areas high in percentages of males were excluded from the trawl surveys. The possibility that fishery biologists conducting the surveys might have consistently made incorrect sex determinations seems highly unlikely because females are determined by the presence of ovarian tissue, whereas males are often designated males simply because no gonadal tissues were found. Any error made because of improper sex determination should have overestimated the number of males in the population. An explanation for the overabundance of female arrowtooth flounder in our observations may come from the length-at-age results.

The difference in length at age between male and female arrowtooth flounders was significant and indicated that for fish over 5 years old, female arrowtooth flounder were larger than male arrowtooth flounder. Our results were supported by earlier AFSC surveys for the eastern Bering Sea (Smith and Bakkala, 1982; Bakkala et al., 1985; Sample et al., 1985; Walters et al., 1988) and Aleutian Islands (Ronholt et al., 1994). These studies show that growth curves for arrowtooth flounder males and females diverge as early as three to five years of age and that females are larger than males. It is doubtful, however, that in past surveys arrowtooth and Kamchatka flounder were regularly separated for otolith collections, because they were not consistently separated for other purposes. Our results differ from the length-at-age data collected from arrowtooth flounder in British Columbian waters, which showed no separation in growth curves between sexes until age 9 (Kabata and Forrester, 1974).

Our findings that female arrowtooth flounder attain a greater size at age than do male arrowtooth founder was supported by sexual maturity studies. Fifty-percent maturity occurs at a larger size in female arrowtooth flounder than in males off both the Washington (37 cm vs. 28 cm, respectively, Rickey, 1995) and Oregon coasts (44 cm vs. 29 cm, Hosie and

Barss[7]). Growth rates of males may decline as they become mature, whereas females, to support the greater reproductive burden of egg production, continue their rapid growth rate and become mature at a larger size (see Roff, 1982).

Difference in size gives arrowtooth flounder females a survival advantage over males because larger fish are better able to avoid predation. Larger fish are also better able to capture and consume larger items of prey, such as walleye pollock, *Theragra chalcogramma*, which are an important part of their diet (Yang and Livingston, 1986). Perhaps this size difference accounts for the high percentage of females in the arrowtooth flounder population.

Although the possibility of cannibalism influencing the sex ratio of arrowtooth flounder cannot be ignored, it is unlikely because cannibalism is uncommon in arrowtooth flounder (Kabata and Forrester, 1974; Yang and Livingston, 1986).

Although the von Bertalanffy growth curve parameters tested as significantly different between male and female Kamchatka flounder, the difference in length at age between the sexes was less than the difference for arrowtooth flounder and perhaps did not afford a significantly higher survival rate for the females. There were no length-at-age results for Kamchatka flounder previously reported in the literature.

The unusually high percentage of females in the arrowtooth flounder population, the greater length at age of female arrowtooth flounder over female Kamchatka flounder, the greater depth preference of Kamchatka flounder over arrowtooth flounder, and the geographic boundaries of the two species defined in the study area all indicate significant interspecies differences. We therefore recommend that arrowtooth and Kamchatka flounder be treated as separate species in resource assessment surveys and for management purposes. Additional information should be gathered on possible differences in mortality of the male and female arrowtooth flounder, the reason for the greater depth preference of Kamchatka flounder, and whether or not the Kamchatka flounder population in the study area is successfully reproducing, or whether it is migrating into the area from the west.

Acknowledgments

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Size-dependent predation risk in larval fishes: mechanistic inferences and levels of analysis

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In any ecological study, the level of observation, as well as the aggregation and analysis of data, affects the inferences that can be drawn. In fisheries science, many studies, covering a wide range of levels of analysis, have examined size-dependent processes, particularly predation, as a primary source of mortality for larval fish (reviewed by Bailey and Houde, 1989; Bertram and Leggett, 1994; Leggett and Deblois, 1994). A general result from those studies is that mortality rate declines as body size increases both across (e.g. Peterson and Wroblewski, 1984) and within species (e.g. van der Veer and Bergman, 1987). However, the use of that general result to forecast survival probabilities at lower levels of aggregation and analysis (e.g. for individual larvae) could lead to erroneous predictions (Pepin and Miller, 1993). Several recent studies have questioned the validity of the generality that increasing larval size reduces predation risk when analyses were conducted at the level of the individual and when the effects of prey size on vulnerability to predation were examined independently of age effects (Litvak and Leggett, 1992; Pepin et al., 1992; Bertram and Leggett, 1994).

The results of Pepin et al. (1992) show that the effect of larval size inversely affects vulnerability to predation, depending on the level at which the information is aggregated and analyzed. Contrasting patterns of larval mortality caused by predation within and between mesocosmic (2.7 m^3 circular tanks) trials were observed in the predation of yolk-sac and first-feeding capelin larvae, *Mallotus villosus*, by threespine sticklebacks, *Gasterosteus aculeatus* (Pepin et al., 1992). Prey age ranged from 1 to 5 d (median post-emergence) and prey size ranged from 5 to 5.8 mm. In each experimental trial, single naive predators were offered a cohort of 500 similar-age prey for 24 h. Comparisons between experiments indicated that greater mean size and age of larvae in the mesocosm reduced mortality due to predation. However, within experiments, larger larvae suffered higher mortality than did smaller individuals of the same age (see also Litvak and Leggett, 1992). Resolving the discrepancy between these results is important because the conclusions differ depending upon the level of observation and analysis. Large size and age were beneficial to larval survival when mean values for each trial were compared over the full range of available prey sizes (i.e. between trial comparisons). Conversely, large size at age was detrimental to larval survival at a lower level of observation and analysis (i.e. within trials) when a reduced range of prey sizes was examined. Patterns and generalizations based on observations from higher levels of aggregation (e.g. cohorts, populations, species) and extended ranges of data, although conceptually appealing, may be misleading for gaining insights into the mechanistic processes that affect larval survival at the level of the individual, where selection acts (Pepin and Miller, 1993). Moreover, to achieve an understanding of the mechanisms that determine overall survival, information from several levels of observation must be integrated (Crowder et al., 1992; Pepin and Miller, 1993). In this study I use fundamental foraging theory to examine an underlying mechanism that could have produced both of the observed mortality patterns in Pepin et al.'s (1992) results at low and higher levels of analysis, within and between trials, respectively.

Pepin et al. (1992) argued that the within- versus between-trial differences occurred because predators actively selected larger larvae within trials ("because of greater encounter or attack probabilities due to greater activity or longer perception distance [i.e. the distance that larvae were visible to the predator] relative to smaller prey") but as the average size of prey increased between trials, the average predation rate decreased owing to greater avoidance capabilities of the larger, older larvae. In accordance with foraging theory (e.g. Stephens and Krebs, 1986), the predators in Pepin et al.'s (1992) study may also have actively selected larger larvae because of their higher caloric value and hence their profitability to a predator within trials (prey handling time was likely to be size-independent in the study system; energetic costs of attack were also assumed to be independent of prey size). Furthermore, the consistently high profitability

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of large larvae to a predator may have more than compensated for the fact that fewer larvae were captured as prey size increased, between trials.

I evaluated this proposition by estimating the total mass of prey that were consumed by predators in each of the 23 predation trials conducted by Pepin et al. (1992). I estimated the total number of prey ingested for each trial in two ways. First, as an estimate of the maximum number of prey ingested, I used the difference between the number of prey present at the beginning and end of each trial (Pepin, unpubl. data). Second, I calculated an estimate for the minimum number of prey ingested by using Equation 2 from Pepin et al. (1992). For each trial I estimated the total mass of prey consumed by multiplying the number of prey ingested by the mass of a capelin larva whose length was equal to the mean of prey lengths used in that trial. To calculate the mass of larvae of average length, I used a general allometric length-weight relationship for capelin (Pepin, 1995). The results demonstrate that the maximum total number of prey consumed per predator decreased significantly with increasing prey length between trials (Fig. 1A; F=22.1, df=1,21, P=0.0001, for the pooled data set). Moreover, the total maximum mass of prey consumed increased significantly with increasing prey length (Fig. 1B; F=52.8, df=1,21, P<< 0.001; see also Fig. 9 in Pepin et al., 1992). The latter result also held within all three categories of prey and predator length ratios.

It is worth noting that the group of triangles below the regression lines (Fig. 1, A and B) represent five trials from an experiment that employed the smallest predators (mean=38.4 mm vs. 50.6 mm for all 18 trials in other experiments; t=3.5, df=21, P=0.002) and the lowest temperatures (mean=11.6°C vs. 13.2°C for all other trials; t=2.6, df=21, P=0.016). It is likely that the low number of prey consumed during those trials (mean=393 vs. 474 for all other trials; t=7.9, df=21, P<<0.001) resulted from the small predator size and low temperature, because smaller predators consume fewer prey (Pepin et al., 1992) and activity and ingestion rates are generally reduced at low temperatures.

The minimum total number of prey consumed also decreased significantly with increasing prey length between trials (F=20.8, df=1,21, P=0.0002, for the pooled data set). The mass of prey consumed also increased with prey length within each prey and predator length category when the minimum number of prey consumed were used. When the results from each prey and predator length category were pooled, the relationship between prey consumption and prey length was not significant owing to the low prey consumption values for the five trials with anomalous temperatures and predator lengths (see above). There was a highly

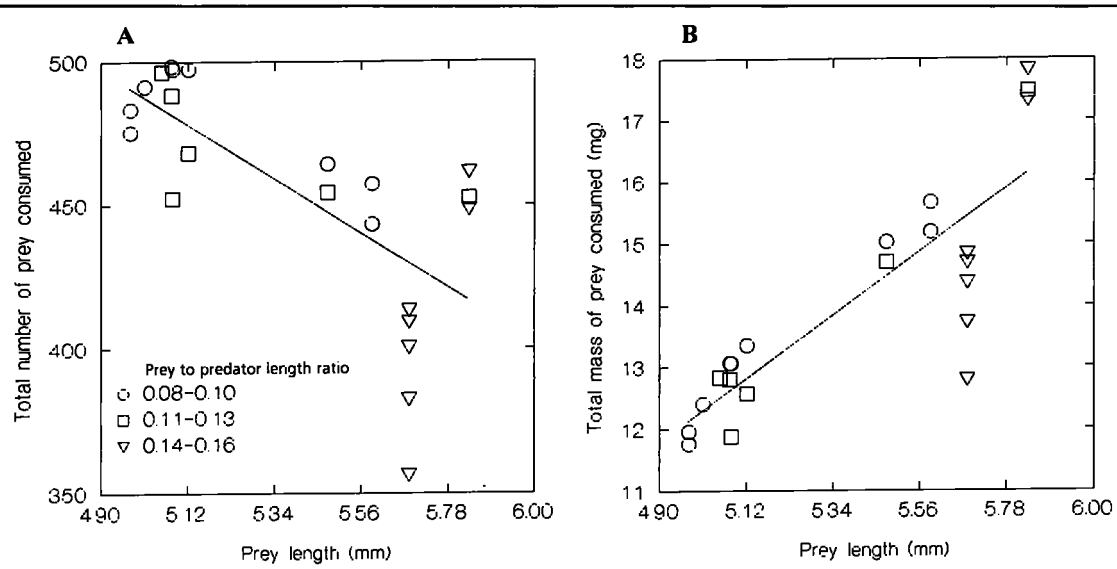

Figure 1

The total mass and number of larval capelin, *Mallotus villosus*, consumed by threespine stickleback, *Gasterosteus aculeatus*. Estimates of the maximum total number (**A**) (y=918–85.9x) and mass (**B**) y=–11.1+4.7x) of prey consumed by sticklebacks versus the mean length of capelin larvae from 23 predation trials conducted by Pepin et al. (1992). The categories of prey and predator length ratio were assigned arbitrarily (on the basis of unpubl. data from P. Pepin). Regression equations were based on the pooled data set.

significant positive relationship between the minimum mass of prey consumed and prey length when those five trials were excluded from the analysis (F=43.9, df=1,16, P<<0.001). Thus, both estimates of prey consumption indicate a positive relationship between prey length and total mass of prey consumed.

My analysis is consistent with the interpretation that predators actively select the largest, most profitable prey to maximize both the mass of prey consumed and the caloric gain from an attack, as predicted by foraging theory. Because of this pattern of prey selection, predators consumed significantly more biomass as prey size increased, between trials, despite a decline in average predation mortality. More generally, the result confirms that larger larvae may be subject to higher rates of predation notwithstanding that their overall vulnerability to predation is inversely related to length. A future challenge will be to incorporate this result from several levels of analysis into longitudinal studies that examine the effects of mortality caused by predation on the size structure of cohorts of growing prey.

The above arguments on prey profitability are consistent with the interpretation of Pepin et al. (1992) that predators actively select larger prey because of greater encounter or attack probabilities that result from greater activity or a longer perception distance (i.e. the distance that a larva is visible to a predator) relative to smaller prey. Indeed predators may have selected larger prey because of the combined effects of higher profitabilities and encounter rates for larger prey. It is noteworthy, however, that prey encounter rates and profitability may not always increase in unison with increasing prey size because encounter rates will be dependent on prey behavior and the perception capabilities and size of the predator. Separating the general effects of prey encounter rate and profitability on predator size-selectivity (see also Juanes and Conover, 1994) will require mechanistic studies and modelling efforts that address prey behavior, profitability of the prey to a predator, as well as encounter, attack, and capture rates, all of which will require corresponding information on predator foraging technique and perception capabilities over a broad range of prey sizes and prey-to-predator size ratios.

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Stomach contents of juvenile cobia, *Rachycentron canadum*, from the northern Gulf of Mexico

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The cobia, *Rachycentron canadum*, is a monotypic member of the family Rachycentridae. It is a migratory pelagic fish that occurs worldwide in tropical, subtropical, and warm temperate seas, except in the central and eastern Pacific Ocean (Shaffer and Nakamura, 1989). In the western Atlantic, the cobia occurs from Massachusetts and Bermuda to Argentina (Briggs, 1958) but is most common in the Gulf of Mexico (Migdalski and Fichter, 1983), ranging from Key West, Florida, along the Gulf coast to Campeche, Mexico (Dawson, 1971).

Some individual cobia are seasonal migrants, moving from wintering grounds near the Florida Keys into the Gulf of Mexico during spring, generally entering northern Gulf waters from April through May and returning to the wintering grounds during late fall and early winter (Franks et al., 1991; Biesiot et al., 1994). The timing of these migrations may relate to the availability of important prey species (Darracott, 1977).

A few observations on the food habits of adult *R. canadum* from the Gulf (Gulf of Mexico) have been reported. Knapp (1951) listed the stomach contents of 24 cobia taken near Port Aransas, Texas, and Miles (1949) briefly discussed the foods of 11 cobia from Aransas Bay, Texas. Reid (1954) mentioned the stomach contents of a single adult taken in the vicinity of Cedar Key, Florida, and Boschung (1957) remarked on the prey in four cobia collected off coastal Alabama. Christmas et al.[1] reported the prey of 11 adult cobia taken off Mississippi. A brief review of reported foods of cobia was presented by Shaffer and Nakamura (1989). Stomach contents of 287 cobia caught by hook and line in the northern Gulf of Mexico recreational fishery, mostly adults taken off Mississippi, were reported by Meyer and Franks (1996). None of these studies identified which prey, if any, were specifically consumed by juvenile cobia, rather, these observations were reported either for adults, for a size range comprising both juveniles and adults, or for cobia "in general." This paper represents the first study describing specifically the diet of juvenile *R. canadum*.

Knowledge of the feeding habits of juvenile cobia is necessary for understanding the role of diet in the recruitment processes of this economically important species and is a necessary prerequisite for management of this resource. The specific objective of this study was to analyze quantitatively the diet of juvenile cobia from the northern Gulf of Mexico.

Methods

Juvenile cobia were collected by trawl during fisheries resource surveys conducted in the northern Gulf of Mexico by the National Marine Fisheries Service (NMFS), Southeast Fisheries Science Center, Pascagoula, Mississippi. Fish were collected in July (n=7) and September (n=40) 1993 and in March (n=2) 1994 north of lat. 28°32'N and between long. 85°40'W and long. 93°55.4'W (Fig. 1). Most of the specimens (71%) were collected during September 1993 off Mississippi and Alabama. Bottom water depth ranged from 9 to 6 m.

Collection gear included a 28-m high-profile fish trawl with 0.6-cm codend mesh; a 19-m "western jib" shrimp trawl with 4-cm codend mesh; a 17-m "mongoose" shrimp trawl with 4-cm codend mesh; and

[1] Christmas, J. Y., A. Perry, and R. S. Waller. 1974. Investigations of coastal pelagic fishes. Gulf Coast Research Laboratory, P.O. Box 7000, Ocean Springs, MS 39566-7000. Completion Rep. to the U.S, Bur. Comm. Fish, Proj. 2-128-R, 105 p.

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Fishery Bulletin 94:374–380 (1996).

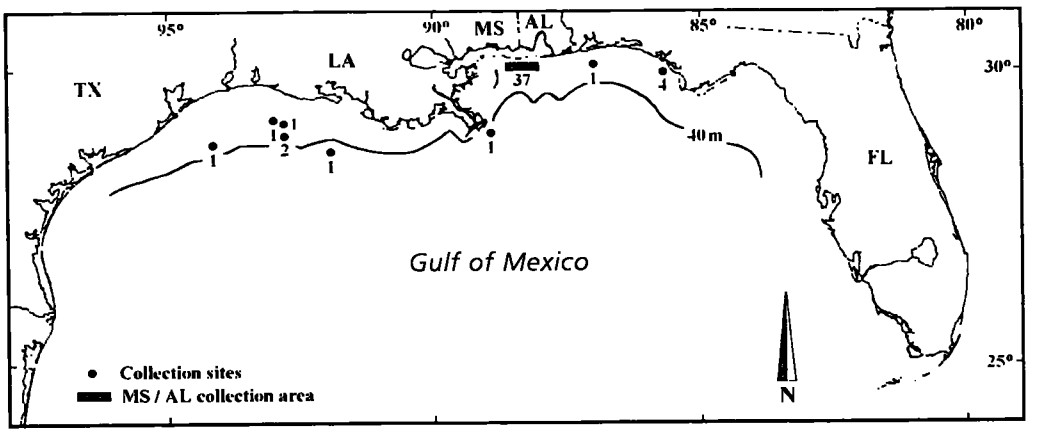

Figure 1

Collection sites and sample sizes of juvenile cobia, *Rachycentron canadum*, from the northern Gulf of Mexico. The MS/AL collection area comprised 17 collection sites.

a 13-m otter trawl with 4-cm codend mesh. Towing speed was 2.5 knots, and the duration of tows ranged from 0.25 to 1 h. Time and location were recorded for each tow. Juveniles were collected in 25 net hauls (18 by day; 7 at night). Whole specimens were frozen aboard the research vessel, generally <0.5 h following capture. In our laboratory, specimens were thawed, measured to the nearest mm fork length (FL), and weighed to the nearest 0.1 g total weight (TW). Stomachs were removed, opened, and designated either as containing food or as empty. Stomach contents were fixed in 10% buffered formalin and then placed in 50% ethanol. A cursory examination revealed that intestinal contents were too digested to be identified; thus, intestines were separated from stomachs at their confluence and discarded.

Stomach contents were placed onto a 0.840-mm mesh screen sieve and gently washed with fresh water. Prey were identified to the lowest taxa possible, counted, weighed (blotted wet weight) to the nearest 0.1 g, and measured volumetrically to the nearest 0.1 mL by water displacement in a graduated cylinder. Prey too digested for unequivocal identification were assigned to one of the appropriate principal prey categories (fish, crustaceans, or cephalopods) as "remains" and included in the determination of the contributions of those principal categories to the diet.

Stomach-content data were pooled for all stomachs and analyzed for percent numeric abundance (*%N*), percent of total volume (*%V*), and percent frequency of occurrence (*%F*) of prey items to describe quantitatively the diet, where *%N* = (number of individuals of one prey taxon divided by total number of all prey individuals) × 100; *%V* = (volume of one prey taxon divided by total volume of all prey) × 100; and *%F* = (number of stomachs containing prey of one taxon divided by total number of stomachs that contained any prey items) × 100. These methods have been reviewed by Windell (1971) and Hyslop (1980). These values were used to calculate an index of relative importance (*IRI*) (Pinkas, 1971), where the importance of an item is directly related to the size of the value:

$$IRI = (\%N + \%V) \times \%F.$$

Percent *IRI* (*%IRI*) was also calculated and consisted of the *IRI* value of each prey taxon divided by the sum of the *IRI* values (Eggleston and Bochenek, 1989). Empty stomachs were excluded from the above computations.

A small number of other items found in stomachs (e.g. mollusc shells and both larval and postlarval crustaceans and parasitic worms) were considered miscellaneous or nonfood items probably ingested incidentally in normal feeding. These were not used in calculating percentages or indices describing relationships of food items in the diet.

A stomach fullness index was calculated by dividing the total prey weight of each cobia by its total body weight × 100 (Sullivan and Gillman, 1993; Rooker, 1995). Stomach fullness was tested between daytime and nighttime captures, and to further examine diel feeding periodicity based on stomach fullness, cobia were grouped by time of capture into 6, 4-h periods: 0000–0400 (n=2); 0400–0800 (including dawn) (n=5); 0800–1200 (n=15); 1200–1600 (n=10); 1600–2000 (including dusk) (n=8); and 2000–2400 (n=9). A one-way analysis of variance (ANOVA) was used to test for differences in mean fullness between time intervals.

Chi-square (χ^2) 2 × 2 contingency table analyses and Fisher's exact test were used to test for differences in frequency occurrence of principle prey cat-

egories (fish, crustaceans, and cephalopods) between two size (FL) groups of juvenile cobia, small (236–338 mm) and large (340–440 mm), that represented all juveniles with food in their stomachs. The χ^2 test and Fisher's exact test were used to identify significant differences in frequency occurrence of principle prey categories between two geographic areas of juvenile collection (east of long. 89°W; west of long. 89°W), essentially described as east and west of the Mississippi River delta. The diet was also examined for seasonal differences in the occurrence of principal prey.

Results

Stomach contents of 49 juvenile *R. canadum* ranging from 236 to 440 mm FL (mean 335 mm) and from 0.08 to 0.81 kg TW (mean 0.34 kg) were examined. Thirty-nine of the 49 (80%) stomachs examined contained prey. The diet comprised three principal categories: fish, crustaceans, and cephalopods (Table 1).

Fishes occurred in 31 (79.5%*F*) of the stomachs containing food and represented 40.9% of the total number of prey and 37.7% of the total volume of prey (Fig. 2). The fish category dominated the *%IRI* (60.0%) (Fig. 2). Fish prey were represented by nine species (Table 1). Other fishes, owing to various states of digestion, could be identified only to genus (*Anchoa* sp. and *Symphurus* sp.) or family (Serranidae).

Anchovies were by far the predominant fish prey items, accounting for 19.7%*N* and 18.4%*V* of all items in the diet (Table 1). The striped anchovy, *Anchoa hepsetus*, was the dominant species by %*V* (9.2), *IRI* (163.8), and *%IRI* (4.9). The bay anchovy, *Anchoa mitchilli*, exhibited the highest numeric percentage (8.4) among fish in the diet; however, all specimens of *A. mitchilli* occurred in one stomach. The dominance of anchovies would be even greater if one considered that unidentifiable fish remains (15.1%*N*, 6.9%*V*, and 74.4%*F*) were primarily anchovies.

Crustaceans ranked first in importance numerically (42.7%*N*) and second by volume (37.4%*V*) and occurred in 59.0% of the stomachs (Fig. 2). Decapods were the most common crustaceans encountered (Table 1). The roughback shrimp, *Trachypenaeus similis*, was the dominant food item in the diet on the basis of %*N* (19.2), but all of these specimens occurred in only two stomachs. Other decapod species were brown rock shrimp, *Sicyonia brevirostris*, lesser rock shrimp, *Sicyonia dorsalis*, and iridescent swimming crab, *Portunus gibbesii*. Other decapods were identifiable only to Portunidae, Xanthidae, or Brachyura. *Sicyonia brevirostris* and *P. gibbesii* contributed 9.1%*V* and 5.9%*V* to the total diet, respectively (Table 1). Decapod remains (2.2%*V*) were categorized as being either those of shrimp (11.8%*N*, 33.3%*F*) or crab (0.8%*N*). The mantis shrimp, *Squilla empusa* (Stomatopoda), contributed 6.4%*V* but only 2.1%*N* to the diet.

Cephalopods were present in 17.9% of the stomachs and comprised 16.3%*N* and 24.9%*V* of prey organisms (Fig. 2). This group was represented by two species, the slender inshore squid *Loligo plei*, and the longfin inshore squid, *Loligo pealei*. Overall, *Loligo plei* dominated the diet among identifiable prey (17.0%*V*, 15.4%*F*, 494.3 *IRI* and 14.9% *IRI*) and was the second most important food item based on %*N* (15.1) (Table 1). *Loligo pealei* was the fifth ranking food item by volume, contributing 7.7%.

The proportion of empty stomachs was significantly greater for juveniles collected during the night (40%) than during the day (12%) (χ^2=3.518, df=1, P<0.05). Mean stomach fullness was found to vary significantly (with 95% confidence) between daytime (3.13) and nocturnal (0.92) collections (ANOVA, df=1, P<0.05) (Fig. 3). When further measured for specific time intervals of capture, mean fullness values were 0.08 (0001–0400), 2.00 (0400–0800), 3.29 (0800–1200), 2.45 (1200–1600), 3.70 (1600–2000), and 0.73 (2000–2400)

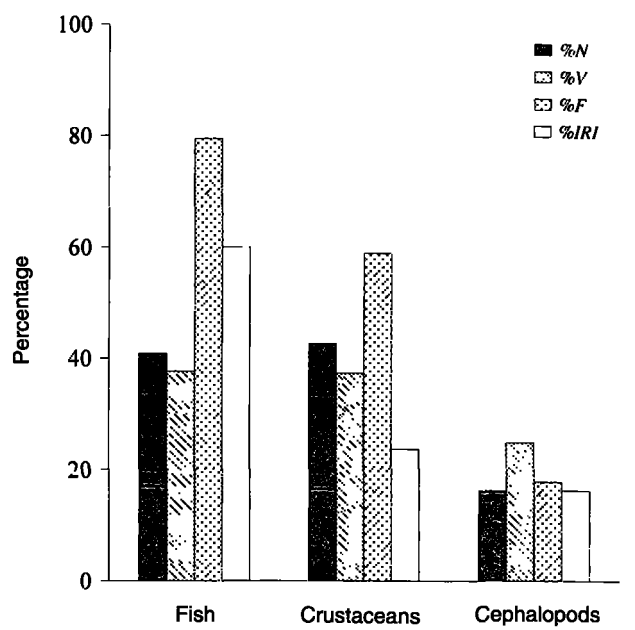

Figure 2

Percent numerical abundance (%*N*), percent total volume (%*V*), percent frequency of occurrence (%*F*), and percent index of relative importance (%*IRI*) for primary prey categories in the diet of juvenile *Rachycentron canadum* from the northern Gulf of Mexico.

(Fig. 4); however, the difference between these means was not statistically significant (ANOVA, df=5, $P>0.05$).

Comparison of the percent occurrence of principal prey categories between the diets of two groups of juvenile cobia based on length (group 1=236–338 mm FL; group 2=340–440 mm FL, Fig. 5) showed that the smaller juveniles fed primarily on crustaceans and fish, whereas fish were the primary foods of group 2. Crustaceans were found in 21 of 25 (84%) stomachs of fish in group 1 but in only 5 of 14 (36%) stomachs of fish in group 2. This indicated a highly significant (χ^2=8.469, df=1, $P<0.05$) difference in diet and was directly related to the greater frequency occurrence of shrimp (including shrimp remains) in the diet of group-1 fish. Fish were important prey for both groups of juveniles (Fig. 5), and although we encountered fish more frequently in the stomachs of group-2 fish, fish occurrence between the two

Table 1

Prey items occurring in the stomachs of 39 juvenile cobia, *Rachycentron canadum*, from the northern Gulf of Mexico, 1993–94. % Frequency of occurrence is based on stomachs containing food (n=39). Unid = unidentified.

Prey	Number of individual prey items	% Number	Volume (mL)	% Volume	% Freqnency of occurrence	Index of relative importance (IRI)	% IRI
Class Osteichthyes							
Anchoa hepsetus	16	6.7	36.0	9.2	10.3	163.8	4.9
Anchoa mitchilli	20	8.4	29.0	7.4	2.6	41.1	1.2
Anchoa sp.	11	4.6	7.0	1.8	12.8	81.9	2.5
Saurida brasiliensis	2	0.8	7.0	1.8	2.6	6.8	0.2
Prionotus rubio	1	0.4	8.5	2.2	2.6	6.8	0.2
Centropristis philadelphica	2	0.8	5.0	1.3	2.6	5.5	0.2
Unid. serranid	3	1.3	0.5	0.1	2.6	3.6	0.1
Stenotomus caprinus	1	0.4	12.5	3.2	2.6	9.4	0.3
Abudefduf saxatilis	1	0.4	1.0	0.2	2.6	1.6	0.1
Trichiurus lepturus	1	0.4	1.0	0.2	2.6	1.6	0.1
Symphurus plagiusa	2	0.8	10.5	2.7	5.1	17.9	0.5
Symphurus sp.	2	0.8	3.0	0.7	5.1	7.7	0.2
Fish remains	36	15.1	27.0	6.9	74.4	1,636.8	49.5
Class Crustacea							
Stomatopoda							
Squilla empusa	5	2.1	25.0	6.4	7.7	65.5	2.0
Squilla chydaea	3	1.3	1.5	0.4	2.6	4.4	0.1
Squilla sp.	2	0.8	1.0	0.3	5.1	5.1	0.2
Decapoda							
Trachypenaeus similis	46	19.2	44.5	11.4	5.1	156.1	4.7
Sicyonia brevirostris	3	1.3	35.5	9.1	5.1	53.0	1.6
Sicyonia dorsalis	2	0.8	4.0	1.0	2.6	4.7	0.1
Portunus gibbesii	7	3.0	23.0	5.9	2.6	23.1	0.7
Unid. portunid	2	0.8	1.5	0.4	2.6	3.1	0.1
Unid. xanthid	1	0.4	0.5	0.1	2.6	1.3	0.1
Unid. brachyuran	1	0.4	1.0	0.2	2.6	1.6	0.1
Shrimp remains	28	11.8	8.5	2.1	33.3	462.9	13.9
Crab remains	2	0.8	0.5	0.1	5.1	4.6	0.1
Class Cephalopoda							
Loligo plei	36	15.1	66.5	17.0	15.4	494.3	14.9
Loligo pealei	2	0.8	30.0	7.7	5.1	43.4	1.3
Squid remains	1	0.4	1.0	0.2	2.6	1.6	0.1
Total	239		392.0			3,309.2	
Total stomachs analyzed	49						
No. (%) containing food	39 (80%)						
No. (%) empty	10 (20%)						

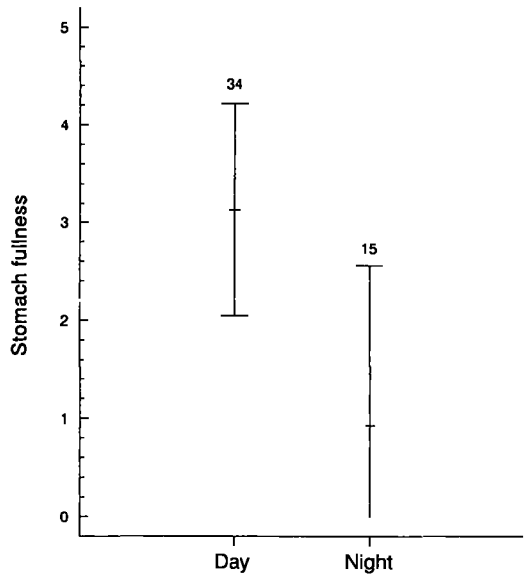

Figure 3

Comparison of day and night mean stomach fullness values (±95% CL) for juvenile *Rachycentron canadum* from the northern Gulf of Mexico. Number of fish sampled is given for each time period. Stomach fullness = prey weight/predator weight·100.

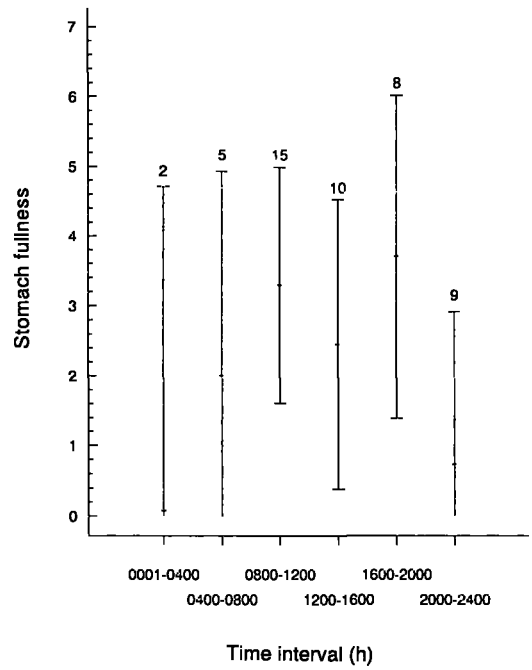

Figure 4

Diel feeding periodicity based on mean stomach fullness (±95% CL) for juvenile *Rachycentron canadum* from the northern Gulf of Mexico. Numbers over each series of values are sample sizes. Stomach fullness = prey weight/predator weight·100.

groups was not statistically different. The percent occurrence of cephalopods (squid) was low for both groups and differed insignificantly.

Chi-square contingency analysis suggested that geographic location did not significantly affect the diet, although we did observe that cephalopods (squid) were absent in the stomachs of all juveniles (n=6) collected west of the Mississippi River. The stomachs of the 2 cobia collected in March (spring) contained, collectively, the only specimens of sea bass (Serranidae, n=3) and xanthid crab (n=1) encountered in the study. The only other prey found in the stomachs of the juveniles collected in March were anchovies which, notably, were the predominant fish prey among the summer (July and September) cobia. A larger sample size is needed to assess accurately any geographic or seasonal variations in diet.

Discussion

We found that juvenile cobia captured by trawl in the northern Gulf of Mexico during fall 1993 and early spring 1994 were carnivorous and fed exclusively on small fish, crustaceans, and squid. Fish, crustaceans, and cephalopods also comprised the diet of adult cobia collected in the northcentral Gulf of Mexico (Meyer and Franks, 1996). On the basis of the frequency occurrence of prey in the diet of cobia caught near Aransas Bay, Texas, Knapp (1951) reported the predominance of fishes (83%), followed by stomatopods (58%), penaeid shrimps (46%), portunid crabs (42%), and squid (17%). Meyer and Franks (1996) reported that the percent frequency of occurrence and numeric percentage of crustaceans (79.1%F, 77.6%N) dominated that of fishes (58.5%F, 20.3%N) and cephalopods (13.2%F, 2.2%N). Our results showed that fish and crustaceans were present in the diet in approximately equal volumes, and, as reported by Miles (1949) and Christmas et al.)[1] for cobia taken off Texas and Mississippi, respectively, occurred in nearly equal numbers; however, we found that fish occurred in the diet with somewhat greater frequency than did crustaceans. Based on IRI calculations, the relative importance of fishes (IRI=1,984.5) as prey items was approximately three times that of shrimp (IRI=676.7) and three and one-half times that of squid (IRI=539.3).

In our study, anchovies were the dominant prey among the fish consumed and were major contributors to the diet. Unidentified fish remains, probably anchovies, occurred in almost 75% of the stomachs

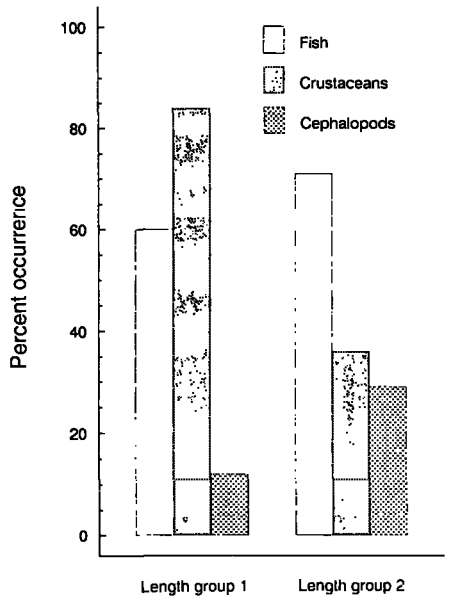

Figure 5

Principal prey of two length groups of juvenile *Rachycentron canadum*: Group 1 (236–338 mm FL, n=25) and Group 2 (340–440 mm FL, n=14), expressed as percent frequency of occurrence.

and were demonstrably important in the overall diet, exhibiting the highest *IRI* (1,636.8) and *%IRI* (49.5) of all food items. We observed that anchovies occurred in 36% of group-1 juveniles, whereas only 14% of the stomachs of group-2 juveniles contained anchovies. Because anchovies were rarely encountered (0.3%*F*) in the diet of northern Gulf adult cobia (Meyer and Franks, 1996), our findings may suggest a possible ontogenetic shift in feeding between juveniles and adults.

Trachypenaeus similis was a key component of the juvenile cobia diet on the basis of numeric and volumetric percentages, and our data show that shrimp, including shrimp remains, occurred in more than 41% of the stomachs, exceeded only by fish in percent frequency occurrence of prey. We found that crustaceans, primarily shrimp, occurred at a significantly higher frequency in the stomachs of smaller juveniles (84%) than in larger juveniles (36%). In contrast, Meyer and Franks (1996) reported that crustaceans, primarily portunid crabs, were the primary foods of adult cobia, based on percent occurrence, and essentially dominated the adult diet.

Loligo plei was one of the most important identified prey consumed by juvenile cobia. This species of squid is abundant in the northern Gulf of Mexico, particularly in shallower Gulf waters during spring and fall of the year (Hixon, 1980). Knapp (1951) reported the percent occurrence for *Loligo* in the diet of cobia as 17%. We report a similar percentage (18%) for *Loligo* and a percent occurrence of 21% for all loliginids combined. Meyer and Franks (1996) reported the percent occurrence of loliginids as ~12%.

Evaluation of diel feeding periodicity based on stomach fullness showed that juvenile cobia feed primarily during daylight. Although fullness peaked during the day, notably during late afternoon through dusk, there was no significant difference in fullness between daytime collection time intervals, including those containing dawn, noon, or dusk. Diana (1979) remarked that when fish with diel feeding cycles are collected at different intervals of time, some stomachs should be empty. We found that 20% of the stomachs we examined were empty.

Field observations in this study did not include reference to regurgitation of prey (i.e. everted stomachs or partially digested food in the mouth). Bowman (1986) stated that undetected regurgitation relative to fish food studies could produce severe underestimation of prey consumption, and he[2] reported that regurgitation is frequently observed in fishes trawled from depths exceeding 100 m. In our study only two cobia were collected at depths >40 m (i.e. 56 m and 66 m), and the stomach of each contained food. Incidentally, the juvenile from the 66-m site contained the second highest volume of food measured from all juvenile stomachs. Most cobia in our study (94%) were trawled from waters <30 m in depth. Even though somewhat limited by the small sample size of stomachs with prey, we were able to observe that increasing size (length) in juveniles appeared to influence an apparent ontogenetic shift from crustacean to piscine prey. Diet composition of juvenile cobia showed no marked changes in prey taxa between seasons or geographic locales.

Cobia are strong swimmers, quick enough to catch fish, squid, and decapod crustaceans. Personal observations, made by the senior author of cobia in culture systems and in natural habitats, reveal that *R. canadum* is a very aggressive feeder and quite capable of catching motile prey. Interestingly, prey species in this study demonstrate considerable diversity in the foraging behavior of juvenile cobia. Anchovies and squid are important components of the open-water nekton. Portunid crabs are both nektonic and benthic organisms. The shrimps and the Brachyuran crab, though capable of swimming, are

[2] Bowman, R. E. 1981. Examination of known and potential causes of variation in fish feeding studies. Northeast Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, 166 Water St., Woods Hole, MA 02543. Woods Hole Lab. Ref. Doc. 81-23, 29 p.

predominantly benthic inhabitants. Other prey, such as the blackwing searobin, *Prionotus rubio*, rock sea bass, *Centropristis philadelphica*, Atlantic cutlassfish, *Trichiurus lepturus*, longspine porgy, *Stenotomus caprinus*, and blackcheek tonguefish, *Symphurus plagiusa*, are essentially demersal. The variety of the diet in this study suggests that juvenile cobia often feed in the water column and possibly near the surface but primarily on or near the sea floor, exhibiting opportunistic feeding behavior comparable to that reported for adults (Meyer and Franks, 1996).

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Winter capture of a harbor porpoise in a pelagic drift net off North Carolina

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Harbor porpoise, *Phocoena phocoena*, of the Bay of Fundy and Gulf of Maine are among the best-studied small cetaceans owing to their coastal nature, frequent encounters with commercial fisheries, and subsequent accessibility to researchers. Unfortunately, our knowledge of these animals is limited primarily to observations made during summer. In autumn most porpoises leave these coastal waters, and their winter distribution is unknown. Various hypotheses have been constructed to explain the apparent disappearance of these animals during the winter months, including that of migration to offshore banks or to a southern coastal area (Gaskin, 1984). Information on the winter distribution of harbor porpoises in the northwest Atlantic is needed to understand better the effects of human activities on this population, which is subject to large removals in coastal gill nets during the spring, fall, and summer (Read et al., 1993).

Existing information on the winter distribution of porpoises comes from strandings and a small number of dedicated surveys. From January to May, porpoises strand on the coasts of Massachusetts to North Carolina (Polacheck et al., in press), but most of these individuals are very young. Stranded adults are seldom encountered. Winter surveys are hampered by poor sighting conditions and so far have failed to find any significant concentrations of porpoises (Palka[1]). In this report, we document the incidental capture of a harbor porpoise in a pelagic drift net off the coast off North Carolina, during winter. The record is significant for two reasons. First, it is the southernmost incidental capture of a harbor porpoise in the northwest Atlantic. Second, observations of the stomach contents of this specimen suggest that the ecology of this population may be quite different in winter than in summer months.

The porpoise was captured on 25 February 1993, 75 km east of Nag's Head, North Carolina, at 35°55'N and 74°47'W, in water 229–293 m deep. Surface water temperature was 12–13°C. The net was set the previous evening and hauled early (0630–0830 h) in the morning. The float line was approximately 10 m below the surface of the water, and the porpoise was entangled near the top of the net. The porpoise was examined at sea by an observer, who noted that the porpoise had been killed recently "because the insides were steaming." Also in the net were a basking shark (*Cetorhinus maximus*), 2 ocean sunfish (*Mola mola*), 2 swordfish (*Xiphias gladius*) and 3 bluefish (*Pomatomus saltatrix*).

The porpoise was male, with a standard length of 129 cm and mass of 28.5 kg. Measurements of girth and blubber thickness indicated that the animal was healthy and robust. The observer collected life history tissues (teeth, stomach, and reproductive tract) from the carcass and transported them to Woods Hole. The age of the porpoise was estimated in the laboratory from counts of dentinal growth layers in thin, decalcified, and stained sections of teeth. Two independent estimates of the age of the animal were made, both indicating that the porpoise was born between April and June 1991. One testis measured 5.3 × 2.4 × 1.2 cm and weighed 11 g without the epididymis. Histological examination of the testis and epididymis (Read and Hohn, 1995) revealed that the porpoise was sexually immature.

The forestomach contained the remains of many small mesoplagic prey not recorded from other harbor porpoises in the northwest Atlantic (Smith and Gaskin, 1974; Recchia and Read, 1989; Fontaine

[1] Palka, D. 1995. Preliminary cruise report of the spring distribution survey of harbor porpoises in the mid-Atlantic. Northeast Fisheries Science Center, Natl. Mar. Fish. Serv., Woods Hole MA 02543.

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et al., 1994). Approximately 99% of the contents (145 g wet weight) comprised partially digested remains of a single species of lanternfish, *Ceratoscopelus maderensis*. Other prey were represented only by hard parts, such as otoliths and squid beaks. Cephalopod prey remains included 7 upper and one lower beak of *Selenoteuthis scintillans* and 2 lower beaks of *Loligo pealei*. In total, 1,994 otoliths from at least 8 fish species were recovered from the stomach (Table 1). The state of digestion of stomach contents suggested that the porpoise had been feeding mostly at night and in the early morning on small-bodied fish and squid.

Of the prey items we identified from this porpoise, only silver hake, *Merluccius bilinearis*, are common prey of harbor porpoises in the Gulf of Maine. In summer, harbor porpoises in the Bay of Fundy and Gulf of Maine feed primarily on Atlantic herring, *Clupea harengus*, augmenting this with silver hake and other demersal species (Smith and Gaskin, 1974; Recchia and Read, 1989). Recent analyses of the stomach contents of harbor porpoises from the southern Gulf of Maine indicate a shift to smaller-bodied prey, such as pearlside, *Maurolicus weitzmani*, during autumn (Read et al.[2]).

These observations lead us to suggest that harbor porpoises in the northwest Atlantic are not tied to shallow nearshore waters during winter. The stomach contents of this specimen indicate that porpoises can forage successfully on midwater prey in deep water. Similar prey remains have been recovered from the stomach of a harbor porpoise taken in Irish waters (Rogan and Berrow[3]). Porpoises can dive to depths of more than 225 m (Westgate et al., 1995), although deep-feeding excursions would not be necessary if mesopelagic prey are taken at night when they migrate toward the surface. Adult *Ceratoscopelus maderensis*, for example, are found at depths of 33–250 m at night (Scott and Scott, 1988). If porpoises are able to use the shelf edge and slope waters during winter, a large expanse of suitable habitat is available from the Grand Banks to Cape Hatteras. This hypothesis is supported by the observations of Stenson and Reddin,[4] who reported the incidental capture of harbor porpoises in experimental drift nets set during winter and spring off the slope of the Grand Banks outside the 1,000 m isobath.

A largely offshore winter distribution of harbor porpoises would explain the paucity of sightings of this species outside the summer and fall months. The Gulf of Maine population of harbor porpoises is believed to number more than 45,000 individuals (Palka, in press); such a large number of animals would have been detected in coastal waters, even during winter. We hypothesize that the population disperses to the south during winter and is found in low densities over the shelf and slope waters, possibly mixing with porpoises that summer in the Gulf of St. Lawrence and Labrador. Molecular genetic techniques are being used to address the question of stock mixing during winter (Rosel[5]). The many young porpoises that strand along the mid-Atlantic coast during this season, most of which are less than a year old, may have been segregated from the remainder of the population after they were weaned from their mothers.

We recognize that it is difficult to test this hypothesis of offshore dispersion during winter. Traditional visual census techniques are ineffective with very low densities of harbor porpoises, particularly given the weather conditions that prevail during this season. Few fisheries that might capture harbor porpoises are operative during this season; pelagic driftnet fishing effort is currently limited to only a few

Table 1

Fish remains in the stomach of a harbor porpoise, *Phocoena phocoena*, killed in a pelagic drift net off Cape Hatteras on 25 February 1993.

Family	Species	Number of otoliths
Ophichthidae	*Myrophis punctatus*	2
Myctophidae	*Ceratoscopelus maderensis*	1,920
	Ceratoscopelus warmingii	1
	Myctophum affine	2
	Hygophum hygomii	4
Moridae	*Laemonema* sp. (?)	29
Merlucciidae	*Merluccius bilinearis*	4
Percomorph	Unidentified	32

[2] Read, A. J., J. E. Craddock, and D. Gannon. 1994. Life history of harbor porpoises and pilot whales taken in commercial fishing operations off the Northeast United States. Northeast Fisheries Science Center, Natl. Mar. Fish. Serv., Woods Hole, MA 02543. Final Contract Rep. 50-EANE-2-00082.

[3] Rogan, E., and S. D. Berrow. 1995. Aspects of the biology of the harbour porpoise, *Phocoena phocoena*, in Irish waters. Paper SC/47/SM40 presented at the 47th meeting of the Scientific Committee of the International Whaling Commission, Dublin, Ireland.

[4] Stenson, G. B., and D. G. Reddin. 1991. Incidental catches of small cetaceans in drift nets during salmon tagging experiments in the Northwest Atlantic. *In* Harbor porpoise in eastern North America: status and research needs; workshop held 5–8 May 1992 at Northeast Fish. Sci. Cent., Natl. Mar. Fish. Serv., Woods Hole, MA 02543.

[5] Rosel, P. 1995. Department of Zoology, Univ. New Hampshire, Durham NH 03824. Personal commun.

trips each winter. Instead, alternative techniques, such as tracking the movements of individual porpoises by satellite telemetry and the use of nontraditional census techniques (e.g. acoustic surveys), may reveal where these animals spend their winter months.

Acknowledgments

We thank the observer, Dianne Borgaard, for her careful observations and meticulous dissection at sea. Damon Gannon identified the cephalopod prey remains, Eugenia Bohlke identified the worm eel, Stephanie Fernandez prepared the tooth sections, and Aleta Hohn read the tooth and testis sections. This research was supported by Contract 50-EANE-2-00082 from the Northeast Fisheries Science Center, NMFS/NOAA.

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Erratum

Erratum: Fishery Bulletin 94(1), p. 173.

Lang, Kathy L., Frank P. Almeida, George R. Bolz, and Michael P. Fahay.

The use of otolith microstructure in resolving issues of first year growth and spawning seasonality of white hake, *Urophycis tenuis*, in the Gulf of Maine–Georges Bank region.

Correction: Text and Figure 4 (page 173) should read as follows:

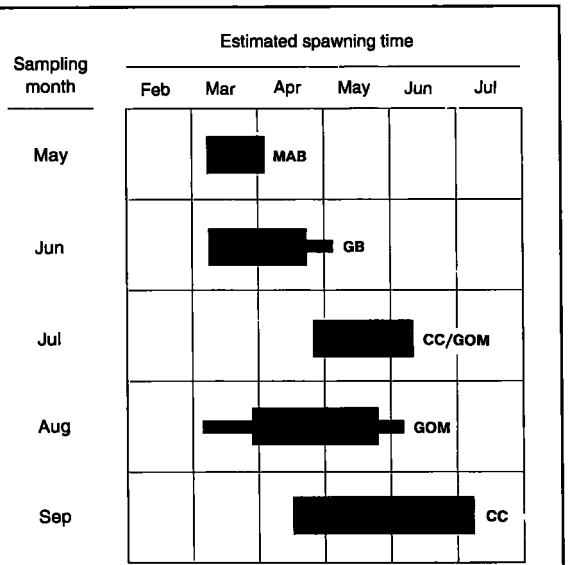

Figure 4

Back-calculated spawning times of juvenile white hake, *Urophycis tenuis*. Narrow bars indicate single observations. (MAB = mid-Atlantic Bight; GB = Georges Bank; CC = Cape Cod; and GOM = Gulf of Maine.)

Back-calculated spawning dates indicated that peak spawning occurred in the spring for fish collected from the mid-Atlantic Bight and Georges Bank (smaller, younger individuals), whereas peak spawning occurred in late spring/early summer (May–June) for fish collected along coastal New England (larger, older individuals) (Fig. 4).

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Age and growth of larval Atlantic herring, *Clupea harengus*: a comparative study

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Abstract.—Age and growth of 1,746 Atlantic herring, *Clupea harengus*, larvae collected in the Nantucket Shoals–Georges Bank region during the autumn–winter seasons of 1976–77, 1988–89, 1989–90, 1990–91, 1991–92, 1992–93, and 1993–94 were determined by enumerating the daily growth increments of their sagittal otoliths. Growth with respect to length for each of the years was best described by a Gompertz curve. Owing to severe weather events in November, January, and February of the 1976–77 season which disrupted the fishes' feeding regimen, growth was much slower (0.16 mm/d) than in more recent years. Lower daily food consumption was reflected in the rapid and continual decrease in otolith diameter during the autumn and winter of 1976. Growth for the other six years was strong, showed only minor interseasonal fluctuations (0.22–0.24 mm/d), and ranged intraseasonally from a high of just over 0.40 mm/d in October to a low of 0.04 mm/d in February.

A general model of larval herring growth was constructed with data from six recent field seasons. Inverse regressive methods were employed to generate a composite growth curve with confidence limits for predicting age (days) for a given standard length (mm) from hatching until the onset of metamorphosis.

Analysis of otolith growth revealed a dramatic increase in the growth rate of the lapillus at about 2.5 months (29.0 mm). It is suggested that this increase may coincide with, or immediately follow, the filling of the otic bullae with gas and may provide an easily obtainable marker for estimating the timing of this critical event. The importance of this phase in the life of larval herring is discussed, particularly with reference to the 1976–77 season.

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Based on the general assumption that fluctuations in the year-class strength of fish stocks are often determined by the rate of mortality during the first year of life (Hjort, 1914; May, 1974; Sissenwine, 1984), ichthyoplankton surveys have been conducted in the Nantucket Shoals–Georges Bank region for more than twenty years. From 1971 to 1979, research cruises designed to gain a better understanding of the early life history of Atlantic herring, *Clupea harengus*, and its relationship to recruitment and spawning stock size were undertaken monthly throughout the autumn and winter. These surveys were coordinated by the International Commission for the Northwest Atlantic Fisheries (ICNAF). The United States participation in the program was conducted concurrently as part of the MARMAP (Marine Resource Monitoring, Assessment, and Prediction) program of the Northeast Fisheries Science Center (Sherman, 1980). The MARMAP program was designed to measure long-term changes in the variability of larval fish abundance off the Northeast coast of the United States and is ongoing.

In the 1970's, intense fishing pressure by distant-water fleets led to a steady decrease in herring abundance on Georges Bank (Anthony and Waring, 1980). Estimates of initial larval abundance declined by 95% from 1975 to 1976 (Lough et al., 1985). Herring populations in the region began to increase once again in the late 1980's, and this trend has continued into the 1990's (Smith and Morse, 1993). An examination of the age and growth of herring larvae, based on the enumeration of daily otolith increments, was initiated in 1976 (Lough et al., 1982). To understand better the recovery of Atlantic herring in the Georges Bank area, microstructural analysis of larval otoliths was incorporated as a routine procedure for each season beginning in the autumn of 1988. To date, otoliths from more than 1,700 larvae have been aged.

The primary goal of this study was to construct an age-at-length curve and a key for field-caught Atlantic herring larvae that describe their growth from hatch until onset of metamorphosis. Additionally, we compared larval growth during the autumn and winter of 1976–77 with that during six recent seasons of 1988–89, 1989–90, 1990–91, 1991–92, 1992–93, and 1993–94. Otolith growth was analyzed to determine whether changes in the fishes' daily food rations, attributable to severe weather, could be de-

tected (Methot, 1983; Karakiri et al., 1989; Maillet and Checkley, 1991). Estimated standard lengths at hatching and metamorphosis were calculated and compared.

We also examined how developmental changes in the acoustico-lateralis system might relate to sensory thresholds that are critical in predator avoidance. Larval herring begin to demonstrate their characteristic C-shape startle response to environmental stimuli at a length of approximately 27–30 mm SL (Batty, 1989). This behavior does not become fully functional until the otic bullae are filled with air (22–30 mm), the air bladder and its connection to the acoustico-lateralis system are complete, and the larvae acquire the ability to swallow air at the surface (30–40 mm). Blaxter and Fuiman (1990) state that "filling the bullae with gas is probably the most significant event in the development of the anatomy of the sensory systems so far as predator evasion is concerned." They observed that successful attacks by predators were reduced from 77% to 32% following the filling of the bullae. Without a mechanism to adjust the volume of air with pressure changes, the fish are restricted in their ability to migrate vertically, limiting their ability to search for prey, to avoid predators, and to control transport (Hoss et al., 1989). Because it is virtually impossible to determine the condition of the otic bullae in field-collected larvae, the otolith to fish-length relationship was analyzed to determine its usefulness in estimating the timing of this critical developmental landmark.

Methods

Atlantic herring larvae were collected on 24 cruises at selected stations within a standard grid of sampling stations covering the western Gulf of Maine, Georges Bank, and Nantucket Shoals during the autumns and winters of 1976–77, 1988–89, 1989–90, 1990–91, 1991–92, 1992–93, and 1993–94 (Fig. 1; Table 1). The samples were collected with a continuous double-oblique haul by using a 61-cm bongo net sampler (0.505- and 0.333-mm mesh) deployed to a maximum depth of 200 m (100 m in 1976–77) or to within 5 m of the bottom in shallower areas. Further details of the sampling gear and protocols can be found in Posgay and Marak (1980) and Sibunka and Silverman (1984). Atlantic herring larvae were removed for otolith analysis immediately following the haul and preserved in 95% ethanol.

In the laboratory, larvae representative of the size-range collected were selected for analysis. Standard length was measured to the nearest 0.1 mm prior to removal of the otoliths. Differential shrinkage with respect to standard length was corrected by using Theilacker's (1980) algorithm, which was specified and discussed in Bolz and Lough (1983). The 2 sagittae and 2 lapilli were dissected from each fish and mounted whole on microscope slides with Permount. The growth increments on most of the otoliths were discernible without any further preparation.

The sagittae were viewed under a Zeiss compound microscope with transmitted light. The number of

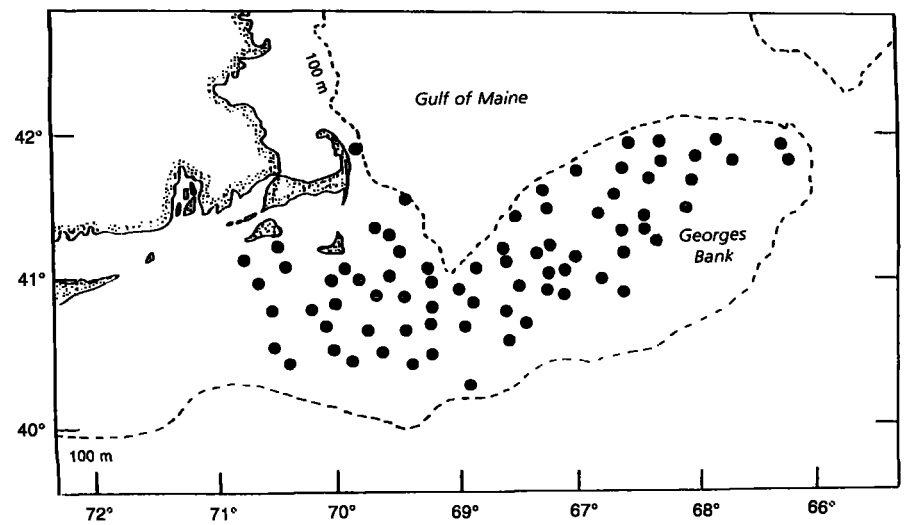

Figure 1

Station locations in the Gulf of Maine–Georges Bank region where larval herring were collected for otolith ageing.

growth increments were counted from the image projected by a drawing tube onto a Hewlett-Packard graphics tablet interfaced with an HP-87 microcomputer. All counts were made at a magnification of 800×. Three counts were made on one sagitta from each larva, and those otoliths with a repeatable increment count of >90% were used in the growth analysis. The other sagitta was counted once for comparison. Campana et al. (1987) found that detection of increments during the first 15–20 days posthatch are probably too fine to be resolved. In a previous study by Lough et al. (1982), it was found that the mean age of a 3-increment larva was approximately 22 d; consequently, a correction factor of 19 was added to the number of increments recorded in order to establish each larva's estimated age in days from hatch (Stevenson et al., 1989; Townsend et al., 1989). Measurements of the anterior–posterior diameters (otolith length) of the sagittae and the lapilli were made to the nearest micron.

Results

Larval herring growth

Otoliths were dissected, mounted, and analyzed for a combined total of 1,746 larval herring. Growth with

Table 1

Cruise information for larval Atlantic herring, *Clupea harengus*, specimens collected for otolith analysis during the autumn–winter field season in the Nantucket Shoals–Georges Bank region.

Vessel	Cruise no.	No. of sta.	Cruise sampling dates	No. of larvae	Mean length (mm)	Mean age (d)
1976–77						
Wieczno	76–03	1	14 Oct–03 Nov	18	16.9	31.1
Researcher	76–01	5	27 Nov–11 Dec	90	21.5	52.0
Mt. Mitchell	77–01	4	13 Feb–24 Feb	48	30.3	131.1
Anton Dohrn	77–01	1	15 Mar–21 Mar	34	31.8	148.4
1988–89						
Delaware II	88–12	4	31 Oct–11 Nov	43	14.4	27.3
Albatross IV	88–11	5	29 Nov–10 Dec	34	21.8	44.5
Delaware II	89–01	11	05 Jan–20 Jan	77	25.4	63.2
1989–90						
Delaware II	89–07	6	06 Nov–16 Nov	117	17.3	31.5
Delaware II	89–09	9	27 Nov–16 Dec	159	23.4	50.5
Delaware II	90–01	6	04 Jan–17 Jan	106	28.0	74.8
1990–91						
Delaware II	90–12	15	30 Oct–08 Nov	112	15.9	30.9
Delaware II	90–14	18	29 Nov–14 Dec	102	22.2	48.8
Delaware II	91–01	16	04 Jan–16 Jan	100	24.3	60.7
Delaware II	91–03	5	17 Feb–22 Feb	100	29.7	89.1
1991–92						
Delaware II	91–11	15	04 Nov–14 Nov	87	13.5	27.1
Delaware II	91–13	14	04 Dec–13 Dec	85	24.8	53.9
Delaware II	92–01	10	06 Jan–13 Jan	96	25.8	65.5
Delaware II	92–02	12	29 Jan–12 Feb	96	28.6	81.2
1992–93						
Delaware II	92–12	9	26 Oct–04 Nov	74	14.1	31.0
Delaware II	92–14	5	01 Dec–18 Dec	50	24.9	59.0
Delaware II	93–01	6	05 Jan–21 Jan	101	27.7	80.5
1993–94						
Delaware II	93–12	5	02 Nov–10 Nov	50	17.0	31.7
Delaware II	93–14	6	30 Nov–10 Dec	50	22.1	46.9
Delaware II	94–01	4	06 Jan–18 Jan	50	27.7	68.6

respect to length for each of the seven field seasons studied was best described by a Gompertz-type curve. The methodology for fitting the curve is discussed in Pennington (1979). Previous uses of the Gompertz growth curve are presented in Al-hossaini et al. (1989) and Jearld et al. (1993). The Gompertz curve not only permits the calculation of growth rate but also provides mean hatching size (length at age 0) and predicted length at metamorphosis (the asymptotic limit of mean larval growth).

Analysis of the seven field seasons resulted in the following relationships, where L = standard length in mm and Age = number of days (increments plus 19) from hatch:

$$1976/77\ L = 33.5381e^{-1.1055e^{-0.0197Age}} \quad [n=187,\ r^2=0.8965];$$

$$1988/89\ L = 38.9217e^{-1.5483e^{-0.0213Age}} \quad [n=139,\ r^2=0.8951];$$

$$1989/90\ L = 35.2189e^{-1.6232e^{-0.0271Age}} \quad [n=379,\ r^2=0.8914];$$

$$1990/91\ L = 36.0859e^{-1.6104e^{-0.0240Age}} \quad [n=382,\ r^2=0.9161];$$

$$1991/92\ L = 34.1978e^{-1.9677e^{-0.0320Age}} \quad [n=313,\ r^2=0.8540];$$

$$1992/93\ L = 34.1176e^{-2.1559e^{-0.0312Age}} \quad [n=204,\ r^2=0.9085];$$

$$1993/94\ L = 37.4796e^{-1.8986e^{-0.0276Age}} \quad [n=142,\ r^2=0.9435].$$

A summary of the growth parameters generated by the above equations may be found in Table 2. Plots of the Gompertz curves fitted to standard length vs. age in days are presented in Figure 2.

In order to compare the rate of growth for the seven seasons, the Gompertz curves were linearized and examined for homogeneity of slope with t-tests (Table 3; Fig. 3). With this method, three groupings were discernible: 1) the 1976–77 season; 2) the 1988–89, 1989–90, and 1990–91 seasons; and 3) the 1991–92, 1992–93, and 1993–94 seasons. Larval growth for the 1976–77 season was the slowest (0.16 mm/d) of the time series, and although larvae for this season had the greatest hatch length, standard length at 120 days posthatch was 2.2 to 4.8 mm less than that in the other six years. There was no significant difference at the 0.05 level between the 1988–89, 1989–90, and 1990–91 seasons. Hatching length for these three seasons differed by less than 1.5 mm, and overall rates of growth for the first 120 days were identical. The rate of growth during the overwintering period of 1988–89 was the greatest of the seven years and compensated for the relatively slow growth earlier in the season. Larvae were on average 2.7 mm smaller at hatching in the autumns of 1991, 1992, and 1993 than in the preceding three years. The rate of growth for the first 40 to 60 days was considerably faster than that in previous years; however, this initial rapid increase in length was followed in 1991–92 and 1992–93 by a period of slower than average growth. The overall higher rates of growth in these two years were not enough to compensate for the small size of larvae at hatching (4.0–4.8 mm), and projected lengths at metamorphosis (34.1–34.2 mm) were smaller than in all previous years except 1976–77. Although hatching lengths in 1993–94 were small, growth was good throughout the season, and the average length at 120 days posthatch (35.0 mm) was the largest of the time series.

Predictability

A generalized growth model for larval herring was created by pooling data (n=1,559) from the six most recent field seasons (1988–94) and by fitting them with a Gompertz curve:

$$L = 34.9959e^{-1.7424e^{-0.0281Age}} \quad [r^2=0.8863].$$

The model tracks growth for the first four months of life from an estimated hatch length of 6.1 mm to a predicted length at 120 days posthatch of 33.0 mm (0.22 mm/d). Figure 4 shows the growth curve with 95% confidence intervals for predicting standard length (mm) for a given age in days. This information is also presented in Table 4 along with age-specific growth rates.

Because it is desirable, especially during field surveys when direct analysis of otoliths is impossible, to be able to estimate the age of larvae based on their length, inverse regression (Draper and Smith, 1966) was performed on the Atlantic herring composite growth curve to establish confidence intervals for predicting age from a given standard length. In its reduced form the equation obtained for herring was

$$\left.\begin{matrix} X_U \\ \\ X_L \end{matrix}\right] = \frac{\ln\left(\dfrac{1-X_0 \pm 0.0470t}{\left(\left(\left(X_0-0.7523\right)^2/26.5957\right)+(1+1/n)\right)^{1/2}}\right)}{-0.0281}$$

where X_U and X_L = upper and lower confidence limits;
X_0 = $1-e^{-0.0281}$; and
n = sample size.

Table 2

Summary of larval Atlantic herring growth parameters based on otolith anaylsis for the autumn–winter field seasons of 1976–77, 1988–89, 1989–90, 1990–91, 1991–92, 1992–93, and 1993–94.

	1976	1988	1989	1990	1991	1992	1993
Sample size	187	139	379	382	313	204	142
Corrected standard length (mm)							
Hatching length	11.1	8.3	6.9	7.2	4.8	4.0	5.6
Inflection of lapillus	—	—	29.1	29.1	28.9	29.4	—
120 days posthatch	30.1	34.5	33.1	33.0	32.9	32.4	35.0
Metamorphosis length	33.5	38.9	35.2	36.1	34.2	34.1	37.5
Growth rate (mm/d)							
Age (d)							
0	0.24	0.27	0.31	0.28	0.30	0.26	0.29
20	0.23	0.30	0.35	0.32	0.41	0.39	0.38
40	0.20	0.28	0.30	0.29	0.35	0.36	0.35
60	0.16	0.23	0.22	0.23	0.23	0.26	0.26
80	0.12	0.18	0.15	0.16	0.14	0.16	0.18
100	0.09	0.13	0.09	0.11	0.08	0.09	0.11
120	0.06	0.09	0.06	0.07	0.04	0.05	0.07
Overall	0.16	0.22	0.22	0.22	0.23	0.24	0.24

Table 3

Summary statistic comparing growth curves for the seven field seasons analyzed. Values in boldface indicate no significant difference at the 5% level.

	t-value						
	1976–77	1988–89	1989–90	1990–91	1991–92	1992–93	1993–94
1976–77	—						
1988–89	–5.9188	—					
1989–90	–10.4849	**–1.7146**	—				
1990–91	–10.6624	**–1.3390**	**–0.6648**	—			
1991–92	–15.0114	–6.4908	–6.6106	–7.5418	—		
1992–93	–17.5134	–8.5801	–9.5920	–10.7229	–2.7409	—	
1993–94	–13.5369	–5.4810	–4.9987	–5.8684	**0.9600**	–3.5349	—

Table 5 provides predicted ages of Atlantic herring for given standard lengths with 70% and 95% confidence limits, and Figure 5 shows the fitted growth curve bracketed by its confidence limits.

Otolith growth

Because past studies have demonstrated a strong relationship between mean otolith diameter (μm) and age (d) (Bolz and Lough, 1987), sagittal growth for the seven seasons was analyzed and compared. The extremely slow growth in otolith diameter during the 1976–77 season was dramatically different from the other six years and resulted in a one-third smaller diameter at metamorphosis (Fig. 6). During 1988–89 and 1993–94, there appeared to be a decoupling of somatic and otolith growth, such that 120-day-old larvae were approximately 1.4–2.6 mm longer than those in the four other recent field seasons and had a smaller otolith diameter.

Beginning with the 1989–90 season, the length of the lapilli, as well as that of the sagittae, was measured. A plot of diameter of the lapillus versus age in days showed an abrupt increase in its rate of growth at approximately 2.5 months of age (Fig. 7). In 1989–90 and 1990–91 the point of flexion occurred at a length of 29.1 mm SL when the larvae were 79 and 84 days old, respectively. Change in the growth of

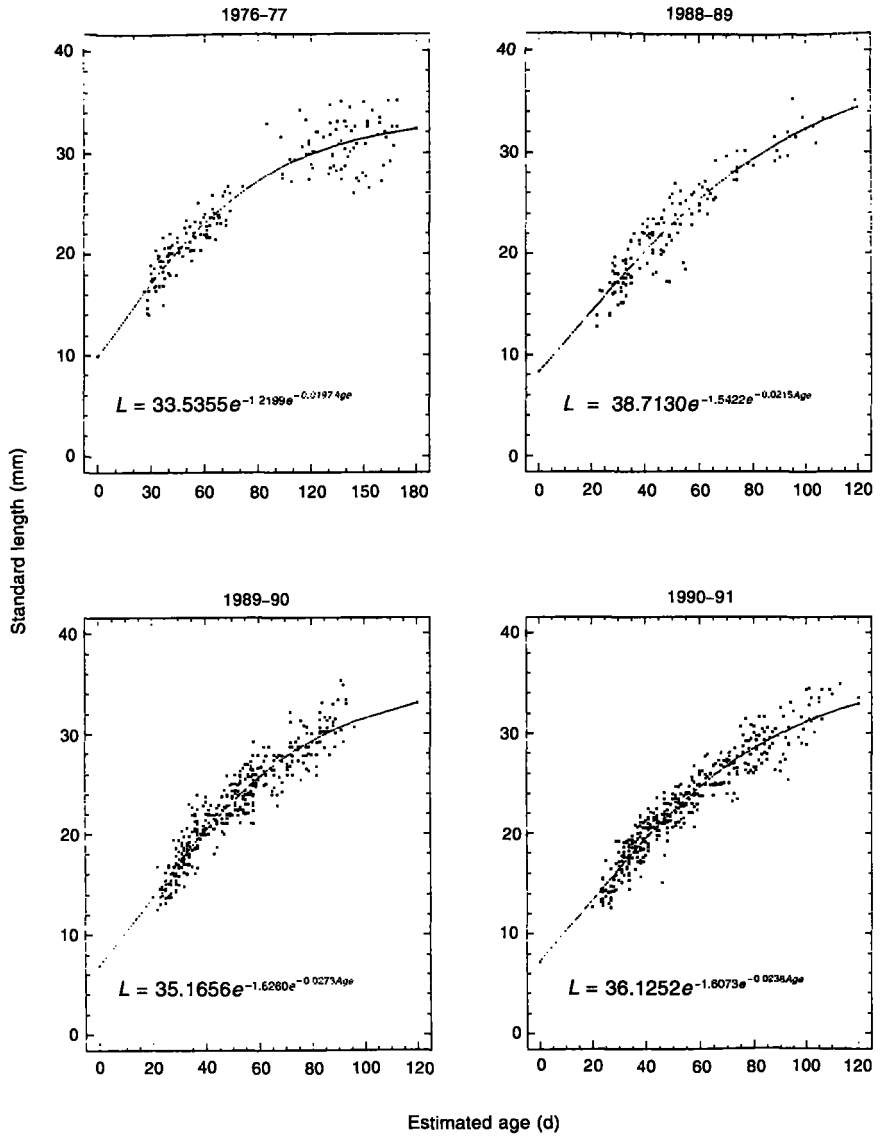

Figure 2

Gompertz growth curves and equations fitted to plots of standard length and estimated age in days (number of otolith increments plus 19) for larval Atlantic herring collected in the Nantucket Shoals–Georges Bank region during the autumn–winter field season.

the lapillus occurred at 77 days in 1991–92 and at 86 days in 1992–93 when the fish were respectively 28.9 and 29.4 mm SL. Owing to the small number of larger individuals sampled during the 1993–94 season, it was not feasible to determine when inflection took place.

Discussion

With the collapse of the herring fishery in the Nantucket Shoals–Georges Bank region during the autumn of 1976, initial larval abundance dropped from an estimated 62.5×10^{12} larvae in 1975 to 2.8×10^{12} in 1976 (Lough et al., 1985). This low abundance was further diminished by strong and persistent northerly winds that occurred during November, January, and February of the 1976–77 season (Wright, 1979; Bolz and Lough, 1984). The computed Ekman transport indices (Lough et al., 1979) are indicative of strong southerly transport. These winds with their resultant offshore surface drift would have disrupted the normal spatial distribution of prey (Maillet and Checkley, 1991).

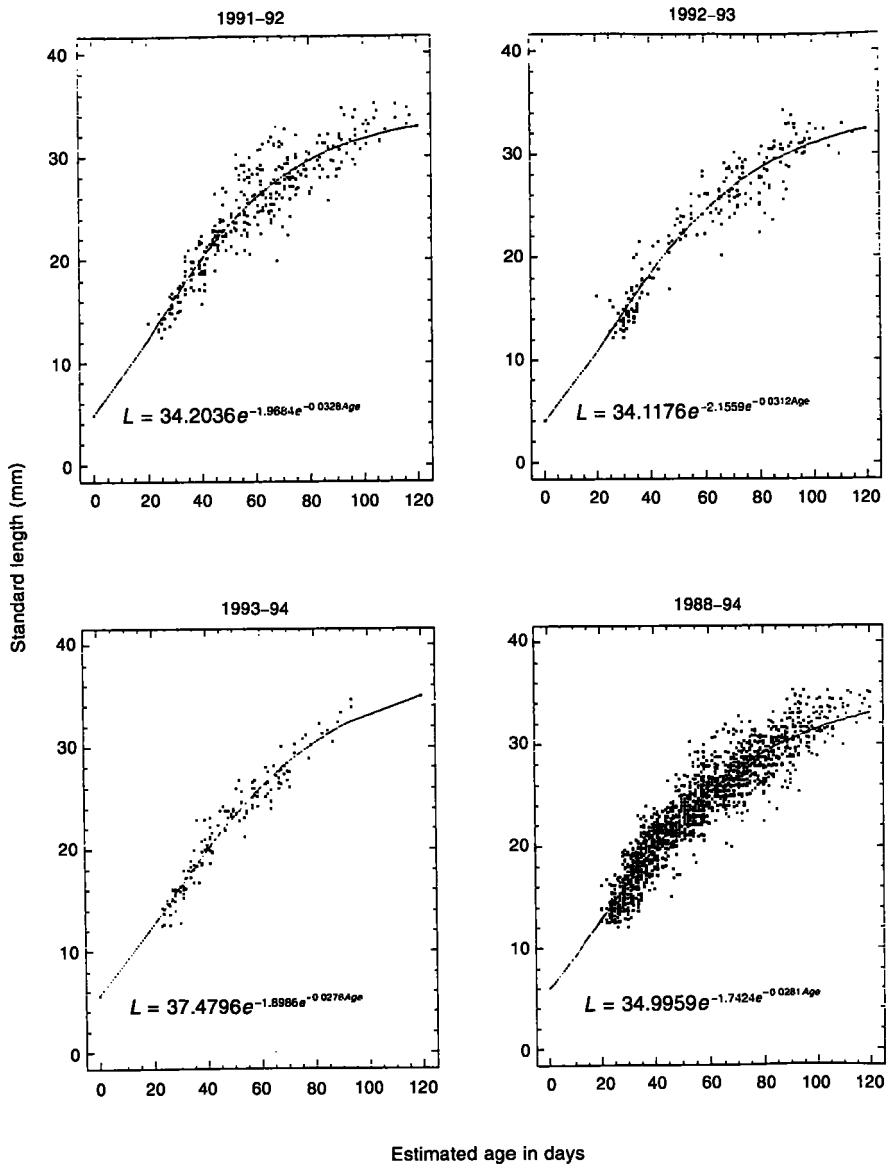

Figure 2 (continued)

Fish hatched in 1976 were longer by 2.8 to 7.1 mm SL than those collected during the 1980's and early 1990's. Since temperatures in the autumn of 1976 did not differ significantly from the long-term average (Mountain and Holzwarth, 1989), a density-dependent function is the most likely explanation for this difference. It is possible that the less dense beds enhanced growth by permitting eggs to be oxygenated better or that the diminished spawning population produced eggs with greater food reserves (Blaxter and Hunter, 1982). Despite their initially robust appearance, larvae during the 1976–77 season exhibited poor growth and high mortality (Lough et al., 1979). The severe storms discussed above most likely dispersed the prey of larval herring and led to a reduction in daily food rations. Poor feeding is reflected in the rapid lessening of mean otolith diameter noted during 1976–77. This observation is in agreement with the previous study of Cohen and Lough (1983), where larvae collected during the 1976 season had lower prey numbers and biomass per larva than those in 1974 and 1975. Similar results were found by Karakiri et al. (1989) in their study of age-0 plaice (*Pleuronectes platessa* L.). They also concluded that food limitation accounted for an observed difference in growth between two years with similar

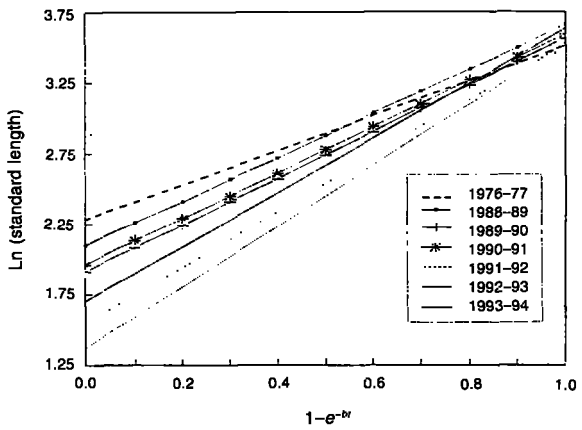

Figure 3

Comparison of the regression lines for the seven field seasons analyzed (b = rate of exponential decay; t = age in days).

Table 4

Mean standard length at age, 95% prediction limits, and growth rate of larval Atlantic herring from hatch through 120 days, estimated from the Gompertz growth model fit.

Age (d)	Mean length (mm)	95% prediction limits		Growth rate (mm/day)
		Lower	Upper	
0	6.1	5.1	7.1	0.30
10	9.2	7.9	10.9	0.35
20	12.8	10.9	15.1	0.36
30	16.4	13.9	19.3	0.35
40	19.7	16.8	23.2	0.32
50	22.7	19.3	26.7	0.28
60	25.3	21.5	29.7	0.23
70	27.4	23.3	32.2	0.19
80	29.4	24.7	34.2	0.15
90	30.4	25.9	35.8	0.12
100	31.5	26.8	37.1	0.09
110	32.3	27.5	38.1	0.07
120	33.0	28.0	38.8	0.06

Table 5

Predicted age in days, with 70% and 95% prediction limits, of larval Atlantic herring for a given standard length.

Observed standard length (mm)	Predicted age (d)	70% prediction limits		95% prediction limits	
		Lower	Upper	Lower	Upper
6.1	0	—	1.7	—	3.2
8.0	5.9	3.9	7.9	2.2	9.6
10.0	11.7	9.4	14.0	7.4	16.0
12.0	17.3	14.6	20.0	12.3	22.3
14.0	22.8	19.6	26.0	17.1	28.5
16.0	28.4	24.7	32.1	21.8	35.0
18.0	34.2	29.9	38.5	26.5	41.9
20.0	40.3	35.3	45.3	31.3	48.3
22.0	46.9	41.0	52.8	36.4	57.4
24.0	54.3	47.1	61.5	41.7	66.9
26.0	62.8	53.9	71.7	47.5	78.1
28.0	72.9	61.5	84.3	53.7	92.1
30.0	86.0	70.5	101.5	60.7	111.3

temperature regimes and that the difference was likewise reflected in daily otolith increment widths.

Several studies have observed a poor correlation between otolith length and fish length (Secor et al., 1989; Moksness and Wespestad, 1989), and this was partly the case in the present work. Since increments may continue to be deposited during periods of slow or negative somatic growth, caution must be exercised in estimating age based solely on length relationships. After 120 days of growth, the fish in the 1988–89 and 1993–94 seasons showed smaller mean otolith diameters than did fish in 1989–90, 1990–91, 1991–92, and 1992–93 seasons, despite their having larger mean standard lengths. There is, however, a strong relationship between mean otolith increment width and the somatic rate of growth as expressed in mm/d of SL. From 60 to 120 days of age, larval herring grew very slowly in 1976–77 and exhibited thin increments; whereas in 1988–89, growth was more rapid and the increments were wider. Secor et al. (1989) found evidence of a lag effect between food ration and its reflection in the otoliths and, until this finding can be demonstrated in herring, it is perhaps best to cite trends rather than attempt to relate a given increment to a specific event.

The predictive model for Atlantic herring growth presented above has to be viewed as general in nature, and the widening of the confidence intervals with increasing length (Tables 4 and 5; Figs. 4 and 5) must be kept in mind. Natural variability of length at age and difficulty in the reading of otoliths increase as fish become older and make precise age determinations extremely difficult. For example, the ability to predict correctly the age of an individual herring larva at the 70% confidence level decreases from ±2 days at 8 mm SL to ±2 weeks at 30 mm. In spite of this problem, otolith ageing of field-caught larvae provides a degree of precision not possible with indirect methods based on size-frequency analysis (Ebert, 1973).

The inflection noted in the rate of otolith growth (Fig. 7) occurs at an age when the otic bullae would

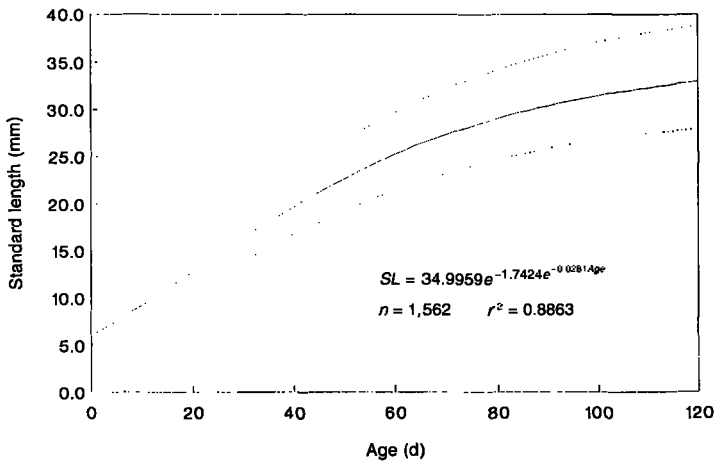

Figure 4

Gompertz growth curve for larval Atlantic herring with 95% confidence intervals for predicting standard length (mm) for a given age in days.

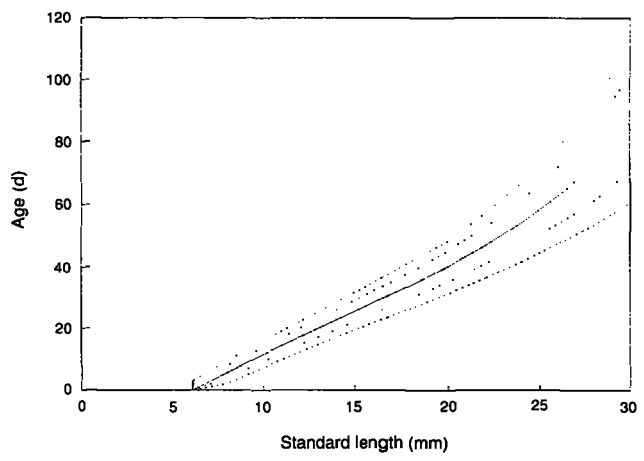

Figure 5

Inverse regression of Atlantic herring growth curve with 70% and 95% confidence intervals for predicting age in days for a given standard length (mm).

be expected to fill with air. Enlargement at this time of the lapilli and, less dramatically, of the sagittae and maculae would allow larvae to take greater advantage of the wave amplification conferred by a full air bladder and bullae. In order to successfully avoid predation and to control vertical migration, this should occur at as early an age as possible. Analysis of otolith growth is probably the only way to estimate the timing of this developmental landmark in field-caught larvae. Knowing when this occurs may permit a better understanding of population anomalies. The necessary morphometric data are lacking for the 1976–77 season; however, from the analysis of recent seasons, the storm events in late November 1976 would be expected to have occurred while many of the larvae were at this critical life stage. This co-occurrence of storm events and critical life-stage events would have caused additional mortality to an already stressed population.

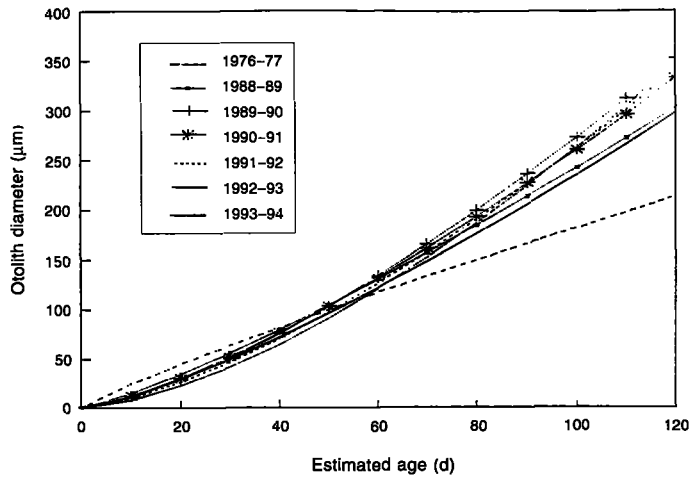

Figure 6

Comparison of changes in otolith growth for larval herring during the autumn-winter period of the seven years in the study.

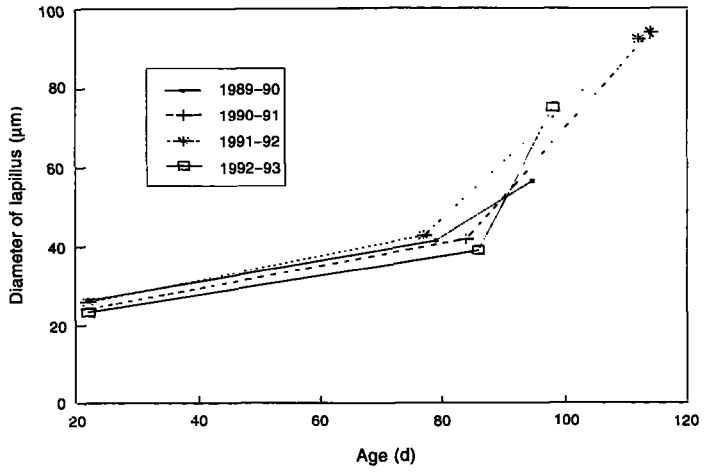

Figure 7

Growth of larval herring lapillus showing increase in rate of growth at approximately 2.5 months of age.

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Estimated paralarval drift and inferred hatching sites for *Ommastrephes bartramii* (Cephalopoda: Ommastrephidae) near the Hawaiian Archipelago

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Abstract.—Research was conducted to test the hypothesis that spawning of the oceanic squid *Ommastrephes bartramii* in the central North Pacific is related to the proximity of the Hawaiian Archipelago. Paralarvae were collected during five plankton surveys near the Hawaiian Island chain during the 1991–93 spawning seasons. In total, 1,720 *O. bartramii* paralarvae were collected from 406 tows. Estimation of ages and hatch dates of all squid was inferred from analysis of statolith microstructures from 85 specimens. A well-defined relationship existed between the number of statolith growth increments and the dorsal mantle length of the paralarvae. Estimated hatch dates of individuals collected during the three years surveyed ranged between mid-January and early April. Spawning sites were then estimated from hatch dates by backcalculating with physical data on the speed of ocean currents near the archipelago. Although estimated spawning of *O. bartramii* did often occur along the island chain, spawning was not limited to nearshore waters. Some animals hatched, on the basis of estimated current speeds, at least 646 kilometers away from the archipelago. Projected hatching locations of more than 72% of all collected paralarvae were at least 10 kilometers from shore. Data do not support the hypothesis that the location of the spawning grounds in this region is solely related to the position of the Hawaiian Archipelago.

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The neon flying squid, *Ommastrephes bartramii* (Lesueur), is an oceanic species occurring worldwide in subtropical and temperate waters (Roper et al., 1984). In the North Pacific, *O. bartramii* paralarvae have been collected from several areas: from January through May, paralarvae are found southeast of Honshu Island, Japan (Okutani, 1968, 1969; Saito and Kubodera, 1993); and during May, paralarvae are found along 25–26°N latitude between 143–166°E longitude, and along 29°N latitude between 161–160°E longitude (Hayase, 1995). Paralarvae also occur near the Hawaiian Archipelago from February to May (Young and Hirota, 1990; Hayase, 1995; Bower et al.[1]; Hayase[2]). A study of paralarvae collected near the Hawaiian Archipelago during 1991–93 found no systematic relationship between the distribution and abundance of *O. bartramii* paralarvae and distance from the archipelago (Bower et al.[1]). This study, however, did not account for the effects of age and paralarval drift on the distribution patterns found. The present study attempts to identify more clearly possible spawning areas by considering these factors.

Statoliths from teuthoid squids commonly contain growth increments that can be used for age determination. After conducting a detailed age analysis of *Loligo opalescens*, Spratt (1978) argued that some increments in the statolith were deposited daily, as in fish otoliths. Since then, a number of studies have been conducted to determine the frequency of increment formation (Dawe et al. [1985] on *Illex illecebrosus*; Hurley et al. [1985] on *I. illecebrosus*; Lipinski [1986] on *Alloteuthis subulata*; Jackson [1989, 1990]; and Nakamura and Sakurai [1991] on *Todarodes pacificus*; also see reviews by Rodhouse and Hatfield [1990] and Jackson [1994]). The data provide strong support for the hypothesis that growth increments form at the rate of one per day in both loliginid and ommastrephid squids. Although validation of the growth increments of *O. bartramii* has not been accomplished, I have assumed that they form daily for this study.

[1] Bower, J. R., R. E. Young, J. Hirota, P. Flament, M. Seki, and K. Bigelow. 1996. Distribution and abundance of cephalopod paralarvae near the Hawaiian Archipelago. In prep.

[2] Hayase, S. 1989. Cruise report of flying squid spawning survey by the *Hokuho Maru* in the North Pacific in April–May 1989, 21 p. Document submitted to the Annual Meeting of the International North Pacific Fisheries Commission, Seattle, Washington, 1989 October.

Vertical distribution data suggest that *O. bartramii* paralarvae occur within the 0–40 m depth layer during both day and night (Okutani, 1968; Young and Hirota, 1990). Upon hatching, paralarvae are active swimmers, but owing to their small size remain planktonic for an unknown period, presumably for several weeks. Given the role of ocean currents in the transport of cephalopod paralarvae, any analysis of cephalopod paralarval distribution requires an investigation of the prevailing oceanographic currents to determine from what region the animals have been advected since hatching. Although there are few records of naturally spawned eggs or egg masses from oceanic cephalopods and no observations of *O. bartramii* egg masses, O'Dor and Balch (1985) have suggested that pelagically spawned egg masses may become suspended in the mesopelagic zone, where reduced current speeds would limit transport of egg masses away from spawning sites. I have assumed that each paralarva hatched at the site at which it was spawned.

Korzun et al. (1979) have suggested that spawning locations of *O. bartramii* may be related to the position of islands. The present study was undertaken to determine whether and how the spawning locations of *O. bartramii* from the North Pacific are related to the proximity of the Hawaiian Archipelago. This objective was addressed by examining the distribution and ages of paralarvae captured during five plankton surveys near the Hawaiian Island chain from 1991 to 1993 with ocean current data derived from Lagrangian tracers and by estimating geostrophic flow.

Materials and methods

Collection and ageing of paralarvae

Five plankton surveys were conducted near the Hawaiian Archipelago to collect cephalopod paralarvae (Fig. 1). Plankton samples were collected during 6–15 February 1991, 5–26 February 1992, and 4–19 February 1993 with the Hokkaido University (Japan) ship FTS *Hokusei Maru*, and during 5–20 February 1991 and 22 March–7 April 1992 with the RV *Townsend Cromwell* of the National Marine Fisheries Service (NMFS). The standard sampling procedure during all surveys was to conduct 30-minute oblique tows to 100 m depth.

The *Hokusei Maru* February 1991 (*HM*-Feb 91) survey sampled paralarvae at seven stations along an inshore–offshore transect to the northeast of the Hawaiian Island chain from Kauai Island (Kauai transect), including a lone station in the lee of Hawaii Island. Windward stations were positioned 9, 16, 106, 235, 349, 460, and 583 kilometers offshore. Thirty-six tows (mean depth=95 m; SD=9 m) were taken. Sampling consisted of five back-to-back replicate tows at each station. This and subsequent *Hokusei Maru* surveys used a 4-m^2 ring net equipped with 0.505-mm mesh, a General Oceanics flowmeter, and a Benthos time-depth recorder.

The *Townsend Cromwell* February 1991 (*TC*-Feb 91) survey sampled at ten stations along the archipelago. Transects orthogonal to the archipelago were

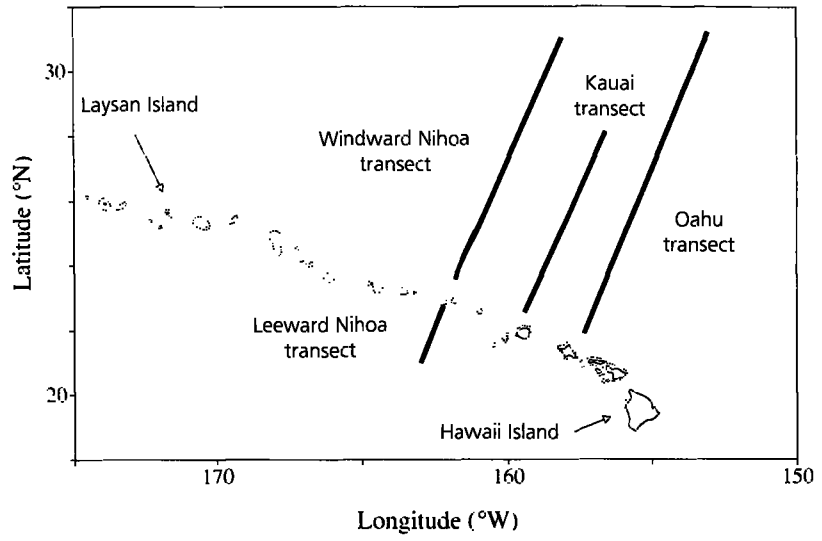

Figure 1

Map of the Hawaiian Archipelago showing the study area and transects surveyed during the five cruises.

abandoned because of inclement weather north of the ridge, restricting most sampling to nearshore waters. Stations were located 13, 14, 15, 16, 25, 28, 28, 207, 228, and 232 kilometers offshore. Forty-four tows were conducted in a stepped oblique fashion (mean depth=93 m; SD=12 m). Sampling consisted of between one and seven back-to-back replicate tows at each station with a 4-m^2 ring net equipped with 0.505-mm mesh.

During the *Hokusei Maru* February 1992 (*HM*-92) survey, paralarvae were collected along the windward Nihoa and Kauai transects, including three stations southwest of the archipelago along the leeward Nihoa transect and a lone station in the lee of Oahu Island. The Kauai transect included stations sampled during the *HM*-91 survey. One hundred thirty-one tows were collected at sixteen sampling stations (mean depth=70 m; SD=14 m). Owing to high variability in the catch rates from the *HM*-91 survey, the number of tows taken at each sampling station was increased from five to between seven and ten back-to-back replicate tows. Stations along the Kauai transect were located 11, 41, 142, 235, 337, 471, 585, and 713 kilometers offshore. Nihoa transect stations were located 26, 181, and 269 kilometers windward, and 25, 126, and 256 kilometers leeward of the archipelago. Four scheduled stations along the windward Nihoa transect were canceled because of inclement weather.

During the RV *Townsend Cromwell* March–April 1992 (*TC*-92) survey, four to eight replicate tows were conducted at fourteen stations along the windward Nihoa and Oahu transects. One hundred tows (96 with a 2-m^2 ring; 4 with a 4-m^2 ring) were conducted in a stepped oblique fashion (mean depth=94 m; SD=13 m). The net carried a Wildlife Computers time-depth recorder. Stations were located between 52 and 1,161 kilometers offshore.

During the *Hokusei Maru* February 1993 (*HM*-93) survey, paralarvae were collected along the same two transects, northeast of the Hawaiian Island chain, that had been sampled in February 1992, including three stations southwest of the archipelago (leeward Nihoa transect) and a lone nearshore test station (only two tows conducted) northeast of Oahu Island. Ninety-five tows (mean depth=92 m; SD=23 m) were collected at twelve sampling stations. Seven to ten back-to-back replicate tows were taken at each station.

Specimens from the *Hokusei Maru* surveys were fixed in 4% formalin and preserved in 50% isopropyl alcohol within 3–6 hours to prevent possible acidic degradation of the calcareous statoliths. *TC*-91 survey samples were fixed in 10% formalin and preserved in 50% isopropyl alcohol. *TC*-92 survey samples were fixed in 6% formalin and preserved in 50% isopropyl alcohol. Statoliths from specimens stored in formalin longer than six hours darkened and proved unreadable.

Paralarvae of the family Ommastrephidae were identified to genus and species level according to figures and descriptions of Hawaiian ommastrephids published by Young and Hirota (1990) and Harman and Young (1985). The dorsal mantle length of each *O. bartramii* paralarva was measured to the nearest 0.1 mm with an ocular micrometer in a stereomicroscope.

Statoliths were removed from the paralarvae with fine dissecting forceps under a stereomicroscope. First, the paralarval funnel was removed, revealing the ovate statocyst. Statoliths were clearly visible within the statocyst as paired, white, opaque structures. The excised statocyst was transferred to a microslide, where it was gently pulled apart, permitting one of the statoliths to fall onto the slide. The statocyst with the remaining statolith inside was then transferred to a separate slide where the statolith was similarly removed. Statoliths were rinsed in distilled water and air-dried before analysis. When dried, statoliths were embedded in thermal plastic by heating the plastic to 77°C.

Statoliths from 85 animals (mantle length: 1.0–4.7 mm) were used for growth increment analysis. Paralarvae used for statolith examination were collected during the *HM*-91, *HM*-92, and *TC*-92 surveys. Growth increments on *O. bartramii* statoliths consisted of two components, a broad, translucent ring and a narrow, dark ring. Using a Zeiss compound microscope (400×), increments were counted from the nucleus to the outer margin of the dorsal end of the lateral dome. Examinations were made with transmitted light. Counts of each statolith were conducted on three separate occasions and averaged for a mean increment value. Increments in the outermost portion of the lateral dome and the innermost portion near the nucleus could not be counted in some cases; therefore the number of increments on those portions was estimated by extrapolation.

Data treatment

Age for each of the 85 paralarvae used for growth increment analysis was determined from the mean of the three counts of statolith growth increments. The exponential equation $y=ae^{bx}$ was fitted to the data for the mantle-length–increment-count relationship. Age estimates of all other paralarvae were based on this relationship curve.

Estimated ocean current speeds and directions

Patterns of ocean currents near the Hawaiian Archipelago were defined by the trajectories of near-

surface drifters and by dynamic height measurements from conductivity-temperature-depth (CTD) probes. Four ARGOS-tracked drifters released by the National Marine Fisheries Service were used as Lagrangian tracers of the surface currents during the 1992 survey periods to assess "typical" current speeds and directions near the Hawaiian Archipelago. Drifter positions were recorded every six hours over the survey period. Each drifter's Lagrangian net path was plotted. Geostrophic flow measurements were calculated between each pair of successive sampling stations during the three *Hokusei Maru* surveys on the basis of dynamic height measurements taken at each sampling station from CTD casts to 1,200 m. Sampling stations averaged approximately 110 km and 24 hours apart.

Results

A total of 1,720 *O. bartramii* paralarvae was collected at 41 of the 59 sampling stations, making up 16.5% of the cephalopod paralarvae caught. Sizes of *O. bartramii* ranged from 0.9 mm to 8.3 mm ML.

Age–mantle-length relationship

Statolith growth increment counts ranged from 3 to 22.7 (Table 1). A well-defined relationship existed between the number of statolith growth increments and the dorsal mantle length of the paralarvae, with the exponential function yielding a good fit for the regression (r^2=0.88) of the number of increments on the dorsal mantle length (Fig. 2). The following exponential model was fitted to the data:

$$ML = 0.95e^{(0.067x)},$$

where ML is the dorsal mantle length in millimeters and x equals the number of increments. This equation was used to estimate the ages (x) of the 1,635 paralarvae not examined during statolith increment analysis. The y-intercept of the exponential function (a=0.95 mm) is close to the actual hatching length (ca. 1 mm).

Size structure, ages, and projected hatch dates

The dorsal mantle length ranges of *O. bartramii* paralarvae varied slightly among surveys (Fig. 3). The largest range of size occurred during the *TC*-91 survey (0.9–8.3 mm), and the smallest range of size occurred during the *HM*-91 survey (1.0–5.6 mm).

Estimates of paralarval ages for total samples, predicted from the exponential mantle length on age model, ranged from 1 to 30 days. Projected paralarvae hatch dates for the five surveys are summarized in Figure 4. During the *HM*-91 and *TC*-91 surveys, captured paralarvae were estimated to have hatched between 13 January and 8 February. During the *HM*-92 and *TC*-92 surveys, estimated hatch dates of captured paralarvae fell between 22 January and 1 April. During the *HM*-93 survey, estimated hatch dates of captured paralarvae fell between 11 January and 6 February.

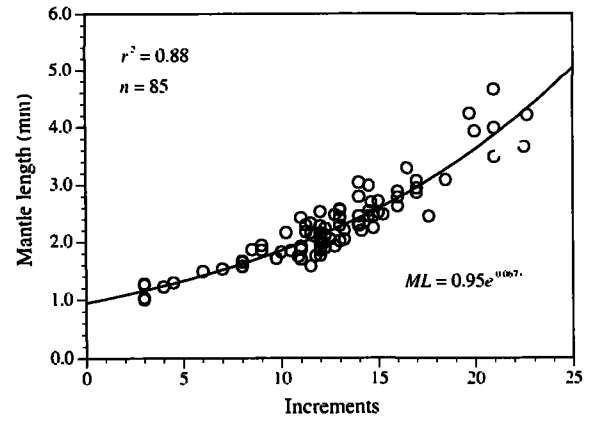

Figure 2

Relationship between paralarval mantle length and number of daily growth increments in statoliths of *Ommastrephes bartramii*, and proposed growth curve.

Paralarval size with distance offshore

Mean mantle lengths at each station were compared with distance from the archipelago (Fig. 5). The mean mantle lengths at each station were not significantly correlated (P>0.05; Student's t-test) with distance offshore for any of the five surveys.

Hydrographic observations

No clear advective current patterns could be estimated from the ARGOS-tracked drifters' tracks (Fig. 6). Average net displacement of the four drifters near the Hawaiian Archipelago was 2.5 km per day. During the *HM*-91 survey, CTD data revealed surface to 50-m flows ranging from 4.1 to 16.0 cm per second relative to 1,000 m in reversing bands relative to the archipelago north of the island chain. During the *HM*-92 survey, CTD data revealed flows ranging from 0.0 to 13.8 cm per second relative to 1,000 m in reversing bands relative to the archipelago both north and south of the island chain; *HM*-93 CTD data revealed

flows ranging from 1.6 to 23.6 cm per second relative to 1,000 m in reversing bands both north and south of the island chain.

In summary, mean current speeds near the Hawaiian Archipelago range between 0.30 and 0.42 knots for geostrophic flow normal to the transects and about 0.06 knots for ARGOS-drifter–measured displacement, with flow near the islands complex and highly variable. The drifter data are considered to be the more reliable estimate of mean-surface drift.

Projected spawning grounds

An average current speed (2.5 km per day) estimated from the four drifters tracked in the region was used together with age estimates to infer possible areas of spawning for *O. bartramii*. To determine whether paralarvae captured at some distance from the archipelago could have been carried to their position by currents from a spawning site next to the archipelago, a "best-case" scenario was used that assumed

Table 1

Size frequency of *Ommastrephes bartramii* paralarvae for 85 statoliths examined with statolith mean increment count, standard deviation (SD), and increment count range for each dorsal mantle length (DML). Specimens were collected from *Hokusei Maru* February 1991, *Hokusei Maru* February 1992, and *Townsend Cromwell* March–April 1992 surveys.

				Count range		
DML (mm)	*n*	Count mean	SD	min	max	range
1.0	2	3.0	0.0	3.0	3.0	0
1.1	0					
1.2	1	4.0	—	—	—	—
1.3	3	3.5	0.9	3.0	4.5	1.5
1.4	0					
1.5	2	6.5	0.7	6.0	7.0	1.0
1.6	4	8.9	1.8	8.0	11.5	3.5
1.7	4	9.9	1.4	8.0	11.0	3.0
1.8	4	11.1	1.0	10.0	12.0	2.0
1.9	9	10.8	1.6	8.5	12.8	4.3
2.0	5	12.6	0.5	12.0	13.3	1.3
2.1	4	11.9	0.3	11.5	12.3	0.8
2.2	7	12.5	1.6	10.3	14.8	4.5
2.3	6	12.6	1.2	11.3	14.0	2.7
2.4	7	14.0	2.0	11	17.6	6.6
2.5	5	13.9	1.4	12	15.3	3.3
2.6	3	14.0	1.7	13	16	3.0
2.7	2	14.8	0.3	14.6	15	0.4
2.8	2	15.0	1.4	14	16	2.0
2.9	3	16.7	0.6	16	17	1.0
3.0	2	14.3	0.4	14	14.5	0.5
3.1	2	17.8	1.1	17	18.5	1.5
3.2	0					
3.3	1	16.5	—	—	—	—
3.4	0					
3.5	1	21.0	—	—	—	—
3.6	0					
3.7	1	22.5	—	—	—	—
3.8	0					
3.9	1	20.0	—	—	—	—
4.0	1	21.0	—	—	—	—
4.1	0					
4.2	2	21.2	2.1	19.8	22.7	2.9
4.3	0					
4.4	0					
4.5	0					
4.6	0					
4.7	1	21.0	—	—	—	—
Total	85					

a unidirectional flow away from the islands. Table 2 shows the estimated percentage of paralarvae taken at each sampling station that could not have been spawned within 10 km of the archipelago. The projected spawning grounds of individuals collected during the five surveys are shown in Figures 7–11.

Discussion

New information was obtained on the estimated spawning areas of the squid *Ommastrephes bartramii* with respect to the Hawaiian Archipelago over the 1991–93 winter spawning seasons. The objective of the study was to determine whether a spatial relationship exists between the Hawaiian Archipelago and *O. bartramii* spawning grounds. The results presented here suggest that although estimated spawning of *O. bartramii* did often occur along the island chain, spawning was not limited to nearshore waters; on the basis of estimated current speeds, some animals hatched at least 646 kilometers away from the archipelago. For a minimum of 72% of all paralarvae from the five surveys, projected hatching sites were located at least 10 kilometers from shore.

Statolith analysis is the most effective method for estimating age in many natural squid populations, yet preparing statoliths for counting growth increments is time-consuming, and frequently increments prove unreadable. This study showed that when a sample size is large, analysis of paralarval mantle lengths measured from a representative subsample can be used as an alternate, easier, and faster method

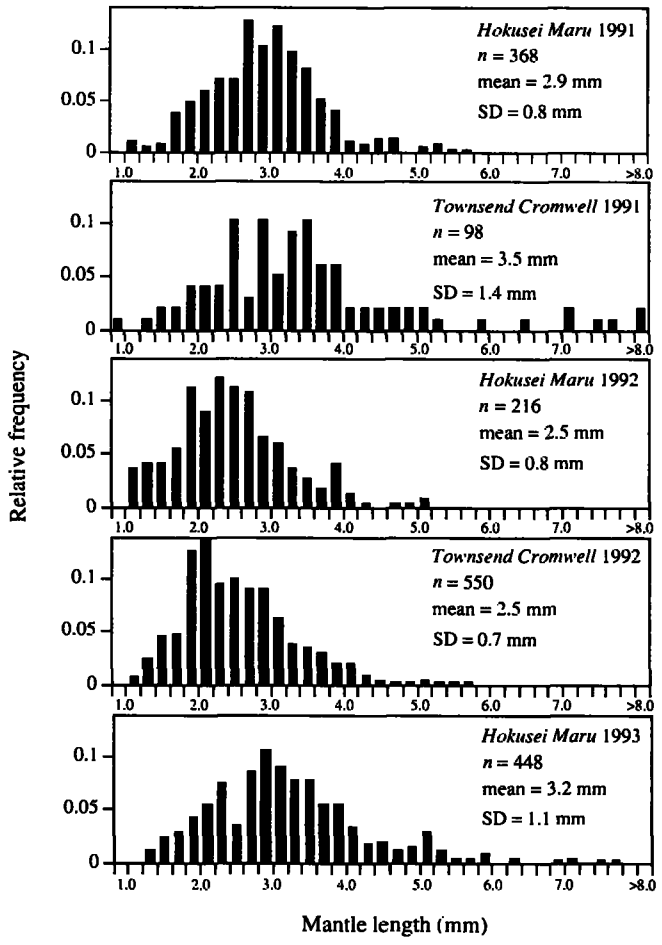

Figure 3

Size-frequency distribution of *Ommastrephes bartramii* paralarvae captured during each cruise.

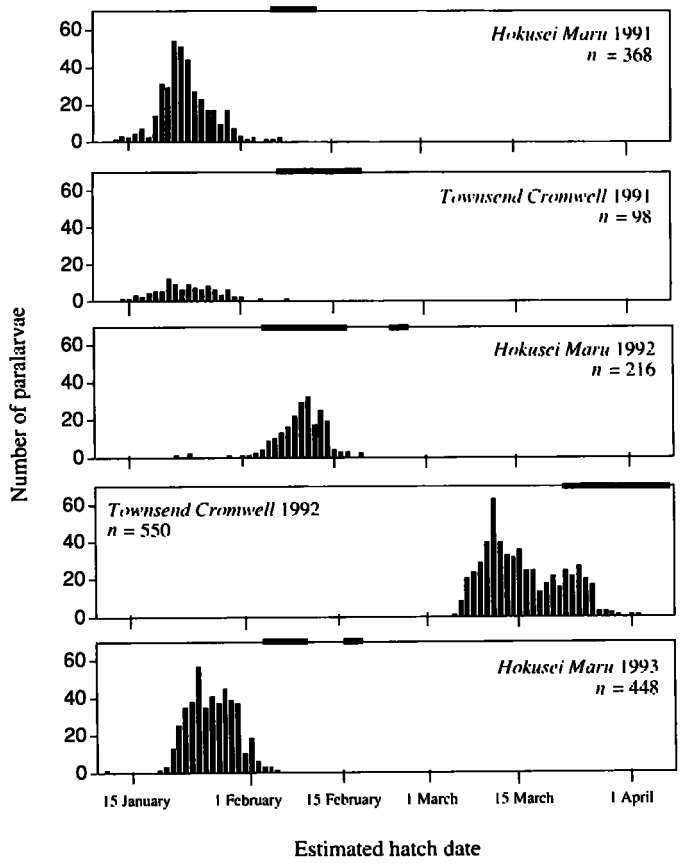

Figure 4

Frequency of projected hatch dates for *Ommastrephes bartramii* paralarvae captured during five surveys. Horizontal bars represent sampling dates.

to obtain good estimates of ages and hatch dates of *O. bartramii* paralarvae.

Growth in mantle length of *O. bartramii* paralarvae was characterized as exponential for at least 23 days after hatching. This observation agrees with that of Bigelow and Landgraf (1993), who found that growth in length of this species is exponential for at least 35 days posthatching. The growth rates of other posthatching ommastrephids have also been shown to be exponential (*Illex* sp., Balch et al., 1988; *Illex argentinus*, Arkhipkin, 1989; *Stenoteuthis oualaniensis*, Bigelow, 1991). Because growth in ommastrephids during later life tends to be linear or nearly linear, these data suggest that the overall form of growth may be approximately described as sigmoidal.

Estimated hatch dates of individuals collected during the three years surveyed ranged between mid-January and early April. Young and Hirota (1990) estimated that paralarvae caught in 1986 were spawned between late February and early April. As noted by Young and Hirota (1990), spawning may occur over a longer period, but synoptic surveys were conducted only between February and April. Surface plankton tows, conducted while the vessel drifted, and nighttime jigging at a sampling station 100 kilometers north of Oahu during March 1992, June 1992, December 1992, and April 1993, caught neither adult nor paralarval *O. bartramii* (Bower, personal observ.). More extensive nighttime jigging off the northeast coast of Oahu during mid-September–early October 1992 failed to capture adult *O. bartramii* (Bower, personal observ.). Harman and Young (1985) failed to catch *O. bartramii* paralarvae off leeward Oahu during December 1983, April 1984, August 1984, and October 1984.

Paralarvae captured over the five surveys showed a fairly broad size range of about 1–8 mm mantle

length at each station, suggesting several possible spawning scenarios. If spawning were isolated to specific geographical areas, synoptic sampling would pick up different size ranges of paralarvae, depending on the proximity of the sampling site to the spawning site. Consistently large size ranges suggest that spawning is not spatially isolated. Furthermore, they suggest that spawning by the local population does not occur in intermittent bursts but is occurring over an extended period. Estimated hatch dates confirm this. The largest squid caught was 8.3 mm, suggesting that this is approximately the size at which paralarvae are fully capable of avoiding the 4-m^2 plankton trawl or that they leave the upper 100

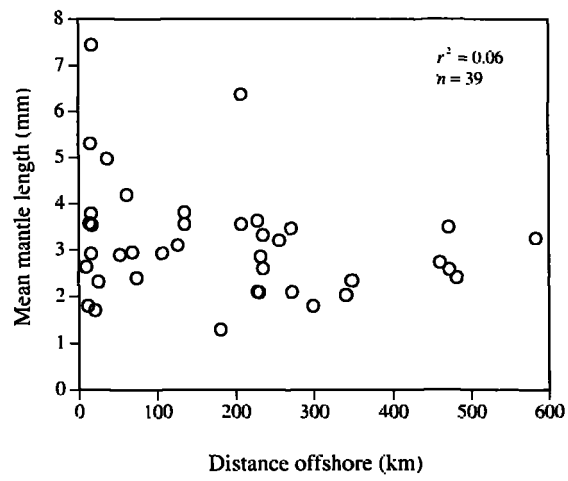

Figure 5

Relationship between mean mantle length of *Ommastrephes bartramii* paralarvae collected from each station and distance of station from land. Data from all five cruises are combined. Correlation is not significant ($P>0.05$; Student's t-test).

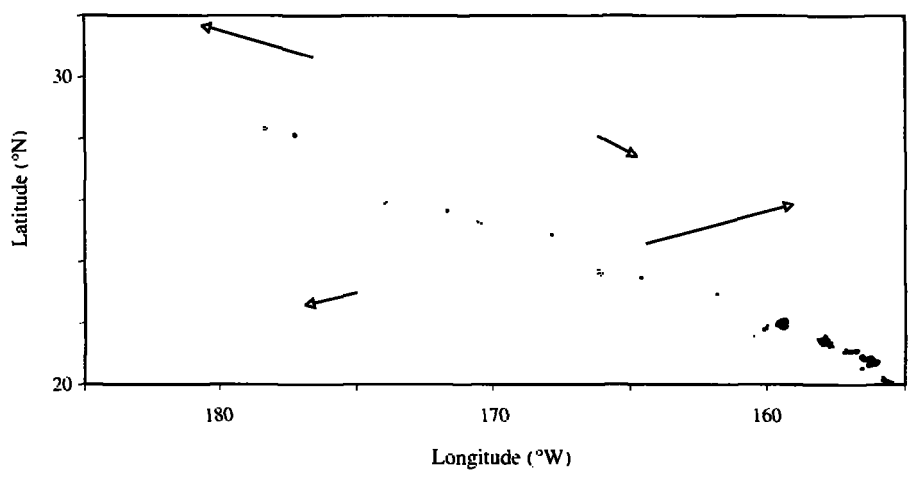

Figure 6

Net distance traveled by four ARGOS-tracked drifters near the Hawaiian Archipelago during the 1992 *Hokusei Maru and Townsend Cromwell* cruises. Time period: 22 January–1 April 1992.

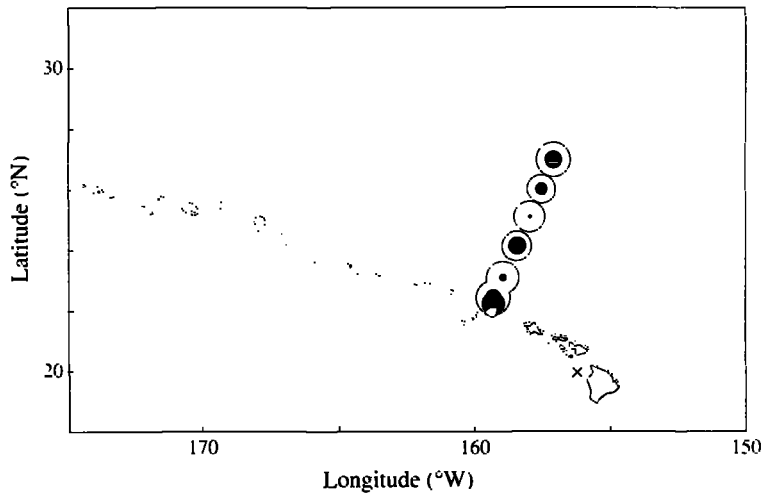

Figure 7

Map of the Hawaiian Archipelago showing the projected spawning grounds of *Ommastrephes bartramii* paralarvae captured during the 1991 *Hokusei Maru* survey. Open circles represent the estimated spawning area for all paralarvae from each station. Closed circles represent the estimated spawning area for the youngest paralarvae from each station. × = station with no *O. bartramii* paralarvae present.

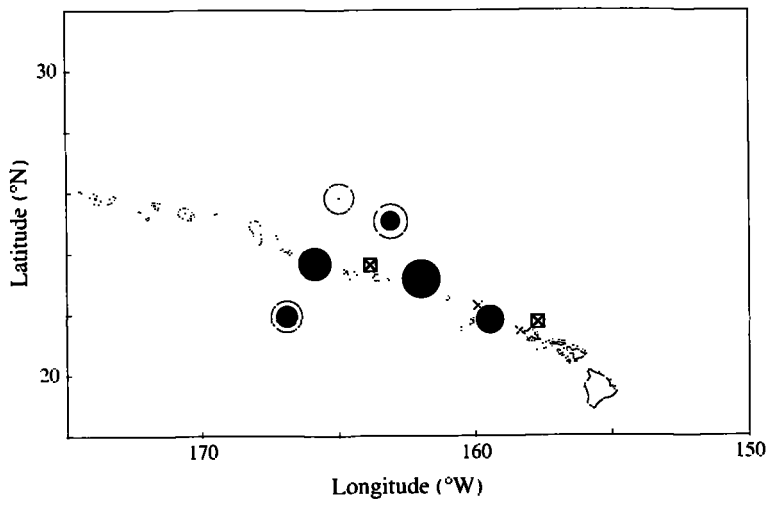

Figure 8

Map of the Hawaiian Archipelago showing the projected spawning grounds of *Ommastrephes bartramii* paralarvae captured during the 1991 *Townsend Cromwell* survey. Open circles represent the estimated spawning area for all paralarvae from each station. Closed circles represent the estimated spawning area for the youngest paralarvae from each station. ⊠ = station with one *O. bartramii* paralarva present but no mantle length measurement recorded. × = station with no *O. bartramii* paralarvae present.

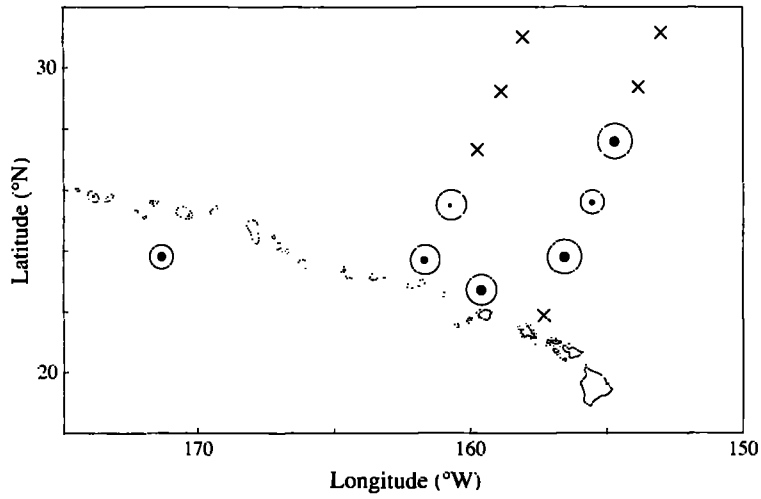

Figure 9

Map of the Hawaiian Archipelago showing the projected spawning grounds of *Ommastrephes bartramii* paralarvae captured during the 1992 *Hokusei Maru* survey. Open circles represent the estimated spawning area for all paralarvae from each station. Closed circles represent the estimated spawning area for the youngest paralarvae from each station. × = station with no *O. bartramii* paralarvae present.

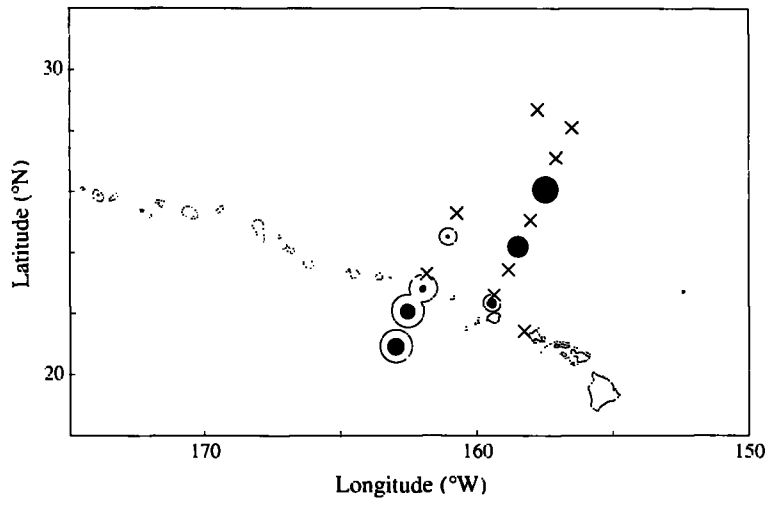

Figure 10

Map of the Hawaiian Archipelago showing the projected spawning grounds of *Ommastrephes bartramii* paralarvae captured during the 1992 *Townsend Cromwell* survey. Open circles represent the estimated spawning area for all paralarvae from each station. Closed circles represent the estimated spawning area for the youngest paralarvae from each station. × = station with no *O. bartramii* paralarvae present.

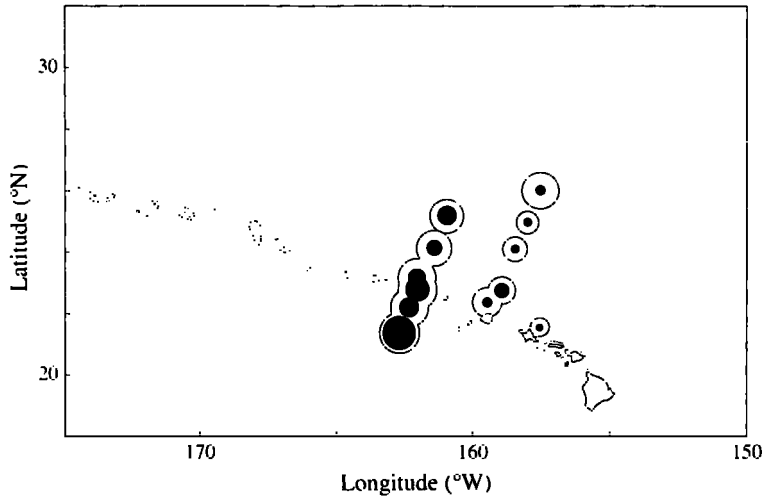

Figure 11

Map of the Hawaiian Archipelago showing the projected spawning grounds of *Ommastrephes bartramii* paralarvae captured during the 1993 *Hokusei Maru* survey. Open circles represent the estimated spawning area for all paralarvae from each station. Closed circles represent the estimated spawning area for the youngest paralarvae from each station.

Table 2

Estimated hatching localities of *O. bartramii* paralarvae relative to the Hawaiian Archipelago (assuming a unidirectional flow away from the archipelago). Stn = station number; DO = station distance from archipelago; Catch = number captured; Min age = age of youngest paralarvae; Max age = age of oldest paralarvae; Max distance traveled = maximum distance the oldest paralarvae could have traveled after hatching; and Minimum distance from land = the closest to the archipelago the largest paralarvae could have hatched. *XX* = indicates spawning of largest animal could have occurred at archipelago. % = percentage of paralarvae of all ages from each station that would have hatched ≥10 km from the archipelago. Cruise total = percentage of paralarvae of all ages from entire survey that must have hatched ≥10 km from the archipelago. Total samples = percentage of paralarvae of all ages from all surveys combined that must have hatched ≥10 km from the archipelago. NC = no increment count.

Stn.	DO (km)	Catch (no.)	Min age (d)	Max age (d)	Max distance traveled (km)	Minimum distance from land (km)	%
***Hokusei Maru* February 1991 survey**							
1	9	2	14.8	14.8	40	*XX*	0
2	16	26	10.7	24.9	62	*XX*	0
3	106	168	4.6	23.7	59	47	100
4	235	56	12.0	21.1	53	182	100
5	349	43	2.2	22.6	56	293	100
6	460	57	8.4	20.5	51	409	100
7	583	16	12.0	24.7	62	521	100
8	33	0	—	—	—	—	—
Cruise total							92
***Townsend Cromwell* February 1991 survey**							
1	228	4	14.8	22.6	56	172	100
2	15	2	22.9	25.6	64	*XX*	0
3	232	59	0.8	21.7	54	178	100
4	207	28	13.2	24.4	61	146	100
5	28	1	NC	NC	—	—	—
6	16	4	26.9	30.1	75	*XX*	0
7	28	0	—	—	—	—	—
8	13	1	19.8	19.8	49	*XX*	0
9	25	1	NC	NC	—	—	—
10	14	0	—	—	—	—	—
Cruise total							93

meters during the day. If spawning was limited to waters near the island chain, a gradient in size with distance from shore would be expected. Presumably smaller animals would be caught nearshore and larger animals farther offshore. No correlation was found between size and distance from shore.

Drifter data confirm the picture of circulation near the Hawaiian Archipelago that flows are complex and highly variable throughout the islands. Although speeds of four drifters were averaged to estimate a general flow speed in the region, determining where particular paralarvae originated could best be deter-

Table 2 (continued)

Stn.	DO (km)	Catch (no.)	Min age (d)	Max age (d)	Max distance traveled (km)	Minimum distance from land (km)	%
***Hokusei Maru* February 1992 survey**							
1	14	0	—	—	—	—	—
2	11	2	6.6	12.6	31	*XX*	0
3	41	0	—	—	—	—	—
4	142	0	—	—	—	—	—
5	235	1	14.8	14.8	37	198	100
6	337	0	—	—	—	—	—
7	471	1	18.7	18.7	47	424	100
8	585	0	—	—	—	—	—
9	713	0	—	—	—	—	—
10	732	0	—	—	—	—	—
11	269	0	—	—	—	—	—
12	181	23	2.2	12.0	30	151	100
13	26	0	—	—	—	—	—
14	25	129	4.6	20.5	51	*XX*	2
15	126	49	10.7	23.7	59	67	100
16	256	37	12.0	23.7	59	197	100
Cruise total							44
***Townsend Cromwell* March–April 1992 survey**							
1	228	65	5.7	17.1	43	185	100
2	52	195	6.6	22.0	55	*XX*	54
3	74	103	4.6	21.1	53	21	100
4	299	38	2.2	22.0	55	244	100
5	526	0	—	—	—	—	—
6	759	0	—	—	—	—	—
7	972	0	—	—	—	—	—
8	1161	0	—	—	—	—	—
9	954	0	—	—	—	—	—
10	709	145	6.6	25.1	63	646	100
11	482	2	3.5	17.1	43	439	100
12	272	8	6.6	24.4	61	211	100
13	61	0	—	—	—	—	—
Cruise total							84
***Hokusei Maru* February 1993 survey**							
1	20	12	4.6	13.2	33	*XX*	0
2	472	6	6.6	26.6	66	406	100
3	341	16	5.7	16.2	40	301	100
4	230	43	5.7	17.5	44	186	100
5	68	20	10.0	19.8	49	19	100
6	15	137	6.6	21.4	53	*XX*	0
7	271	69	13.2	24.4	61	210	100
8	135	18	10.7	25.6	64	71	100
9	15	63	12.0	27.8	69	*XX*	0
10	36	15	16.7	28.6	71	*XX*	0
11	135	53	13.7	27.6	69	66	100
12	207	2	23.7	29.1	73	134	100
Cruise total							51
Total samples							72

mined by sampling near a drifter that had been tracked. Dynamic height variations reveal information about the longitudinal extent of the reversing flows along the Hawaiian Ridge. Measurements from CTD probes support the findings of studies that suggest the existence of bands of fairly strong currents that are immediately adjacent to the windward side of the Hawaiian Ridge and that are flowing in opposite directions (White, 1983; Mysak and Magaard, 1983).

Bower et al.[1] suggested that distribution of *O. bartramii* paralarvae is not related to the position of the Hawaiian Archipelago. The results presented here confirm this and indicate that most paralarvae captured during the five surveys were hatched at least 10 kilometers from shore, so that spawning occurs predominantly in oceanic waters.

Acknowledgments

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Effects of square-mesh panels in codends and of haulback delay on bycatch reduction in the oceanic prawn-trawl fishery of New South Wales, Australia

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Abstract.—Two experiments were conducted in the New South Wales oceanic prawn-trawl fishery, 1) by comparing catch from a conventional codend with that from two new codend designs with square-mesh panels and 2) by showing the effects on catches of a short delay in haulback of trawls with square-mesh panels. The two new codend designs incorporated panels of netting (85-mm mesh) sewn such that the meshes were square-shaped (measuring 7 × 11 bars) and inserted lengthwise and widthwise into the tops of the anterior sections. Simultaneous comparisons among these designs and a conventional codend showed that both designs performed similarly by significantly reducing the weights of bycatch that would be discarded (by 46% and 38%, respectively) without significantly reducing the catch of the prawn *Penaeus plebejus*. The second experiment showed that juvenile red spot whiting, *Sillago flindersi*, an important commercial finfish, escaped from the square-mesh panels in the trawl during a 10–15 second haulback delay. Trawls without any haulback delay showed no significant reduction in the bycatch of this species. The results are discussed in terms of the probable behavior of fish in the modified trawls and in terms of the implications that factors such as haulback delay may have on the survival of fish escaping through square-mesh panels in codends.

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In many of the world's prawn-trawl fisheries, significant numbers of nontarget organisms (collectively termed "bycatch," sensu Saila, 1983) are caught incidentally with targeted prawns. This bycatch often includes a large and diverse assemblage of small fish, some of which are juveniles of commercially and recreationally important species (for reviews see Saila, 1983; Andrew and Pepperell, 1992; Alverson et al., 1994; Kennelly, 1995). The incidental capture and mortality of large numbers of these juveniles has been of worldwide concern in recent years because it may reduce the potential biomass and yield of stocks that form the basis of other fisheries (Gordon, 1988; Foldren, 1989).

In New South Wales (NSW), Australia, oceanic prawn trawling involves approximately 300 vessels that usually operate during the night from 11 ports. This fishery is valued at approximately A$17 million per annum and primarily targets the eastern king prawn, *Penaeus plebejus*, although a significant proportion of the total income is derived from the sale of legally retained bycatch (termed "byproduct"), which comprises several commercially important species of fish, crustaceans, and cephalopods (see Kennelly et al., 1992). However, a recent survey examining the spatial and temporal distributions and abundances of the catch and bycatch from four ports in this fishery showed that juveniles of commercially important species comprised a significant portion of the bycatch (Kennelly[1]). Athough many of these juveniles showed large temporal and spatial variabilitiy in their occurrence, some (e.g. red spot whiting, *Sillago flindersi*, and eastern blue spot flathead, *Platycephalus caeruleopunctatus*), were consistently caught in large numbers throughout the sampling period. Although there are few data available on the population structure and dynamics of the key bycatch species or on the extent of their post-trawl mortalities, the quantities involved have raised concerns regarding potential detrimental impacts of prawn trawling on future stocks of these species (Kennelly, 1993). We therefore began an investigation that examined various modifications to trawling gear and trawling practices that minimize undesirable bycatch while maintaining catches of prawns and commercial byproduct.

[1] Kennelly, S. J. 1993. Study of the bycatch of the NSW east coast trawl fishery. Final report to the Fisheries Research and Development Corporation, P.O. Box 222, Deakin, ACT, 2600, Australia. Project No. 88/108. ISBN 0 7310 2096 0, 520 p.

One suite of modifications to trawls that has been successful throughout the world in reducing bycatches while retaining the target catch involves the use of square-mesh panels in codends (Robertson and Stewart, 1988; Carr, 1989; Briggs, 1992; Broadhurst and Kennelly, 1994; Robertson[2]; Isaksen and Valdemarsen[3]; Suuronen[4]). Quantifying the effectiveness of square-mesh panels in codends has been approached by a variety of experimental methods. At the simplest level, catches and bycatches from control and modified codends have been compared by using alternate tows (Robertson and Stewart, 1988; Broadhurst and Kennelly, 1994), by towing both codends as twin gear (Briggs, 1992), by using trouser trawls (Walsh et al., 1992; Suuronen[4]), or by towing either gear from two adjacent vessels (Thorsteinsson, 1992). Alternatively, covers of small-mesh netting over modified codends have provided estimates of the quantities of fish escaping (Robertson and Stewart, 1988).

Although these kinds of experiments have determined the effectiveness of square-mesh panels in codends, without direct observations by divers or cameras there is no information available on the patterns of behavior of escaping fish or on the period when escapement occurs during tows. The latter point raises an important issue with respect to the survival rates of escaped catch. Because fish are exhausted to varying degrees owing to the stress associated with capture (see Wardle, 1983; Main and Sangster[5]), the ultimate efficiency of square-mesh panels in reducing bycatch mortality is determined by the rate at which nontarget individuals are excluded. The survival of these individuals is probably inversely proportional to the time spent in the trawl, because studies have shown that fish that remain in the codend are subjected to high levels of stress and fatigue (Main and Sangster[5]; Main and Sangster[6]).

Observations from divers, from video cameras, and from towed submersibles, have provided conflicting information on the behavior of escaping fish (Wardle, 1983, 1989; Watson, 1989; Briggs, 1992; Watson et al., 1993). For example, in the Irish Sea, Briggs (1992) observed that the escape of European whiting, *Merlangius merlangus,* occurred continually throughout the duration of the tow. In contrast, Watson et al's (1993) studies in the Gulf of Mexico showed that red snapper, *Lutjanus campechanus,* maintained their position within the codend throughout the tow and escaped only when haulback was initiated.

In the NSW oceanic prawn-trawl fishery there is commonly a delay of up to 15 seconds (s) between slowing the vessel and engaging the winch to haul in the trawl (termed haulback delay). Because of this delay, possible effects, such as those observed by Watson et al. (1993), need to be investigated prior to interpreting the effectiveness of square-mesh panels in codends. Direct observations of such effects, however, always assume that the divers or cameras have no artificial effects on the behavior of the fish or on the normal commercial operation of the gear. While it may be reasonable to assume minimal effects in conditions with adequate light, Wardle (1989) found that the use of cameras with artificial light at night or in turbid conditions (below 10^{-3} lux) disorientated fish and disturbed their behavior. The possibility of such effects makes this technique unsuitable for assessing the effects of haulback delay on square-mesh panels in the NSW oceanic prawn-trawl fishery which operates at night.

Our specific goals in this experiment were 1) to investigate the effectiveness of square-mesh panels in reducing the bycatch from the NSW oceanic prawn-trawl fishery and 2) via a manipulative experiment, to provide an accurate and inexpensive means to determine the effects of haulback delay on the performance of these designs.

Materials and methods

Two experiments were conducted on commercial prawn-trawl grounds east of Yamba, New South Wales (29°26'S, 153°22'E), between August and October 1994 by using a commercial prawn trawler (13.8 m). Three florida flyers (mesh size 42 mm), each with a headline length of 12.8 m, were rigged in a standard triple gear configuration (see Andrew et al., 1991, for details) and towed at 2.5 knots. Each of the identical outside nets were rigged with zippers (no. 10 nylon open-ended auto lock plastic slides) to facilitate changing of the codends (see Broadhurst et al., in press). Because the middle net was not rigged

[2] Robertson, J. H. B. 1983. Square mesh cod-end selectivity experiments on whiting (*Merlangius merlangus* (L.)) and haddock (*Melanogrammus aeglefinus* (L.)). Int. Counc. Explor. Sea, council meeting 1983/B:25, 13 p. [Mimeo.]

[3] Isaksen, B., and J. W. Valdemarsen. 1986. Selectivity experiments with square mesh codends in bottom trawl. Int. Coun. Explor. Sea, council meeting 1986/B:28, 18 p. [Mimeo.]

[4] Suuronen, P. 1990. Preliminary trials with a square mesh codend in herring trawls. Int. Counc. Explor. Sea, council meeting 1990/B:28, 14 p. [Mimeo.]

[5] Main, J., and G. I. Sangster. 1988. Scale damage and survival of young gadoid fish escaping from the cod-end of a demersal trawl. *In* J. DeAlteris (ed.), Proceedings of selectivity and survivability workshop, p. 17–34. Univ. Rhode Island Sea Grant Advisory Service, Narragansett, RI.

[6] Main, J., and G. I. Sangster. 1991. A study of haddock (*Merlanogrammus aeglefinus* (L.)) behavior in diamond and square-mesh codends. Scot. Fish. Work. Paper 19/91, 25 p.

exactly like the outside nets (see Andrew et al., 1991), it was excluded from our analyses.

The codends used in the experiments measured 75 meshes long (3 m) and were constructed from 40-mm mesh netting (Fig. 1). They comprised two panels. The anterior panel was 100 meshes in circumference and constructed of 25 meshes of 48-ply twine attached to 25 meshes of 35-ply twine. The posterior panel was 200 meshes in circumference and constructed of 3-mm diameter braided twine.

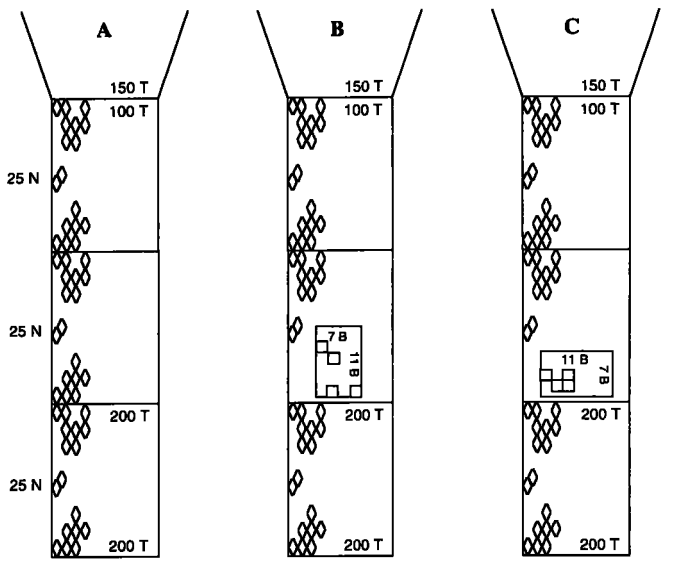

Figure 1

Diagrammatic representation of (**A**) the control codend, (**B**) the 85-mm-long codend and (**C**) the 85-mm-wide codend (T=transversals; B=bars; N=normals).

Experiment 1—evaluation of codends

Three codend designs were compared. The control codend was made entirely of diamond-shaped meshes (Fig. 1A). The second codend (termed the 85-mm-long codend) had a panel of 85-mm netting cut on the bar (7 bars × 11 bars) inserted lengthwise into the top of the anterior section (Fig. 1B). The third codend (termed the 85-mm-wide codend) had the same panel inserted sideways into the top of the anterior section (Fig. 1C).

All three codends were compared against each other in independant, paired trials. That is, in separate tows, the 85-mm-long codend was compared against the control; the 85-mm-wide codend was compared against the control; and the 85-mm-long and 85-mm-wide codends were compared against each other. The particular pair to be compared in a given tow were placed on each outside net of the triple-rigged gear. The position and order of each codend was determined randomly (to eliminate any biases between different nets) and the codends were used in normal commercial tows of 90-min duration (with a haulback delay of 10–15 s) on established prawn-trawl grounds. Over six nights we completed a total of 10 replicate tows of each paired comparison. Prior to the trials and at the end of each night, we rigged the outside nets with normal commercial codends and performed tows to ensure that there were no differences in the fishing characteristics of each net.

Experiment 2—effects of haulback delay

In this experiment the 85-mm-long codend from experiment 1 was tested against the control for possible effects due to haulback delay. The codends were interchanged between tows, and each night we completed two replicate 90-min tows that included 1) a 10–15 s haulback delay (measured as the duration between slowing the vessel and engaging the winch) and 2) no haulback delay. Over 4 nights we completed a total of 8 replicate tows for each type of haulback.

To ensure independence among tows, the location and direction of each tow was randomly selected from the available locations on established grounds northeast of Yamba. The grounds trawled varied in depth and ranged between 20 and 25 fm.

Data collected from the experiments

After each tow in each experiment, the codends were emptied onto a partitioned tray. Prawns and all commercially important species larger than the minimum legal size (retained commercials) were separated from the remaining bycatch. The remaining bycatch (termed discarded bycatch) was then sorted. This included individuals of commercially important species that were smaller than the minimum legal size (discarded commercials). Data collected from each tow were the total weight of prawns and their size (to the nearest 1-mm carapace length); the weight of the discarded bycatch; the weights, numbers, and sizes (to the nearest 0.5 cm) of discarded commercial species and retained commercial species; and the numbers of noncommercial species in the assemblage. All individuals were counted without subsampling. Several commercially important species were caught in sufficient quantities to allow meaningful comparisons. These were eastern king prawn, *Penaeus plebejus*, cuttlefish, *Sepia* sp., Octopus, *Octopus* sp., red spot whiting, *Sillago flindersi*,

eastern blue spot flathead, *Platycephalus caeruleopunctatus*, and smooth bug, *Ibacus* sp.

The paired comparisons done in experiment 1 were analyzed with one-tailed, paired *t*-tests. Data from experiment 2 were analyzed with two-factor analysis of variance (Underwood, 1981) after testing for homogeneity of variances (Cochran's test). Further, treating the data from each haulback-delay period separately, we compared data from the pairing of the 85-mm-long and control codends, using one-tailed, paired *t*-tests. Data from the 85-mm-long codend and its control (which used the haulback delay of 10–15 s in experiment 2) were combined with data from these codends in experiment 1, to provide a larger dataset for analysis of the results for the 85-mm-long codend. Size frequencies of prawns and red spot whiting from both experiments and the combined data were compared by using two-sample Kolmogorov-Smirnov tests (P=0.05).

Results

Experiment 1—evaluation of codends

Both the 85-mm-long and 85-mm-wide codends significantly reduced the weight of discarded bycatch (means reduced by 46% and 38%, respectively) (Fig. 2A; Table 1). The 85-mm-wide codend significantly reduced the number and weight of discarded red spot whiting (by 71% and 75%), and the number of trash species (Fig. 2, D–F; Table 1). There were insufficient data from the 85-mm-long codend to analyze data for red spot whiting (<2 fish per replicate). Neither of the codends with square-mesh panels significantly reduced the catch of prawns (Table 1), although the mean catches were 7.5% lower in the 85 mm long codend and 2.5% lower in the 85-mm-wide codend (Fig. 2G). Apart from a significant reduction in the number of trash species with the use of the 85-mm-long codend (Fig. 2F; Table 1), there were no other detectable differences between the two codends with square-mesh panels. Two-sample Kolmogorov-Smirnov tests comparing the size-frequency distributions for the king prawns and red spot whiting measured from each sample showed no significant differences in the relative size compositions between any of the codends tested.

Experiment 2—effects of haulback delay

There were no significant effects due to haulback delay on the differences in catch between the control and 85-mm-long codends for the weight of bycatch and prawns (Fig. 3, A–B; Table 2). However, haulback delay significantly increased the difference in catch between the control and 85-mm-long codends for the number and weight of red spot whiting and decreased the weight of retained cuttlefish (Fig. 3, C–E; Table 2). There were no significant effects among any of the other variables (i.e. retained octopus, discarded eastern blue-spot flathead, smooth bug, and trash species) due to haulback delay. The number and weight of red spot whiting were significantly differ-

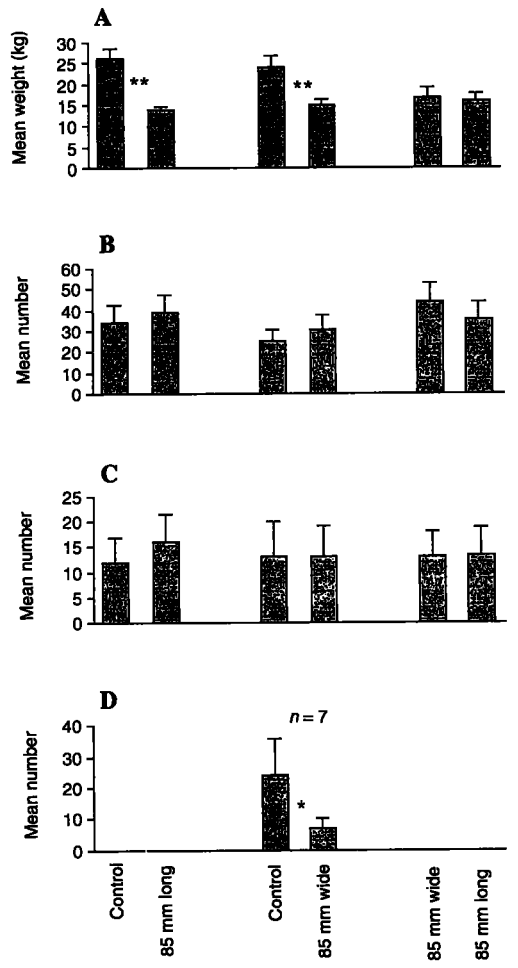

Figure 2

Differences in mean catch (±SE) between each of the codends in experiment 1 (evaluation of codends): (**A**) the weight of discarded bycatch; (**B**) the numbers of retained octopus (*Octopus* sp.); (**C**) the numbers of discarded cuttlefish (*Sepia* sp.); (**D**) the number of discarded red spot whiting (*Sillago flindersi*); (**E**) the weight of discarded red spot whiting (*Sillago flindersi*); (**F**) the number of noncommercial species; and (**G**) the weight of prawns (*Penaeus plebejus*). * = P<0.05; ** = P<0.01; unless stated otherwise, n = 10.

ent among nights in the experiment. No variables displayed significant interactions among haulback delay and nights (Table 2).

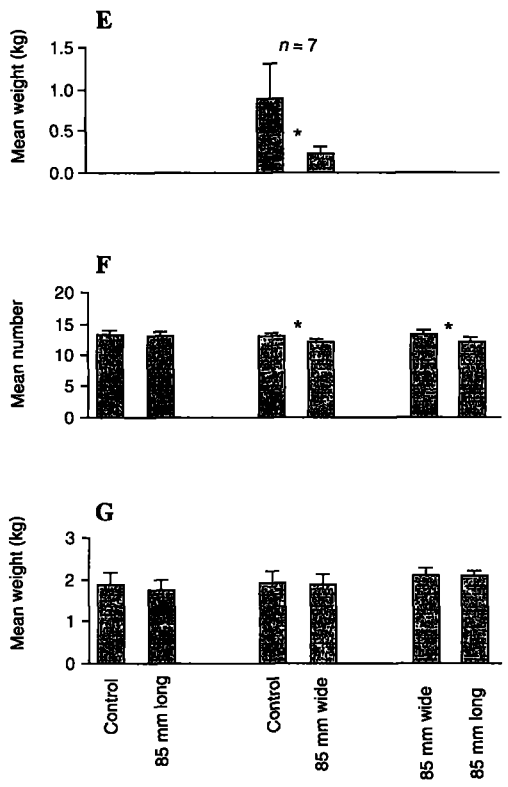

Figure 2 (continued)

One tailed, paired *t*-tests comparing data from the control and 85-mm-long codends showed that the 85-mm-long codend significantly reduced the weight of bycatch and significantly increased the weight of prawns during both a 10–15 s delay and no delay in haulback (Fig. 3, A–B; Table 3). The 85-mm-long codend significantly reduced the number and weight of discarded red spot whiting compared with the control during the 10 to 15 s haulback delay (means reduced by 64% and 56%, respectively) (Fig. 3, D–C; Table 3). There was no significant reduction in these variables for this codend when there was no delay in haulback, although the mean numbers and weights of red spot whiting were reduced by 21% and 25%, respectively (Fig. 3, D–C; Table 3). The weight of retained cuttlefish was significantly decreased in the 85-mm-long codend when there was no delay in haulback (Fig. 3E; Table 3). No other variables showed any differences between the control and 85-mm-long codends either with or without a delay in haulback. Two-sample Kolmogorov-Smirnov tests comparing size-frequency distributions for king prawn and red spot whiting (Fig. 4) measured from each sample showed no significant differences in the relative size compositions between the 85-mm-long and control codends during either a 10–15 s delay or no delay in haulback.

Aggregated data for the 85-mm-long codend

Combining all the data for the 85-mm-long codend, we found that this modification significantly reduced

Table 1

Summary of one-tailed paired *t*-tests comparing number and weight of catch of three different codends. *n* = number of replicates; rsw = red spot whiting.

	Control vs. 85-mm-long			Control vs. 85-mm-wide			85-mm-long vs. 85-mm-wide		
	Paired *t*-value	*P*	*n*	Paired *t*-value	*P*	*n*	Paired *t*-value	*P*	*n*
Weight of prawns	1.458	0.089	10	–0.357	0.635	10	0.000	—	10
Weight of discarded bycatch	6.355	0.0001**	10	5.800	0.0002**	10	0.491	0.317	10
Number of discarded cuttlefish	–2.17	0.971	10	0.638	0.269	9	–0.066	0.526	10
Weight of discarded cuttlefish	–0.656	0.736	10	–0.219	0.584	9	–0.264	0.601	10
Number of retained cuttlefish	0.810	0.219	10	0.819	0.217	10	–1.213	0.871	10
Weight of retained cuttlefish	1.331	0.108	10	–0.599	0.718	10	–0.077	0.530	10
Number of retained octopus	–1.847	0.952	10	–2.202	0.973	10	1.451	0.090	10
Weight of retained octopus	–0.248	0.595	10	–0.972	0.822	10	0.346	0.368	10
Number of discarded rsw	(insufficient data)			2.242	0.033*	7	(insufficient data)		
Weight of discarded rsw	(<2 fish per replicate)			2.223	0.034*	7	(<2 fish per replicate)		
Number of noncommercial sp.	1.246	0.122	10	2.228	0.026*	10	2.283	0.024*	10

*P=<0.05; **P=<0.01.

the weight of bycatch (mean reduction of 37%) and the number and weight of red spot whiting (by 68% and 58%, respectively) (Figs. 5, A–C; Table 4). This codend did not significantly reduce the weight of prawns (although the mean catch was 3% lower) nor any of the other variables (Fig. 5E; Table 4). Two-sample Kolmogorov-Smirnov tests failed to detect any significant difference in the size compositions of prawns between the 85-mm-long and control codends (Fig. 6A). The sizefrequency distributions for red spot whiting, however, were significantly different between these codends (Fig. 6B).

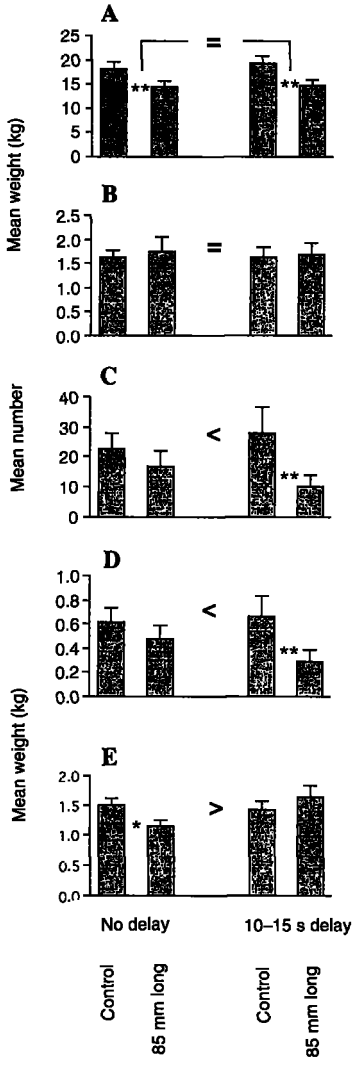

Figure 3

Differences in mean catch (±SE) between the control and 85-mm-long codends in experiment 2 (effects of haulback delay) for no delay and a 10–15 s delay in haulback (<, >, and = indicate direction of differences): (**A**) the weight of discarded bycatch; (**B**) the weight of prawns (*Penaeus plebejus*); (**C**) the number of discarded red spot whiting (*Sillago flindersi*); (**D**) the weight of discarded red spot whiting (*Sillago flindersi*); and (**E**) the weight of retained cuttlefish (*Sepia* sp.). * = $P<0.05$; ** = $P<0.01$.

Discussion

The results of these experiments show that codends with square-mesh panels have the potential to reduce bycatch of nontarget individuals (see also Robertson and Stewart, 1988; Briggs, 1992; Fonteyne and M'Rabet, 1992; Broadhurst and Kennelly, 1994). By experimentally examining the effects of haulback delay, we have also quantified, for the first time, the effects that such operational procedures can have on the escape of some individuals.

In previous experiments, Broadhurst and Kennelly (1994, 1995) showed that square-mesh panels in the anterior sections of codends were effective in releasing small fish (i.e. mulloway, *Argyrosomus hololepidotus*) from prawn trawls in the Hawkesbury River. These results were attributed to the differences in behavior of fish and prawns in their response to

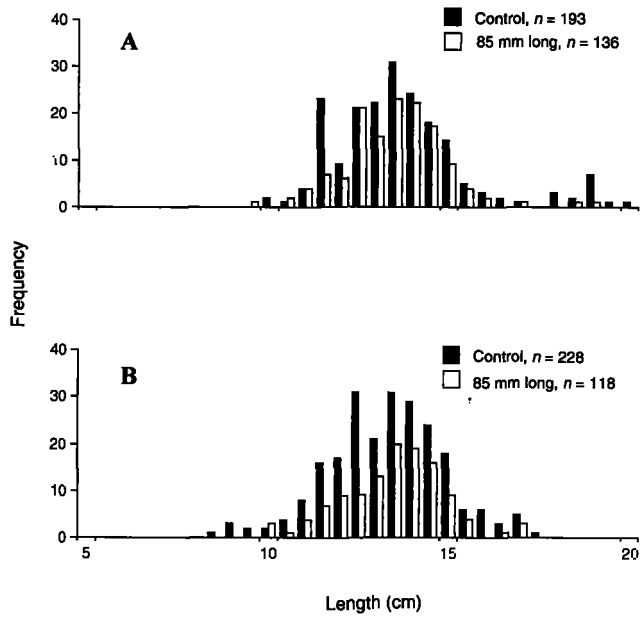

Figure 4

Length-frequency distributions of red spot whiting (*Sillago flindersi*) from the control and 85-mm-long codends for experiment 2: (**A**) during no delay in haulback and (**B**) a 10–15 s delay in haulback.

Table 2

Summary of F-ratios from two-way analyses of variance to determine effects on variables (weight and number of catch) due to haulback delay on different nights.

Treatment	df	Prawns (wt.)	Discarded bycatch (wt.)	Retained octopus (no.)	Retained octopus (wt.)	Retained cuttlefish (no.)	Retained cuttlefish (wt.)	Discarded eastern blue spot flathead (no.)	Discarded eastern blue spot flathead (wt.)	Discarded red spot whiting (no.)	Discarded red spot whiting (wt.)	Discarded smooth bugs (no.)	Discarded smooth bugs (wt.)	Trash species (no.)
Haulback delay (HD)	1	0.25	0.93	0.02	0.01	4.86	9.24*	0.13	0.06	8.25*	7.48*	0.26	2.77	0.02
Nights (N)	3	1.83	1.07	0.12	0.03	0.60	0.91	0.28	0.74	6.13*	5.95*	3.74	0.66	0.57
HD × N	3	2.51	2.26	0.21	1.13	1.78	0.60	0.44	0.96	0.156	0.58	1.07	0.48	1.30
Residual	8													

*$P<0.05$.

Table 3

Summary of one-tailed paired t-tests for the effect of haulback delay on weight and number of catch for control and 85-mm-long codends. $n = 8$ for all comparisons; rsw = red spot whiting; ebs = eastern blue spot flathead.

	No haulback delay		10–15 second haulback delay	
	Paired t-value	P	Paired t-value	P
Weight of prawns	0.903	0.198	–0.595	0.715
Weight of discarded bycatch	7.976	0.0001**	4.610	0.001**
Number of retained octopus	–0.242	0.592	–0.043	0.516
Weight of retained octopus	1.560	0.081	0.979	0.180
Number of retained cuttlefish	1.964	0.045*	–1.085	0.844
Weight of retained cuttlefish	2.694	0.015*	–1.843	0.946
Number of discarded ebs	–0.403	0.951	–0.989	0.823
Weight of discarded ebs	–0.956	0.815	–0.712	0.751
Number of discarded rsw	1.072	0.159	3.464	0.0005**
Weight of discarded rsw	0.778	0.231	3.984	0.002**
Number of discarded smooth bugs	–0.037	0.639	–0.716	0.752
Weight of discarded smooth bugs	–0.333	0.626	–0.477	0.676
Number of noncommercial sp.	0.477	0.334	0.174	0.433

*$P<0.05$; **$P<0.01$.

stimuli from the trawl and to the hanging configurations of the codends. Fish were apparently herded together at the taper of the codend, invoking an escape response to the sides and top of the net. The attachment of an anterior panel of 100-mesh circumference to a posterior panel constructed of heavy twine and 200-mesh circumference, presumably created a back pressure of water that was directed out through the open anterior square meshes, facilitating the escape of fish. This sequence of events was assumed to occur continually throughout the duration of the trawl. The response of prawns to this stimuli appeared fairly limited; other studies have shown that prawns are not capable of maintaining active escape responses to the trawl and are quickly forced against the meshes and towards the back of the codend (Lochhead, 1961; Main and Sangster, 1985; Newland and Chapman, 1989).

The two square-mesh codends used in experiment 1 were designed to take advantage of the theory discussed above by incorporating a panel of square mesh on top of the anterior section only, so that small fish might escape without a reduction in the catch of prawns or of larger commercially important bycatch

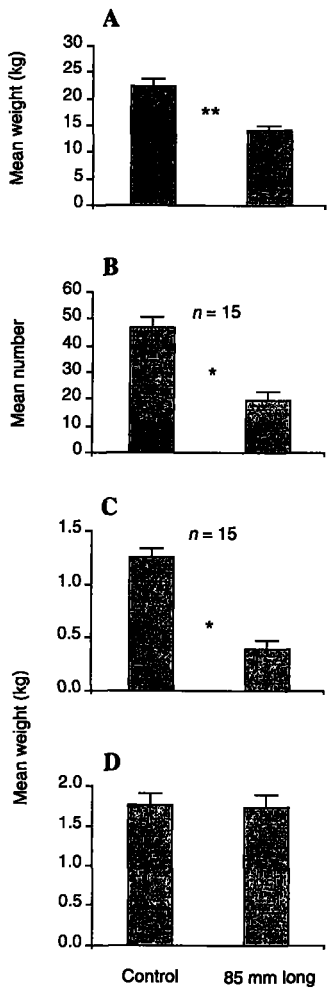

Figure 5

Differences in mean catch (± SE) between the control and 85-mm-long codend, combined across both experiments: (**A**) the weight of discarded bycatch; (**B**) the number of discarded red spot whiting, *Sillago flindersi;* (**C**) the weight of discarded red spot whiting, *Sillago flindersi;* and (**D**) the weight of prawns *Penaeus plebejus*. * = $P<0.05$; ** = $P<0.01$; unless stated otherwise $n = 18$.

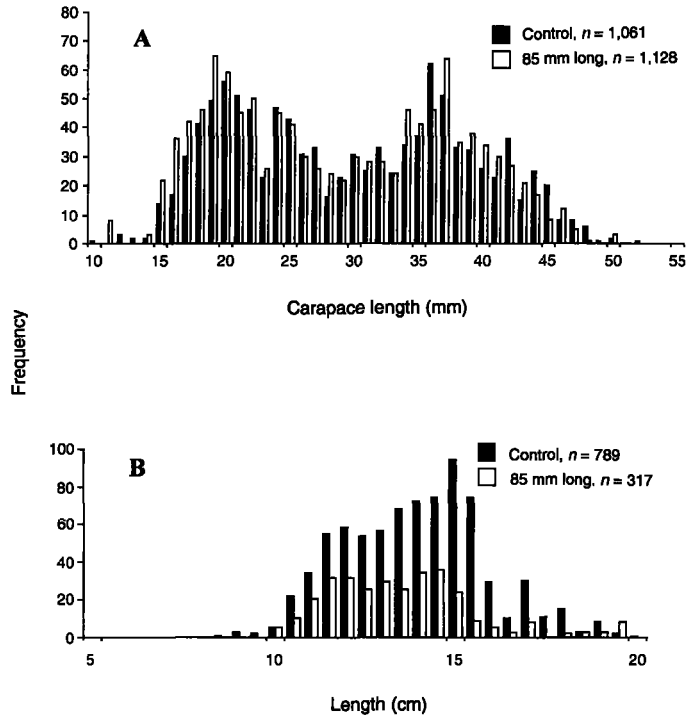

Figure 6

Length-frequency distributions of (**A**) king prawn, *Penaeus plebejus*, and (**B**) red spot whiting, *Sillago flindersi*, from the control and 85-mm-long codends combined across experiments.

species. Both the 85-mm-wide and 85-mm-long codends performed similarly, significantly reducing the weight of discarded bycatch (by 48% and 38% respectively) with no significant reduction in the weight of prawns or retained species (Fig. 2; Table 1). The 85-mm-wide codend also significantly reduced the number and weight of red spot whiting by 71% and 75%, respectively (Fig. 2; Table 1), whereas, based on the aggregated data, the 85-mm-long codend reduced these by 68% and 58%, respectively (Fig. 5; Table 4).

Experiment 2 compared the differences between the control and 85-mm-long codends with and without a short (10–15 s) delay during haulback. The results suggest that the individuals comprising discarded bycatch escaped continually throughout the duration of the tow (Fig. 3A; Table 2). Their behavior and escape from the square-mesh panel may be explained, therefore, according to the theory discussed above. For red spot whiting, however, there was no significant reduction in number or weight when there was no delay in haulback (although the means were reduced by 21% and 28%, respectively), but there was a significant reduction of 64% and 56.6%, respectively, for the tows that included a 10–15 s delay (see Figs. 3 and 6; Table 3). Red spot whiting, therefore, did not appear to exhibit the same behavior as the other species because the majority of these fish appeared to escape during the 10–15 s delay in haulback.

Table 4

Summary of one-tailed, paired *t*-tests comparing control and 85-mm-long codends trialed with a 10–15 s haulback delay, combined over both experiments. *n* = number of replicates; rsw = red spot whiting.

	Control vs. 85-mm-long		
	Paired *t*-value	*P*	*n*
Weight of prawns	1.000	0.165	18
Weight of discarded bycatch	5.720	0.0001**	18
Number of retained cuttlefish	0.355	0.363	18
Weight of retained cuttlefish	0.566	0.289	18
Number of retained octopus	–0.948	0.822	18
Weight of retained octopus	–0.169	0.566	18
Number of discarded rsw	1.935	0.036*	15
Weight of discarded rsw	2.185	0.023*	15
Number of noncommercial sp.	1.587	0.065	18

*$P<0.05$; **$P<0.01$.

A possible reason why few red spot whiting escaped continuously during trawling is that there were insufficient stimuli generated in the codend to invoke an escape response. This hypothesis is supported by previous studies that have shown that physiological and behavioral differences between species are major factors in the effectiveness of escape panels (Robertson and Stewart, 1988; Briggs, 1992; Fonteyne and M'Rabet, 1992). The subsequent escape of red spot whiting from the 85-mm-long codend during the 10–15 s haulback delay may have been a result of additional stimuli generated by changes in the geometry of the codend. For example, Watson (1989) observed that during haulback, differences in the contours of the codend and associated water flow caused fish to aggregate and become disorientated. The fish then increased their swimming speeds and randomly charged the meshes around the codend. By opening the meshes in this area (i.e. by our inclusion of the 85-mm-long square-mesh panel), we may have stimulated some fish to escape the trawl.

The delayed escape of red spot whiting from the 85-mm-long codend raises important questions concerning the extent of their mortality during trawling and after escape. Because previous studies have shown that fish that remain in the codend experience greater stress and fatigue than those that escape continuously, those individuals escaping at the end of the tow may suffer greater mortality. Further, such post-trawl mortality, particularly among smaller fish, may increase in proportion to tow duration. Obviously such effects on red spot whiting should be investigated prior to commercial use of the 85-mm-long codend per se, because, unless most of the escaping fish survive, such designs are of little value.

It may be possible to reduce the problems of trawl mortality for red spot whiting by altering the design of the 85-mm-long codend so that more fish escape continuously during trawling. One possible modification to the design would be to make the square-mesh panel longer (see Briggs, 1992), allowing more red spot whiting to escape at random along the codend. This may also provide juveniles of other commercially important species (i.e. cuttlefish, octopus, and eastern blue spot flathead) the opportunity to escape, although there was little evidence in our experiments to suggest that these species displayed active escape response toward the square-mesh panel (see Figs. 2 and 3; Tables 1–3). Their lack of exclusion is more likely attributable to intraspecific variability in behavioral responses rather than to the design of the square-mesh panel (see also Robertson and Stewart, 1988; Briggs, 1992).

Another modification to allow more red spot whiting to escape the trawl continuously may be to increase the size of mesh used in the panels. However, the size-frequency composition of red spot whiting captured in the 85-mm-long codend and control showed that the size of mesh used in the panel allowed fish within the range of sizes sampled to escape, including some individuals of commercial size (>16 cm) (Fig. 4). Further, this size of mesh resulted in no significant reduction in the weight of prawns, nor were there any significant differences detected in the size composition of prawns between the control and the 85-mm-long or 85-mm-wide codends. Subsequent increases in the size of mesh may, there-

fore, result in further loss of commercial red spot whiting and possibly some reduction in the catch of prawns.

The square-mesh codends tested in these experiments provide further evidence of the effectiveness of this type of exclusion device in reducing the bycatch of unwanted species, while maintaining the catch of prawns and other species of commercial size. Further, for a fishery that retains a range of species, these designs offer a relatively simple and inexpensive method for eliminating a large part of the incidental catch. It is evident from the results, however, that not all species to be excluded behave in a similar manner and that the effects of operational procedures such as haulback delay can significantly influence the rate of exclusion of some species. Therefore, it is imperative that future research into exclusion designs, such as square-mesh panels, include an assessment of such operational factors so that the full impact of bycatch excluders on reducing the mortality of incidentally caught juveniles can be assessed.

Acknowledgments

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Revision of the frigate tunas (Scombridae, *Auxis*), with descriptions of two new subspecies from the eastern Pacific

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Abstract.—Two cosmopolitan species of frigate tunas, *Auxis thazard* (Lacepède) and *A. rochei* (Risso), are differentiated primarily by the width of the corselet under the origin of the second dorsal fin and by the anterior extent of the dorsal scaleless area above the pectoral fin. *Auxis thazard* has five or fewer scales in the corselet under the second dorsal fin, and the dorsal scaleless area extends anterior to the tip of the pectoral fin; *A. rochei* has six or more scales and the dorsal scaleless area does not reach the tip of the pectoral fin. Of nine morphometric characters examined with ANCOVA, four body depth measurements were significantly different between the species. *Auxis rochei* is a slender species with each of the four body depth measurements approximately equal, whereas *A. thazard* is more tuna-shaped, with a deeper, more robust body and with more unequal body depth measurements. For both species, eastern Pacific populations differ from Atlantic and Indo-West Pacific populations at what we consider the subspecific level. The eastern Pacific *A. thazard brachydorax* new subspecies has more gill rakers, usually 43–48 vs. usually 38–42 in *A. t. thazard*. Body depth at anal-fin origin, pectoral-fin length, and corselet width were also significantly different between *A. thazard brachydorax* and *A. t. thazard*. The eastern Pacific *A. rochei eudorax* new subspecies has an even wider corselet than that of *A. rochei rochei*, usually more than 20 scales wide compared with 6–19 scales.

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It is not clear whether there are one or two species of frigate tunas of the genus *Auxis*. In the Indo-West Pacific region, several investigators have distinguished a narrow-corseleted species (N) from a wide-corseleted species (W): Bleeker (1854, 1855) from the East Indies as *A. tapeinosoma* (N) and *A. thynnoides* (W); Kishinouye (1915, 1923) from Japan as *A. hira* (N) and *A. maru* (W); Wade (1949) from the Philippines and Jones (1958) from India as *A. thazard* (N) and *A. tapeinosoma* (W); and Matsumoto (1960a) from Hawaii as *A. thazard* (N) and *A. thynnoides* (W). However, most Atlantic-based workers have considered the frigate tunas to be a single worldwide species which they have identified as *Auxis thazard* (Dresslar and Fesler, 1889; Jordan and Evermann, 1896; Fraser-Brunner, 1950; Rivas, 1951; Zavala-Camin, 1983). Fitch and Roedel (1963) have shown that there are two sympatric species of frigate tunas in the Indo-West Pacific: the narrow-corseleted *A. thazard* (Lacepède) and the wide-corseleted *A. rochei* (Risso) (Fig. 1). They used the name *A. rochei* for the wide-corseleted species on the supposition that only one species occurred in the Mediterranean Sea and Atlantic Ocean and that *rochei* was the earliest name for it. Richards and Randall (1967) have shown that both species occur in the Atlantic, reopening the question of the proper name for Atlantic *Auxis*.

Frigate tunas (*Auxis*) are the smallest members of the tribe Thunnini, the true tunas. *Auxis rochei* reaches a fork length (FL) of 600 mm and *Auxis thazard*, at least 420 mm. To date, frigate tunas have not been greatly exploited, partly because of their small size. Of the total world catch of tunas, bonitos, and billfishes in 1993 (4,654,750 metric tons (t), FAO, 1995), only 4.5% (208,305 t) was *Auxis*. The largest landings are by Asian countries (Philippines 110,357 t; Thailand 36,300 t; Japan 27,896 t; and India 15,684 t). *Auxis* has soft meat and is not suitable for sashimi (slices of raw fish) because of its strong astringent taste, probably due to the high level of free amino acids in the meat (Murata et al., 1994). At least as larvae, *Auxis* are widespread and very abundant (Yabe et al., 1963, fig. 15; Ahlstrom, 1971; Ramíriz-Estévez and Ornelas-

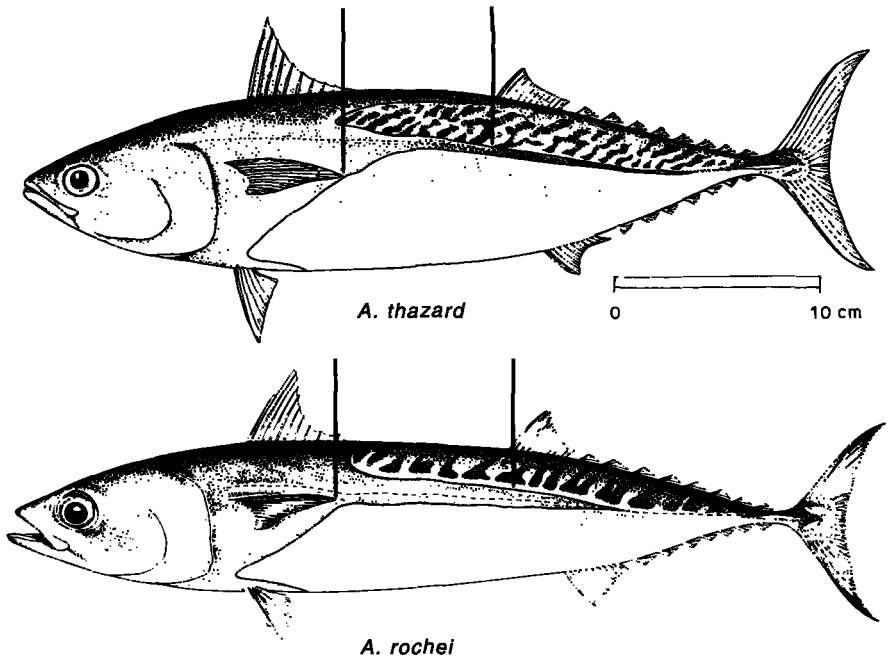


Figure 1

Auxis thazard (top) and *A. rochei* (bottom) showing anterior extent of dorsal scaleless area in relation to distal end of pectoral fin (left line) and width of corselet under origin of second dorsal fin (right line).

Roa, 1991). Richards (1984:28) concluded that *Auxis* "... is the most widely distributed and abundant scombrid in tropical seas." With stocks of other tuna species continually diminishing, there is increased potential for greater exploitation of *Auxis*. Before exploitation increases, it is necessary to establish how many species exist and what their correct names are, to determine how to identify them, and to obtain some idea of the major worldwide populations.

Fitch and Roedel (1963) also showed that the eastern Pacific populations of both species differed significantly from the Indo-West Pacific populations but did not name them pending further work. We confirm Fitch and Roedel's findings that the eastern Pacific population of *A. thazard* has more gill rakers (usually 43–48) than other populations (usually 38–42 in Atlantic and Indo-West Pacific populations), similar to the counts for *A. rochei*. The eastern Pacific population of *A. rochei* has an even wider corselet (usually more than 20 scales wide under the second dorsal fin) than other populations (8–19 scales in populations from the Indo-West Pacific).

This paper distinguishes the two species. We have located the type specimen of *rochei* and designate a neotype for *thazard* to stabilize current use of these names for these species. We evaluate the systematic status of eastern Pacific populations of the two species and describe them as new subspecies, *Auxis thazard* ***brachydorax*** and *Auxis rochei* ***eudorax***.

Materials and methods

Methods follow those used by Collette and Gillis (1992), in a revision of the double-lined mackerels *Grammatorcynus*, and by Collette and Russo (1985) in a revision of the Spanish mackerels *Scomberomorus*. Morphometric characters used in this study are as follows: FL (fork length); HdL (head length); P1L (pectoral-fin length); P1T (distance from pectoral-fin tip to anterior edge of dorsal scaleless area above lateral line); and CW (corselet width under second dorsal-fin origin). Owing to the different shapes of *A. rochei* and *A. thazard*, we postulated that four body depth measurements would illustrate these differences: 1Dor (body depth at origin of first dorsal); 1Dend (body depth at posterior end of first dorsal); 2Dor (body depth at origin of second dorsal); and Aor (body depth at anal-fin origin). *Auxis rochei* is a more slender species and the four body depth

measurements are approximately equal, whereas *A. thazard* is more tuna-shaped, having narrow entering and departing wedges and more unequal body depths.

Morphometric data were analyzed with regression analysis, analysis of covariance (ANCOVA), and principal component analysis (PCA). Regression analysis was run on the combined morphometric data for all populations of *A. rochei* vs. the combined populations of *A. thazard* to determine whether morphometric differences exist between species. Regression analyses were also run on morphometric data for major populations of each species to look for intraspecific differences. The following combinations of geographic populations were tested: for *A. rochei*—western Atlantic (n=36) vs. Mediterranean (n=34) plus eastern Atlantic (n=64), western Pacific (n=82) vs. eastern Pacific (n=37); for *A. thazard*—Gulf of Guinea (n=20) vs. Indian Ocean (n=38), western Pacific (n=75) vs. central Pacific (n=17), and westcentral Pacific (n=92) vs. eastern Pacific (n=69).

PCA was performed with the character variables FL, 1Dor, 1Dend, 2Dor, and Aor to determine whether these characters supported species level separation of *A. rochei* from *A. thazard* and separation between the eastern Pacific population and the other populations for both species. Very little separation was observed with PCA because 97.9% of the variation is explained by principal component 1. This means that almost 98% of the variation can be explained by differences in size, whereas only a little more than 2% of the variation can be explained by character differences among the different populations.

ANCOVA was performed on the variables 1Dor, 1Dend, 2Dor, Aor, P1L, and CW with size (FL) as the covariate to determine whether these characters differentiated *A. rochei* from *A. thazard* and to see whether eastern Pacific populations of each species were different from other populations. ANCOVA showed that morphometric data for each species were the same for all populations, except for the eastern Pacific, and could be combined. For each species, the combined populations were run against the eastern Pacific population to test the level of differentiation of the eastern Pacific population. For *A. rochei,* the combined populations we tested against the eastern Pacific (n=30) were western Atlantic (n=36), Gulf of Guinea (n=64), Mediterranean (n=34), Indian Ocean (n=9), and western Pacific (n=82). For *A. thazard,* the combined populations we tested against the eastern Pacific (n=63) were Indian Ocean (n=38), western Pacific (n=71), central Pacific (n=17), and Australia (n=4).

Material examined is listed at the end of each subspecies account and includes 267 specimens of *A. thazard* and 291 specimens of *A. rochei*. Abbreviations of institutions housing the material examined follow Leviton et al. (1985). CMFRI is the Central Marine Fisheries Research Institute, Cochin, India. ZRC is the current institutional code for the Zoological Reference Collection at the National University of Singapore.

Systematics

Auxis Cuvier, 1829

Auxis Cuvier, 1829:199. Type-species: *Scomber rochei* Risso, 1810, by subsequent designation of Gill, 1862

Diagnosis (Modified from Collette, 1979.) *Auxis* lacks the prominent paired fronto-parietal fenestra in the top of the skull found in all the other tunas, tribe Thunnini (except *Allothunnus*). The dorsal and ventral branches of the cutaneous artery originate separately from the dorsal aorta in *Auxis* (Godsil, 1954); a common cutaneous artery divides into dorsal and ventral branches laterally from the dorsal aorta in the other Thunnini. The ventral branch is very poorly developed, less so than in other Thunnini. The dorsal cutaneous artery lies ventral to the corresponding vein in *Auxis;* it lies dorsal in *Euthynnus* (Godsil, 1954). The vertebral column differs from all other scombrids in having a long pedicel or epihaemal process (1.5–2 times the centrum depth) that forces the dorsal aorta to run much further ventrally from the vertebral column than in other tunas. The interpelvic process is single and very long, equal to or longer than the pelvic fins themselves; it is shorter than the pelvic fins in all other Scombridae.

Description Body robust, elongate, and rounded. Teeth small and conical, in a single series. Two dorsal fins, the first with 10–12 spines, separated from the second by a long interspace (at least equal to length of first dorsal-fin base), the second fin followed by 8 finlets; pectoral fins short; anal fin followed by 7 finlets. Gill rakers 36–49. Body naked except for the corselet, which extends posteriorly along the lateral line past the origin of the second dorsal fin. In *A. thazard*, the extension is only 1–5 scales wide beneath the second dorsal fin, in *A. rochei* it is six scales or more. A strong central keel is present on each side of the caudal-fin base between two smaller keels. Vertebrae: 20 precaudal plus 19 caudal, total 39. Color: dorsum bluish, turning to deep purple or almost black on the head; belly white, usually without stripes or spots, occasionally black spots present on

belly between pectoral and pelvic fins as in *Euthynnus*; pectoral and pelvic fins purple, their inner sides black.

Relationships *Auxis* is related most closely to *Euthynnus* (Kishinouye, 1923; Collette, 1979, 1984; Finnerty and Block, 1995). It has been considered (Collette, 1979) to be the most primitive member (except for *Allothunnus*) of the Thunnini, the true tunas, because it lacks the frontoparietal fenestra present in *Euthynnus, Katsuwonus*, and *Thunnus,* because its subcutaneous circulatory system is more poorly developed than that of the more advanced tunas, and because *Auxis* shows no suturing of the first vertebra to the skull as is present in higher Thunnini. Tunas have a pair of lateral retia which serve the red muscle and act as heat exchangers enabling them to maintain body temperatures several degrees warmer than ambient water (3.5–9.5°C, mean 5.9°C, in the case of *Auxis,* Schaefer, 1985). In addition, *Auxis* and *Euthynnus* share a large central heat exchanger below the vertebral column in a series of enlarged haemal arches. *Auxis* is endothermic at sizes of 200 mm FL and larger (Dickson, 1994). The liver is similar to that in *Euthynnus* in having a very long right lobe running the length of the body cavity (Fig. 2). Prominent branches of the hepatic vein are present on the ventral surface of the liver lobes in both genera. *Auxis* differs from *Euthynnus* in having a greatly reduced left liver lobe; the left and middle lobes are of about equal length in *Euthynnus.* A swimbladder is present in larvae but degenerates by 20 mm as in *Euthynnus* and *Katsuwonus* (Richards and Dove, 1971).

Osteological comparisons Several authors (Kishinouye, 1923; Watanabe, 1962, 1964; Yoshida and Nakamura, 1965; Chi and Yang, 1972; Uchida, 1981; Zavala-Camin, 1983) have reported osteological differences between the species. Watanabe (1962, 1964) found that there were two types of *Auxis* based on long and short parapophyses. The differences were more prominent in specimens larger than 111 mm, especially on the 25th and 27th vertebrae. *Auxis thazard* had long free parapophyses, whereas *A. rochei* (as *A. tapeinosoma*) had short free parapophyses. In addition, in young *A. thazard* the first free parapophysis is developed mostly on the 23rd vertebra, and the first inferior foramen occurs on the 27th or 28th vertebra. In young *A. rochei,* however, the first free parapophysis is usually produced on the 21st or 22nd vertebra, and the first foramen occurs on the 29th or 30th vertebra. Other differences between the two species were the ratio of the caudal vertebral length to precaudal vertebral length and the ratio of body height at anal-fin origin to length from first dorsal to second dorsal origin. Yoshida and Nakamura (1965) found that in *A. thazard* the length of the anterior branch of the haemal process of the 24th to the 28th vertebra was longer and contacted the preceding arch. In *A. rochei* the anterior branches of the haemal processes were short, more fragile, and were never in contact with the preceding haemal arches. The angle between the temporal crests and a line parallel to the supraoccipital crest ranged from 0 to 2 degrees in *A. rochei* and from 3 to 7 degrees in *A. thazard.* In skulls of the same length, skulls of *A. thazard* were wider than those of *A. rochei.*

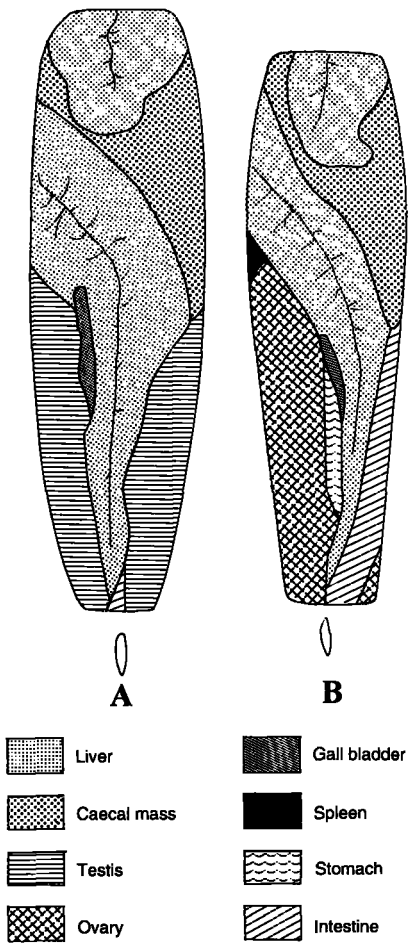


Figure 2
Viscera in ventral view. (**A**) *Auxis t. thazard*, USNM 339045, Philippine Is., 357 mm FL. (**B**) *Auxis r. rochei*, USNM 339044, Philippine Is., 262 mm FL.

Larval differences In several geographic regions, workers have been able to divide their material of larval and juvenile *Auxis* into what appear to be two

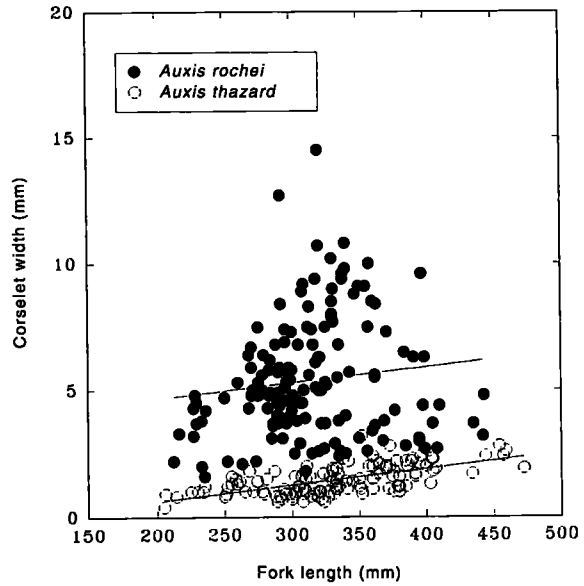


Figure 3

Corselet width under second dorsal-fin origin vs. fork length in *Auxis rochei* (closed circles, $y = 0.005x + 3.933$, r=0.09) and *A. thazard* (open circles, $y = 0.006 - 0.673$, r=0.62).

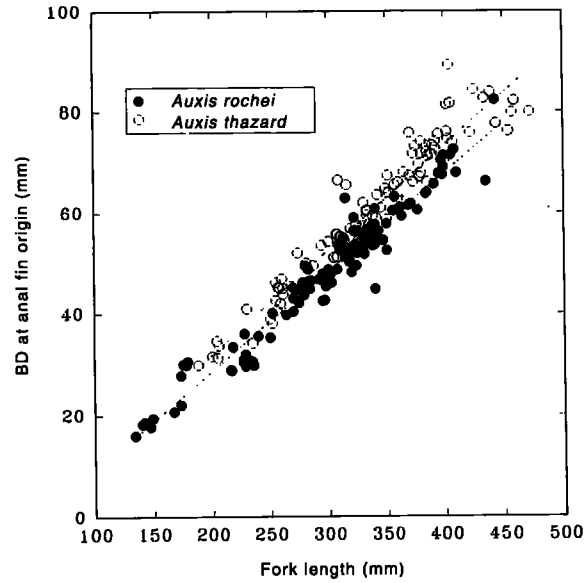


Figure 4

Body depth (BD) at anal-fin origin in *Auxis rochei* (closed circles, $y = 0.17x - 3.06$, r=0.92) and *A. thazard* (open circles, $y = 0.207x - 9.58$, r=0.96).

species (Wade, 1949, Philippines; Matsumoto, 1959; Gorbunova, 1969, 1974, Indian and Pacific oceans; Zhao et al., 1982, and Sun et al., 1986, China; Richards, 1989, western central Atlantic). Juveniles have been successfully identified (e.g. Wade, 1949), but larvae are more difficult to identify to species because the corselet scales and gill rakers that distinguish the adults are not fully developed in the larvae. For brief length intervals, pigment characters are useful in distinguishing two types of larvae.

Gorbunova (1974) distinguished between larvae of the two species. *Auxis rochei* is characterized by a seemingly slower rate of development and a shallower body depth. The relative size of the eye is smaller and the pigmentation on the caudal peduncle is less intense. *Auxis thazard* is distinguished by a more rapid rate of development, a greater body depth, a shorter caudal portion of the body, and more intense body pigmentation. Richards (1989) emphasized the presence of pigment along the lateral line in the posterior part of the body in *A. rochei* and its absence in *A. thazard*.

Biochemical differences The first attempts to separate the two species of *Auxis* biochemically were by Matsumoto (1960b) who found that Hawaiian specimens could be distinguished in a one-dimensional chromatogram. Taniguchi and Nakamura (1970) examined muscle protein of *A. thazard* and *A. rochei* by the cellulose acetate electrophoretic method. They found five components in the electropherograms of both species, but some components were not common to both. Electrophoretic patterns of the two species were clearly distinguishable from each other by the mobility and percentage of each component. Taniguchi and Konishi (1971) used starch gel electrophoresis to detect protein specificity between *A. thazard* and *A. rochei*. No individual variation occurred in the electropherograms of 11 specimens of *A. thazard*, whereas all 170 specimens of *A. rochei* fit into 1 of 3 phenotypic patterns. They hypothesized that these three phenotypes are controlled by two codominant alleles. Distribution of the three phenotypes was independent of age and sex.

Auxis thazard (Lacepède, 1800)

Frigate tuna

Diagnosis *Auxis thazard* has a narrow corselet that is 0.5–3.5 mm, usually 0.5–1.0 mm wide (Fig. 3) but no more than five scales wide under the second dorsal-fin origin (Table 1), a greater body depth at the anal-fin origin (Fig. 4), and the anterior margin of the scaleless area above the corselet extends anteriorly beyond the tip of the pectoral fins (Figs. 1 and 5) unlike that in *A. rochei*. Color pattern: 15 or more

Table 1

Number of corselet scales under second dorsal-fin origin in populations of *Auxis*.

	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	*n*	$\bar{x}$
A. t. thazard																																
W. Atlantic	—	—	4	1	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7	4.0
E. Atlantic	1	2	10	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	14	2.9
Indian O.	1	3	23	7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	34	3.1
W. Pacific	14	7	25	5	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	53	2.5
C. Pacific	—	—	11	3	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	16	3.4
																															124	2.7
A. t. brachydorax																																
E. Pacific	13	8	42	2	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	68	2.6
Galapagos	—	—	1	1	—	1	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	5.6
																															73	2.8
A. r. rochei																																
W. Atlantic	—	—	—	—	2	8	4	7	4	1	—	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	30	7.9
Mediterranean	—	—	—	—	—	—	3	2	1	5	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	13	9.2
E. Atlantic	—	—	—	—	—	—	—	4	3	2	2	9	6	6	3	4	4	3	3	2	1	2	—	1	—	—	—	—	—	—	55	14.3
Indian O.	—	—	—	—	—	—	1	—	—	3	2	3	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	10	11.5
W. Pacific	—	—	—	—	—	—	—	1	—	10	1	7	3	6	6	1	1	—	1	—	—	—	—	—	—	—	—	—	—	—	37	12.6
																															148	11.7
A. r. eudorax																																
E. Pacific	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2	1	1	1	—	2	8	3	2	2	3	—	—	1	1	1	29	21.6

narrow, oblique to nearly horizontal, dark wavy lines in the scaleless area above the lateral line (Figs. 1 and 6). Spots sometimes occur between the pectoral and pelvic fins (see Robins and Ray, 1986: pl. 48), as they usually do in *Euthynnus*.

Geographical distribution Probably cosmopolitan in warm waters (Fig. 7) but there have been relatively few documented occurrences in the Atlantic Ocean. Although we did not examine specimens of either species from the southeastern Atlantic and although Zavalla-Camin (1983) concluded that there was only a single variable species, both species do occur there as can be seen from the anterior extent of the dorsal scaleless area (Fig. 8, 20 specimens of *A. thazard* and 33 specimens of *A. rochei*). On the basis of two specimens of *A. thazard* from Haifa, Israel (HUJ 17480, HUJ 17826) provided by Dani Golani, we believe both species occur in the Mediterranean Sea.

Habitat and biology (From literature summarized in Uchida, 1981, and Collette and Nauen, 1983:29.) An epipelagic, neritic, and oceanic species. In the eastern Pacific, mature fish occur throughout the

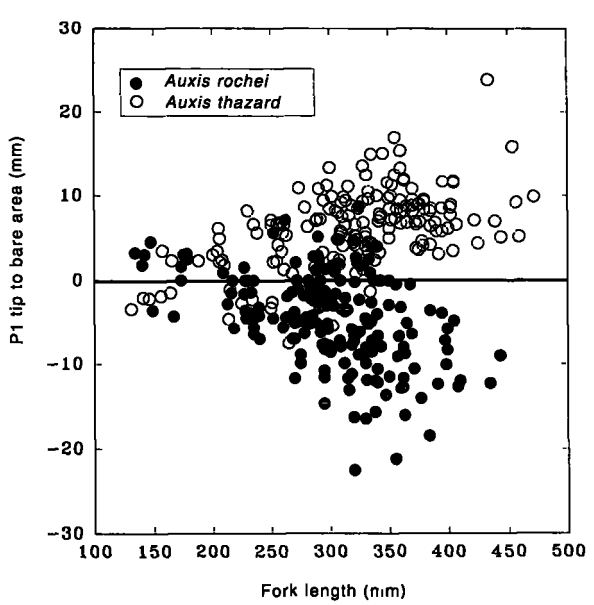
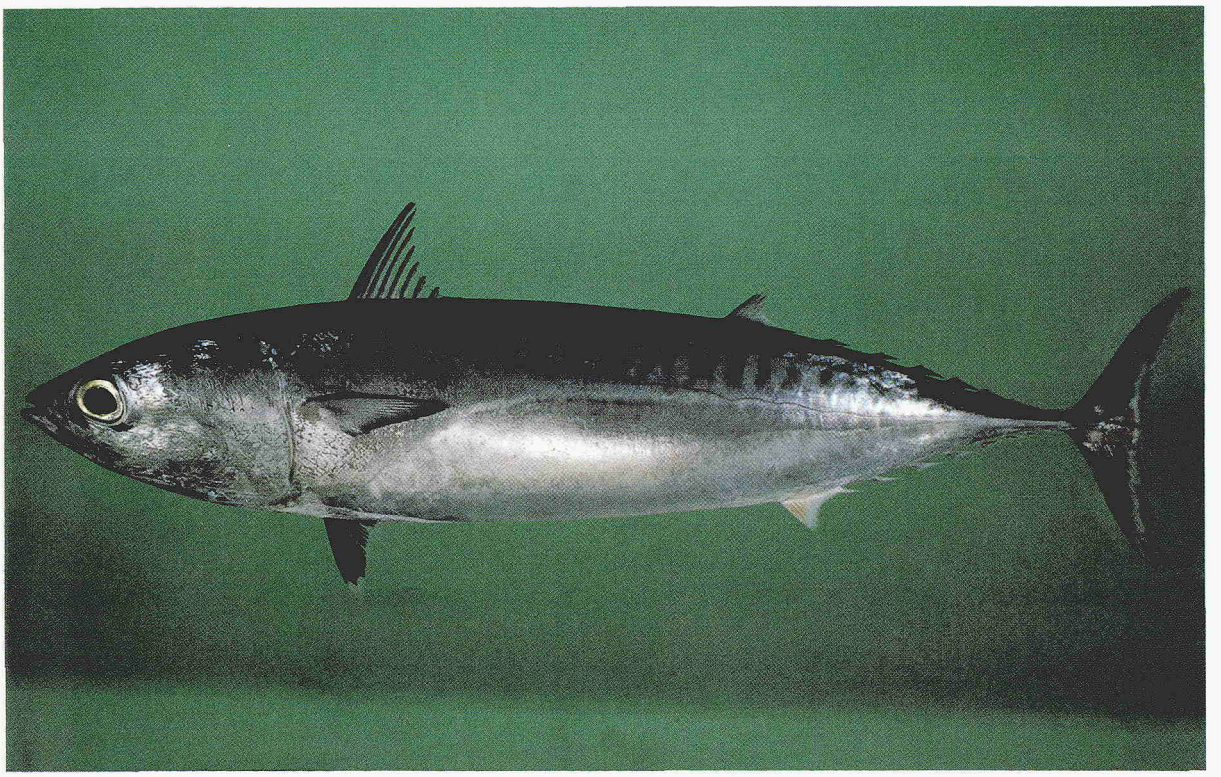


Figure 5

Distance from the tip of the pectoral fin (P1) to the bare area above the lateral line in *Auxis rochei* (closed circles) and *A. thazard* (open circles).



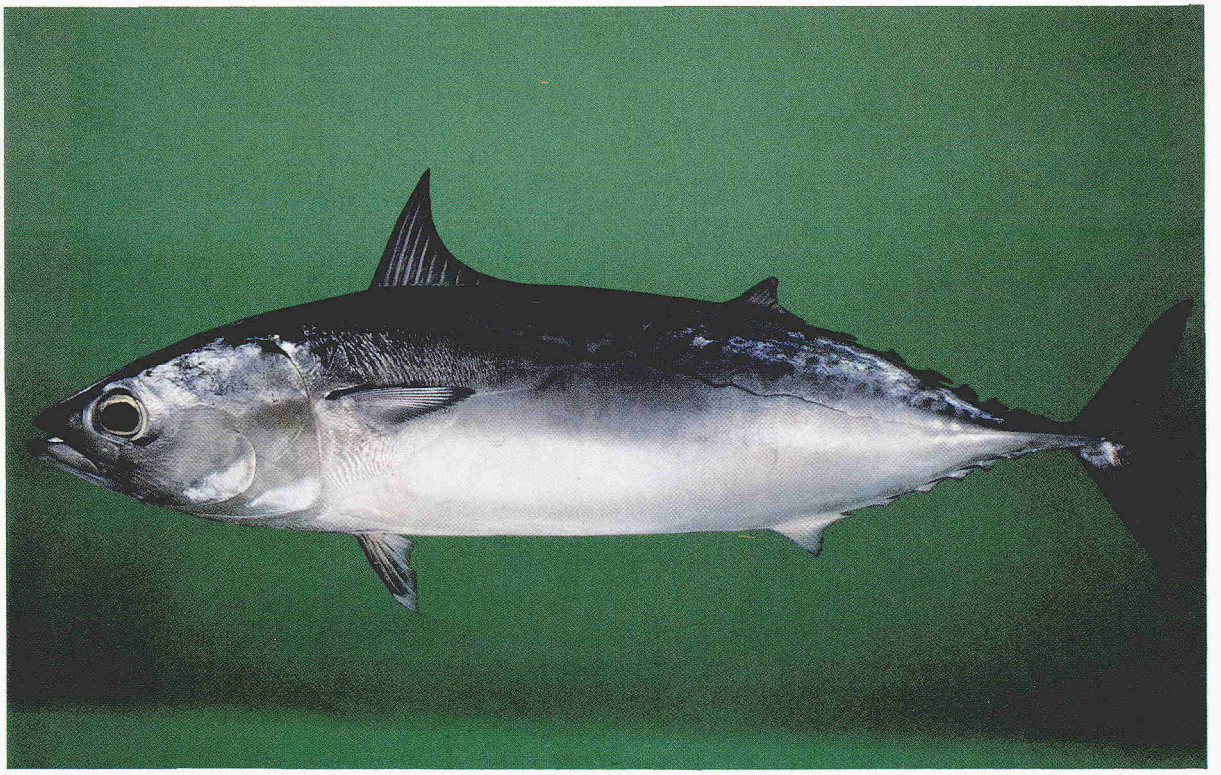


Figure 6

(**Upper photograph**) *Auxis rochei rochei*, 283 mm FL, Indonesia, Bali, Padang Bai; 28 Feb 1984; John E. Randall. (**Lower photograph**) *Auxis thazard thazard,* 267 mm FL, Hawaii, Oahu; 11 Nov 1994; John E. Randall.

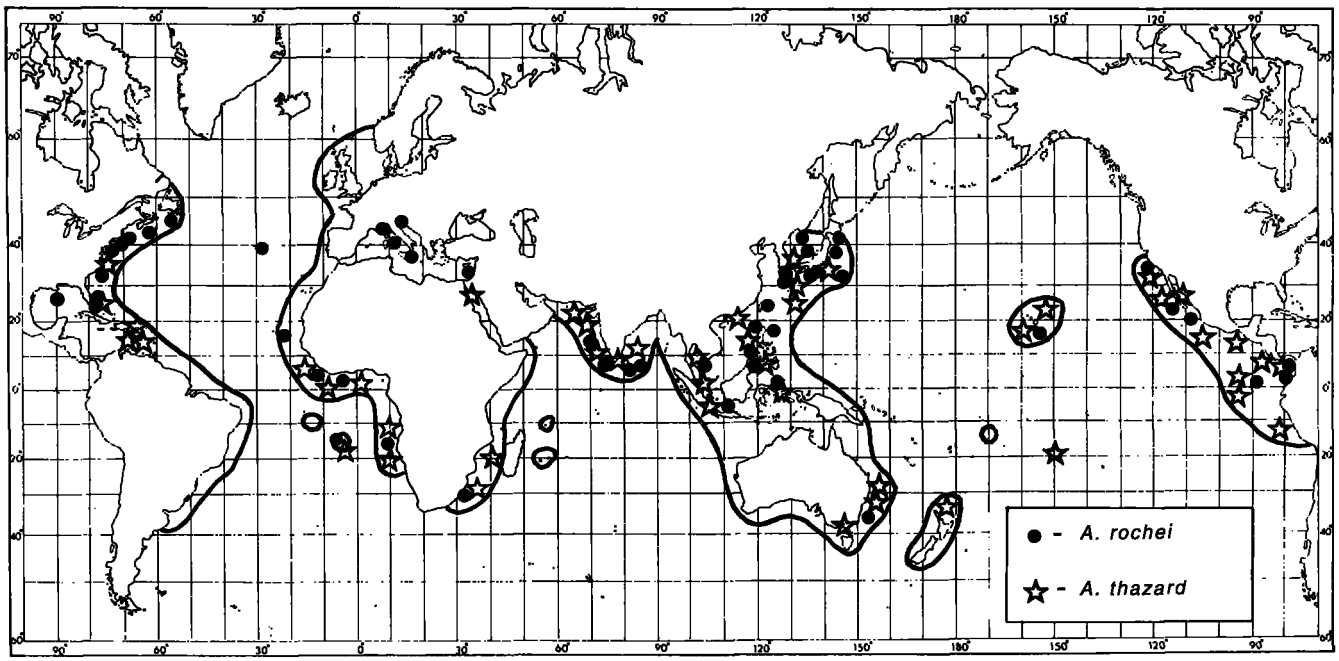


Figure 7

Distribution of *Auxis rochei* and *A. thazard*. Solid lines show approximate limits of distribution; symbols indicate localities of specimens examined.

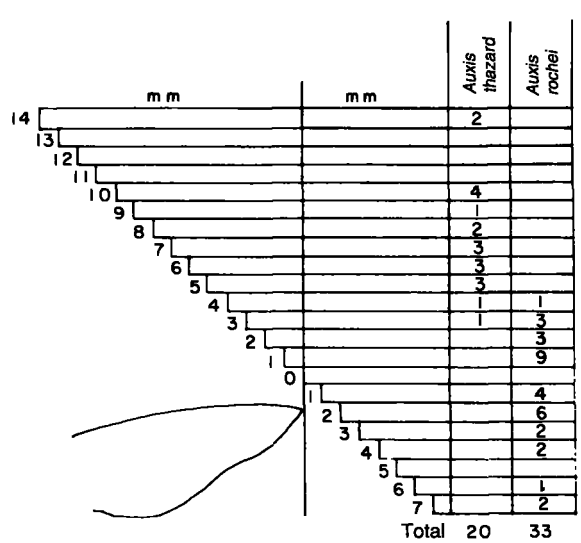


Figure 8

Distance from the tip of the pectoral fin to the anterior extent of the dorsal scaleless area above the lateral line in *Auxis* from southeastern Brazil (from Zavala-Camin, 1983: fig. 4). The scaleless area extends 3–14 mm anterior to the tip of the pectoral fin in 20 specimens of *A. thazard* but falls short of the pectoral-fin tip or extends slightly anterior to it in 33 specimens of *A. rochei*.

year; although off Costa Rica spawning is heaviest from December through April, whereas in Japanese waters it peaks in July as expressed by the index of sexual maturity. In the southern Indian Ocean, the spawning season extends from August to April; north of the equator it is reported from January to April. Fecundity was estimated at about 1.37 million eggs per year in a 44.2-cm-long female. Fecundity of fish in Indian waters ranged between approximately 200,000 to 1.06 million eggs per spawning in correlation with size of females.

Size Maximum fork length from drift net records in the Indian Ocean is 510 mm, but off Sri Lanka it is 580 mm; common lengths range between 250 and 400 mm FL depending on gear type and may also vary seasonally and by region. Size at first maturity is reported at about 290 mm FL in Japanese waters but at about 350 mm around Hawaii. *Auxis thazard* grows to be larger than *A. rochei*.

Subspecies The eastern Pacific population of *A. thazard* has more gill rakers, leading us to describe it as a separate subspecies. Linear regression analyses of morphometric characters for *A. thazard* showed significant differences between the eastern Pacific and the remaining combined populations in four char-

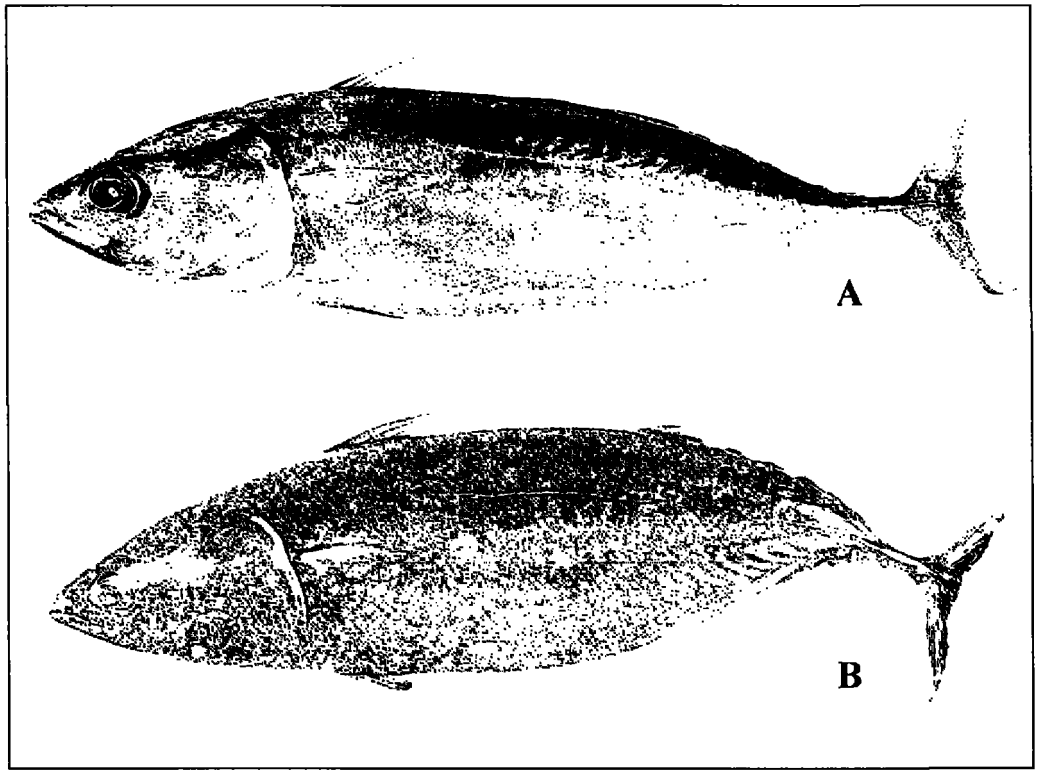


Figure 9

Type specimens of *Auxis thazard*. (**A**) Neotype of *Scomber thazard* Lacepède, 1800; USNM 265418; 274 mm FL; Indonesia, Moluccas, Halmahera I. (**B**) Holotype of *Auxis thazard brachydorax* n. ssp.; USNM 320406; 352 mm FL; 7°51'N, 99°51'W.

acters: CW, P1L, 2Dor, and Aor. ANCOVA showed differences that were significant at the 0.01 level of significance for three morphometric characters: AOR, P1L, and CW, further supporting recognition of an eastern Pacific subspecies of *A. thazard*.

Auxis thazard thazard (Lacepède, 1800)

Fig. 9A

Scomber thazard Lacepède, 1800:599 (original description) Lacepède, 1801:9–13 (description, off New Guinea); no type-specimens extant.

Auxis taso Commerson, 1831 *in* Cuvier and Valenciennes, 1831:146–148 (original description based on *Scomber taso* Commerson, New Guinea).

Auxis tapeinosoma Bleeker, 1854:408–409 (original description, Nagasaki, Japan); holotype: RMNH 6050 (see Boeseman, 1964:465, pl. 3, fig. 10).

Auxis thazard: Dresslar and Fesler, 1889:434 (synonymy, in part). Jordan and Evermann, 1896:867–868 (synonymy, in part). Wade, 1949:230–231, fig. 1 (comparison of both species, Philippines), figs. 3–6 (juveniles, 23.1–57.2 mm FL). Fraser-Brunner, 1950, synonymy, in part:152. Jones, 1958:190–192 (India). Matsumoto, 1960a:174–175, fig. 2 (comparison of both species, Hawaii). Jones and Silas, 1961:377–378, fig. 3. Fitch and Roedel, 1963:1329–1342, fig. 1 (generic review). Jones and Silas, 1963:1781–1786; 1964:20–22 (India). Tortonese, 1963 (Mediterranean population differs from Indo-Pacific populations of wide-corseleted *Auxis*). Richards and Randall, 1967:245–247, fig. 1 (first western Atlantic records). Chi and Yang, 1972 (osteology, morphology, Taiwan). Richards and Klawe, 1972:68–69 (references to eggs and young). Uchida, 1981 (species synopsis). Gorbunova, 1974:48–50 (description of larvae, Pacific and Indian oceans, fig. 12). Collette and Nauen, 1983:30–31 (synonymy, description, distribution, fig.). Robins and Ray, 1986:261 (W. Atlantic), pl. 48 (color fig.). Richards, 1989:32–33 (description of larvae, western central Atlantic; figs. of 7 larvae 4.5 mm NL to 25.0 mm SL).

Table 2

Number of gill rakers in populations of *Auxis*.

	36	37	38	39	40	41	42	43	44	45	46	47	48	49	*n*	$\bar{x}$
A. t. thazard																
Western Atlantic	—	—	1	1	2	2	1	—	—	—	—	—	—	—	7	40.1
Eastern Atlantic	—	—	1	4	6	5	5	—	1	—	—	—	—	—	22	40.6
Indian Ocean	1	2	6	8	7	7	3	1	—	—	—	—	—	—	35	39.6
Western Pacific	—	1	18	18	28	20	9	—	1	—	—	—	—	—	95	39.8
Central Pacific	—	—	—	3	9	7	9	—	—	—	—	—	—	—	28	39.3
Total															187	39.8
A. t. brachydorax																
Eastern Pacific	—	—	—	—	1	1	7	14	19	13	13	6	2	—	76	43.3
Galapagos	—	—	—	—	—	—	—	2	1	1	—	—	2	—	6	45.2
Total															82	43.4
A. r. rochei																
Western Atlantic	—	—	—	1	3	7	11	8	2	2	1	—	—	—	34	43.4
Eastern Atlantic	—	—	—	—	1	8	12	16	26	10	6	2	—	—	81	43.5
Mediterranean	—	—	—	—	1	10	8	8	6	3	—	1	—	—	37	42.6
Indian Ocean	—	—	—	—	—	—	—	1	3	—	1	3	2	—	10	45.8
Western Pacific	—	—	—	—	—	—	1	7	12	29	21	6	3	1	80	45.2
Central Pacific	—	—	—	—	—	—	—	3	3	5	1	1	—	—	13	44.5
Total															255	44.0
A. r. eudorax																
Eastern Pacific	—	—	—	—	—	—	—	1	5	11	5	5	3	—	30	45.6
Total																

Auxis hira Kishinouye, 1915:23–24, fig. 16 (original description, Japan); no type-specimens known. Kishinouye, 1923:462–463, pl. 31, fig. 55 (anatomy).

Diagnosis *Auxis thazard thazard* has fewer gill rakers, 36–44, usually 38–42 (Table 2); a greater body depth at the anal-fin origin (Fig. 10); a longer pectoral fin (Fig. 11); and a wider corselet (Fig. 12) than has *A. thazard brachydorax*.

Description Corselet narrow under second dorsal-fin origin (1–6 scales, usually 3, Table 1). Dorsal scaleless area extends anteriorly beyond P1 tip (1–16 mm, usually 3–12 mm, Fig. 5). Width of corselet under second dorsal-fin origin 0.5–3.5 mm, usually 0.5–1.0 mm (Fig. 3).

Types

Scomber thazard Lacepède, 1800. Neotype USNM 265418 (274 mm FL), Indonesia, Moluccas, Halmahera I., 0°58'N, 127°56'E; 12 Mar 1979; herein designated. Pectoral fin 41.2 mm, anterior extent of dorsal scaleless area 10.9 mm anterior to tip of pectoral fin, width of corselet under second dorsal-fin origin 1.4 mm, 3 scales in corselet under second dorsal-fin origin, gill rakers 10 + 31 = 41. Fig. 9A.

Auxis tapeinosoma Bleeker, 1854. Holotype RMNH 6050 (200 mm FL), Japan, Nagasaki; S.N. Wolff. Pectoral fin 20.5 mm; 2 scales in corselet under second dorsal fin origin; gill rakers 10 + 30 = 40. Photograph of type presented by Boeseman (1964, pl. 3, fig. 10).

Material examined 194 specimens (44.8–472 mm FL) from 94 collections.

Western Atlantic 10 specimens (240–471 mm FL) from 10 collections.

CAS SU 10874 (1, 305); Massachusetts; D.S. Jordan. USNM 23347 (1, 343); MA, Provincetown; Aug 1879; S.F. Baird. USNM 325226 (1, 449); NC, Oregon Inlet. UF 42693 (1, 344); NC, off Morehead City; 3 Jun 1973; G.F. Burgess. UF 38841 (1, 402); FL, Government Cut off Miami; 31 Jul 1971; T. Iwamoto. UF 98890 (1, 240); FL, Marquesas Keys, 24°29'N, 83°00'W; 23 Sep 1992; G.F. Burgess 92-5. UF 46979 (1, 253); Puerto Rico. USNM 325457 (1, 471); Caribbean, west of St. Vincent, 13°16'N, 62°32'W; 27 Mar 1966; RV *Undaunted*, cr. 2, sta. 114 (skeleton). USNM 325238 (1, 426); 10°47'N, 67°03'W; 24 Mar 1966; RV *Geronimo*, cr. 7, sta. 116. MNHN A.5792 (1, 248); Martinique; Plee; paralectotype of *Auxis vulgaris* Valenciennes.

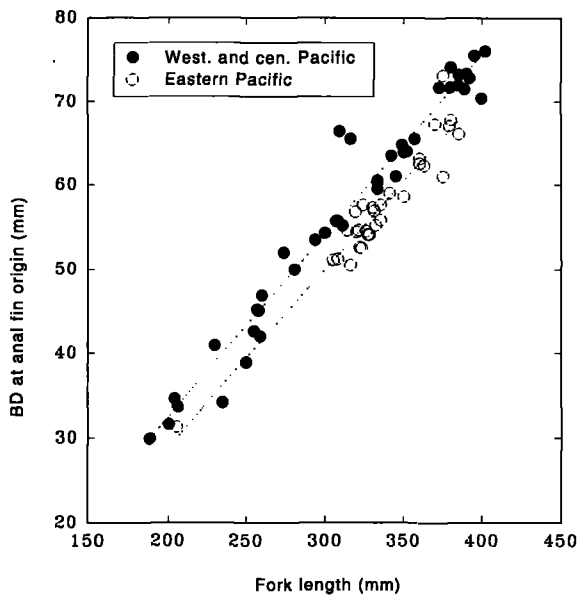


Figure 10

Body depth (BD) at anal-fin origin. Western and central Pacific *Auxis thazard thazard* (closed circles, $y = 0.216x - 10.683$, r=0.98) differ significantly (F=52.06, P<0.00) from eastern Pacific *A. t. brachydorax* (open circles, $y = 0.210x - 13.147$, r=0.96).

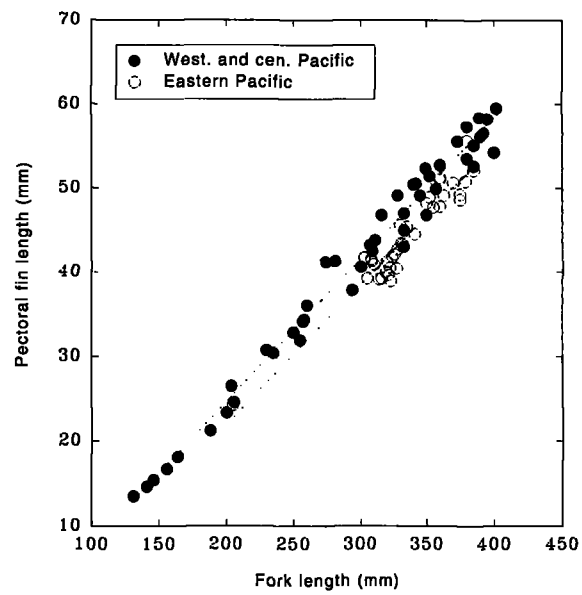


Figure 11

Pectoral-fin length. Western and central Pacific *Auxis thazard thazard* (closed circles, $y = 0.169x - 9.045$, r=0.991) differ significantly (F=24.06, P<0.00) from eastern Pacific *A. t. brachydorax* (open circles, $y = 0.165x - 11.11$, r=0.95).

Eastern Atlantic 24 specimens (261–472 mm FL) from 7 collections.

BMNH 1946.5.23.13–14 (2, 340–383); St. Helena; Colman. HUJ 17480 (1, 323); Mediterranean Sea, purchased in the market at Haifa, Israel; 8 Jun 1993; D. Golani. HUJ 17826 (1, 335); Haifa Bay; 2 Feb 1995; D. Golani. USNM 325237 (1, 442); 5°44'N, 14°28'W; 23 Feb 1965; RV *Geronimo*, cr. 5, sta. 124. USNM 325216 (10, 386–472); Gulf of Guinea; 15 Oct 1967; MV *Caribbean*, set 1. USNM 325956 (1, 261); Ghana; 5 Oct 1967. USNM 325224 (8, 370–439); off Lobito, Angola; fall 1968; MV *Bold Venture*.

Indian Ocean 38 specimens (216–416 mm FL) from 18 collections.

USNM 266918 (1, 310); Israel, Eilat; 21 May 1962. USNM 266919 (1, 330); Israel, Eilat; 1949. USNM 166908 (3, 310–338); Egypt, Ghardaqa; E. Clark. USNM 307773-5 (5, 351–373); north of Tulear, Madagascar, 22°10'S, 43°10'E; 4 Dec 1988; RV *Vityaz* 2657; B.B. Collette 1889. ANSP 93093 (1, 330); Natal coast; 1927; H.W. Bell Marley. CMFRI uncat (1, 415); India, Bombay, Sasson dock; 26 Oct 1979. CMFRI uncat (4, 325–387); India, Mangalore, Kaup; 15 Sep 1979. CMFRI uncat (2, 318–338); India, Vizhinjam; 17 Dec 1979. CMFRI uncat (2, 313–315); India, Veraval. CMFRI uncat (1, 368); India, Veerapandyan patnam, Tuticorin; 23 Oct 1979. CMFRI uncat (1, 416); India, Cochin fishing harbor; 1 Sep 1979. CMFRI uncat (5, 325–360); India, Calicut, off Vellayil; 25 Nov 1979; RSLM Haridas sta. 98. CMFRI uncat (1, 216); India, Cochin fish-

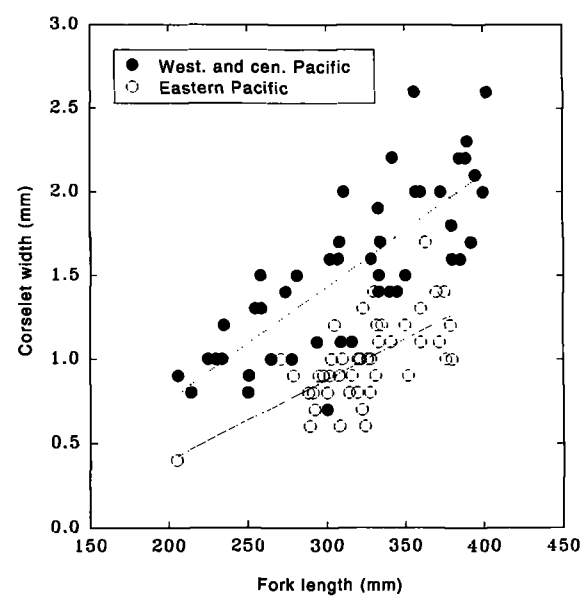


Figure 12

Corselet width under second dorsal-fin origin. Western and central Pacific *Auxis thazard thazard* (closed circles, $y = 0.007x - 0.606$, r=0.79) differ significantly (F=65.94, P<0.00) from eastern Pacific *A. t. brachydorax* (open circles, $y = 0.005x - 0.561$, r=0.65).

ing harbor; 22 Sep 1979. CMFRI uncat (1, 340); India. CMFRI uncat (1, 340); India, northwest Indian Ocean; 25 Mar 1977; MURAENA sta. 78. CMFRI uncat (1, 235); India, Cochin fishing harbor; 22 Sep 1979. USNM 218963 (1, 378); Ceylon, Trincomalee, St. John's market; 13 Sep 1969; P.C. Heemstra. USNM 215024 (6, 252–287); Ceylon; P.C. Heemstra.

Dissections 4 specimens (312–401 mm FL) from 4 collections.

USNM 307773-5 (3, 365–373); Madagascar, north of Tulear; 4 Dec 1988; RV *Vityaz* 2657; B.B. Collette 1889. CMFRI uncat (1, 401); India, Cochin fishing harbor.

Western Pacific 94 specimens (44.8–415 mm FL) from 50 collections.

RMNH 6050 (1, 200), Japan, Nagasaki; holotype of *Auxis tapeinosoma* Bleeker. ZUMT 2475 (1, 234); Japan, Nagasaki Pref.; Aug 1909. ZUMT 23751 (1, 251); Japan, Kagoshima Pref., Taniyama, Kagoshima City; 3 Jul–15 Aug 1930. ZUMT 31281 (1, 334); Japan, Shimane Pref., Matsue; 19 Oct 1935. ZUMT 31286 (1, 302); Japan, Shimane Pref.; 19 Oct 1935. ZUMT 50160 (1, 278); Japan, Nagasaki Pref., Nakadori I., Goto I., Arikawa; 17 Oct 1953. ZUMT 54923-4 (2, 225–250); Japan, Shizuoka Pref., Izu Peninsula; 12 Sep 1981; M. Aizawa. ZUMT 23979 (1, 214); Japan, Kagoshima Pref., Shibushi. CAS SU 24006 (1, 208); Japan, Wakanoura; 1900; Jordan and Snyder. USNM 325231 (1, 308); Japan, south of Tokyo (purchased in Tokyo market); 20 Sep 1966; R.H. Gibbs. USNM 44894 (1, 333); Japan. FMNH 57450 (1, 294); Japan, Sendai; D.S. Jordan. FMNH 57353 (2, 235–250); Japan, Osaka; D.S. Jordan. NMW 14528 (1, 300); Japan; 1900; D.S. Jordan. NMW 14530 (1, 309); Japan, Nagasaki; 1895. ZUMT 16740 (1, 265); Japan, Okinawa Island, Onnason. FMNH 55727 (1, 395); Korea, Fusan; 1911; D. S. Jordan. USNM 325230 (5, 349–402); Hong Kong; Nov 1967; CSM, cr. 10/67. ZRC 3736 (1, 370), South China Sea, 2°15'N, 104°45'E; 26 Mar 1973; RV *Changi*, SEAFDEC. CAS SU 13685 (2, 343–353); Philippine Is., Jolo; 1931; Herre. CAS SU 26430 (1, 238); Philippine Is., Culion; 1931. CAS SU 14524 (1, 263); Philippine Is., Luzon; 1934; Herre. CAS SU 28284 (1, 250); Philippine Is., Culion; Apr 1931; Herre. USNM 218964 (3, 307–342); Philippine Is.; 17 Sep 1963. USNM 150084 (3, 255–258); Philippine Is., Cebu; F. Baker. USM 325232 (1, 260); Philippine Is., Palawan; 25 May 1962; I. Ronquillo. USNM 325235 (3, 200–206); Philippine Is., Manila Bay; 27 May 1962. USNM 339045 (3, 265–357); Phillipine Is., Manila markets; 1–10 Oct 1995; B.B. Collette. CAS 53833 (3, 131–146); Philippine Is., Luzon, Batangas Prov., Batangas market; 24 Apr 1948; Herre. CAS 49634 (2, 156–164); Philippine Is., Batangas Prov., Batangas; 30 Jun 1948. LACM 45781-2 (14, 44.8–75.0); Philippine Is., Luzon, Batangas Bay, Bauan; 27 Mar 1949; M.A. Sabado and D. Leonicio. LACM 45782-2 (3, 62.7–69.2); Philippine Is., Luzon, Batangas Bay, Bauan; 12 Mar 1949; M.A. Sabado and D. Leonicio. LACM 45780-1 (3, 55.8–114); Philippine Is., Luzon, Batangas Bay, Bauan; 27 Sep 1949; M.A. Sabado and D. Leonicio. ZRC 3288 (1, 390); Singapore; Jun 1964; A.K. Tham. ROM 22971 (1, 188); Singapore; 1962–1963; C.C. Linsey. USNM 72629 (1, 230); Java, Batavia; 2 Apr 1909; Bryant and Palmer. SIO 61-735 (3, 206–215); Java Sea, Sunda Straits, 5°37'S, 106°02'E; 22 Mar 1961; Naga Expedition; T. Matsui. BMNH 1892.4.6.74 (1, 257); N. Celebes; Meyer. BMNH 1858.4.21.512 (1, 223); Amboina; Franks. USNM 265418 (1, 274); Moluccas, Kampung Loleba, Wasile district, Halmahera I., 0°58'N, 127°56'E; 12 Mar 1979; neotype of *Scomber thazard* Lacepède and USNM 330940 (1, 281), same data. USNM 215015 (1, 273); Australia, New South Wales, Sydney fish market; 17 Apr 1970; B.B. Collette 1469B. USNM 176970 (1, 300); Australia, New South Wales; Col. Howard. AMS IB 6430 (1, 403); Australia, Botany Bay, New South Wales; Mar 1963; D. Cleaver. AMS IB 845-6 (2, 282–290); Australia, Port Jackson; 3 Feb 1963; Stead. AMS I.21568-001 (1, 355); Australia, New South Wales, Sydney Harbour. AMS I.28544-001 (1, 415); Australia, New South Wales, Long Reef, 33°45'S, 151°19'E; D. Mercer. BMNH 1896.6.17.43 (1, 365); Melbourne market; Degen. NMNZ 9905 (2, 340–357), New Zealand, off Cape Brett, 35°10'S, 174°20'E. NMNZ 6939-42 (4, 290–350); New Zealand area; 16 Apr 1975. NMNZ 7326 (2, 370–372); New Zealand area.

Dissections 2 specimens (312–376) from 2 collections.

USNM 269056 (1, 312); Australia, Port Marquarie, New South Wales; 3 May 1970; B.B. Collette 1474E. USNM 269055 (1, 376); Australia, New South Wales; 17 Apr 1970; B.B. Collette 1469A.

Central Pacific 29 specimens (50.0–400 mm FL) from 10 collections.

LACM 6706-1 (4, 340–400), 6706-2 (4, 333–390), and 6706-3 (4, 345–385); Hawaiian Is. LACM 45778-1 (1, 93.0); Hawaii off Kona; 4 Oct 1962; RV *Charles M. Gilbert* 60-24. LACM 45779-2 (11, 50.0–60.3); Hawaiian Is.; 17 May 1969; RV *Townsend Cromwell* 43-30. CAS SU 12759 (1, 342); Hawaiian Is.; 1901; U.S. Fish Commission. USNM 52748 (1, 259); Hawaii; Bur. Fish. NMW 14529 (1, 316); Hawaii, Honolulu fish market; 1928; Pietschmann. BPBM 35799 (1, 267); Hawaii, Lanai, Cape Kaea; 30 Nov 1957; RV *John R. Manning*, cr. 38. MCZ 26298 (1, 392); Society Is.

Auxis thazard brachydorax Collette and Aadland, new subspecies

Fig. 9B

Diagnosis *Auxis thazard brachydorax* has more gill rakers, 40–48, usually 43–48 (Table 2), a shallower body depth at the anal-fin origin (Fig. 10), a shorter pectoral fin (Fig. 11), and a narrower corselet (Fig. 12) than *A. thazard thazard.*

Description Corselet narrow under second dorsal-fin origin (1–8 scales rows wide, usually 1–3, Table 1). Dorsal bare area extends anteriorly beyond tip of pectoral fins. Width of corselet under second dorsal 0.5–3.5 mm, usually 0.5–1.0 mm (Fig. 3).

Etymology We use the name that Fitch and Roedel used in their manuscript, *brachydorax* from the Greek *brachys* (short) and *dora* (hide) in reference to the narrow corselet. Carl L. Hubbs suggested this

name in a memo dated 1 Feb 1951 to W.I. Follett, concerning an edition of their California fish list, with copies to Fitch and Roedel.

Material examined 73 specimens (205–400 mm FL) from 29 collections.

Holotype USNM 320406 (352 mm FL); 7°51'N, 99°51'W; Olympia; 16 Aug 1991. Pectoral fin 48.9 mm, anterior extent of dorsal scaleless area 10.0 mm anterior to tip of pectoral fin, width of corselet under second dorsal-fin origin 0.9 mm, 3 scales in corselet under second dorsal-fin origin, gill rakers 10 + 35 = 45. See Fig. 9B.

Paratypes from the eastern Pacific 48 specimens (205–400 mm FL) from 21 collections.

LACM 6711-2 (1, 335); CA, Orange Co., 1–2 mi off Huntington Beach; 19 Sep 1960. LACM 34069-1 (1, 330); CA, between Oceanside and San Clemente; 30 Sep 1972. LACM 34254-1 (1, 379); CA, off San Onofre; 20 Jul 1974; MV *Bonanza*. SIO 73-60 (1, 321); CA, La Jolla. SIO 60343 (1, 321); CA, San Diego, off Coronado Hotel. CAS 56979 (2, 355); Baja California, below Holcombe Point; 25 Jul 1958; IATTC. SIO 91-138 (10, 327–350); Baja California, 26°05'N, 113°22'W; 12 Sep 1991; W. Mesa. LACM 34022-1 (1, 205); Baja California, Morgan Bank; Apr 1969; MV *Beverly Lynn;* R. Chikami. LACM 6714-1 (10, 271–302); Baja California, Morgan Bank. SIO 61-257 (2, 312–328); Gulf of California, Ceralbo I., 24°08'N, 104°51.5'W; 22 Jun 1961; W. Baldwin. LACM 6708-1 (1, 335); Gulf of California, 450 Fathom Bank; 24 Mar 1950; MV *Nancy Rose*. CAS 56981 (3, 350–370); Mexico, Sinaloa, 30 mi off Mazatlan; Apr 1951; MV *Gaston Explorer;* field number W 51-151. ANSP 89064 (1, 363); Mexico, Tres Marias, Cleofa I.; 4 Jul 1941; Fifth Vanderbilt Expedition. LACM 6709-5 (2, 360–372); 20°16'N, 105°59'W; 24 Nov 1951; R.C. Wilson 51-S-87. ANSP 89066 (1, 350); Mexico, Colima, 18°00'N, 105°47'W; 29 Jun 1941; Fifth Vanderbilt Expedition. SIO 79-256 (2, 322–328); 15°30'N, 93°30'W; 10 Apr 1974. LACM 6709-2 (1, 376); Gulf of Panama, 9°48'N, 86°00'W; 13 Nov 1951; field number 51-S-82. SIO 80-172 (1, 342); 9°20'N, 94°27'W. LACM 6709-4 (1, 333); Gulf of Panama; field number 51-S-85. USNM 334062 (3, 303–310); 7°51'N, 99°51'W; Olympia; 16 Aug 1991. SIO 58-83-43A (2, 374–395); Peru; 1958; Tomlinson.

Other material examined 26 specimens (305–385 mm FL) from 4 collections.

LACM 6711-8 (4, 360–380); "California"; Jun–Jul 1951; MV *Courageous*. LACM 6711–9 (4, 355–385); "California." UMMZ 160954 (1, 375); "from Mexico"; 16 Sep 1927; L.E. Herr and L.A. Walford. USNM 325223 (17, 305–341); eastern Pacific, exchange from LACM, no other data.

Galapagos Islands 6 specimens (315–400 mm FL) from 4 collections.

LACM 6713-1 (3, 358–375); Isabella I., 5 mi south of Point Cristobal; 8 Mar 1954; MV *Mayflower;* H. Clemens. LACM 39622-1 (1, 385); Skipjack Bank, 01°11'N, 91°03'W; 7 Dec 1952; H. Clemens. ANSP 71417 (1, 315); Charles I.; Feb 1957; South Pacific Expedition; G. Vanderbilt. CAS 56980 (1, 400); Galapagos; Dec 1951; MV *Golden West*; Field Number W51-276.

Auxis rochei (Risso, 1810)

Bullet tuna

Diagnosis *Auxis rochei* has a wider corselet under the second dorsal-fin origin, 5 or more scales wide, usually 7–15 (Table 1), and the anterior margin of the scaleless area above the corselet does not reach the tip of the pectoral fin (Fig. 1). Color pattern: 15 or more fairly broad, nearly vertical dark bars in the scaleless area above the lateral line (Figs. 1 and 6).

Geographical distribution Cosmopolitan in warm waters (Fig. 7). Both species occur off southeastern Brazil (see distribution of *A. thazard*). Most confirmed records of *Auxis* from the Mediterranean Sea are *A. rochei,* with the exception of two specimens of *A. thazard* from Haifa, Israel.

Habitat and biology (From literature summarized in Uchida, 1981, and Collette and Nauen 1983:30.) An epipelagic, neritic, and oceanic species. The spawning season may vary regionally depending on the hydrographical regime. In many parts of the Mediterranean and in the Straits of Gibraltar, maturing fish are common from May onwards, and more than 30% are spent by September. In large areas of the Gulf of Mexico, peaks of batch spawning are reported from March to April and from June to August, whereas in coastal waters from Cape Hatteras to Cuba and in the Straits of Florida, the spawning season begins in February. Indirect evidence suggests that the season extends at least from June through July off Taiwan and from May through August off southern Japan, as indicated by gonad indices and larval counts, respectively. Fecundity ranges between 31,000 and 103,000 eggs per spawning according to size of the fish. Food consists largely of small fishes, particularly anchovies and other clupeids (Etchevers, 1976).

Size Maximum fork length is 500 mm in Japanese catches, commonly to 350 mm. Common fork lengths in the Indian Ocean range between 150 and 250 mm. Fork length at first maturity off Gibraltar is 350 mm for females and 365 mm for males (Rodríguez-Roda, 1966).

Subspecies The eastern Pacific population of *A. rochei* has more scales in the corselet under the second dorsal fin: therefore we describe it as a separate subspecies. ANCOVA on morphometric characters for populations of *A. rochei* were not significant, possibly because of the small size range (300–365 mm) for the eastern Pacific sample, but no significant differences

were found between morphometric features for the eastern Pacific population and other populations.

Auxis rochei rochei (Risso, 1810)

Fig. 13, A and B

Scomber Rochei Risso, 1810:165–167 (original description, Nice); holotype MNHN A. 5808, Nice).
Scomber Bisus Rafinesque, 1810a:45, pl. II (upper fig.) (original description, Sicily); no type material. Rafinesque, 1810b:20 (Sicily).
Thynnus rocheanus: Risso, 1826:417–419.
Auxis vulgaris Cuvier, 1831, *in* Cuvier and Valenciennes, 1831:139–146, pl. 216 (original description, Mediterranean); syntypes: MNHN A. 5808, A. 5815, not located by Bauchot and Blanc, 1961:375, Blanc and Bauchot, 1964:453 or Collette, 1966, but recently located in the MNHN collections during transfer of fishes to the new storage building.
Auxis thynnoides Bleeker, 1855:301 (original description, Ternate, Indonesia); holotype: RMNH 6049 (see Boeseman, 1964:464–465, pl. 3 fig. 9). Jones 1958:192–193, fig. 2 (India). Matsumoto, 1960a:

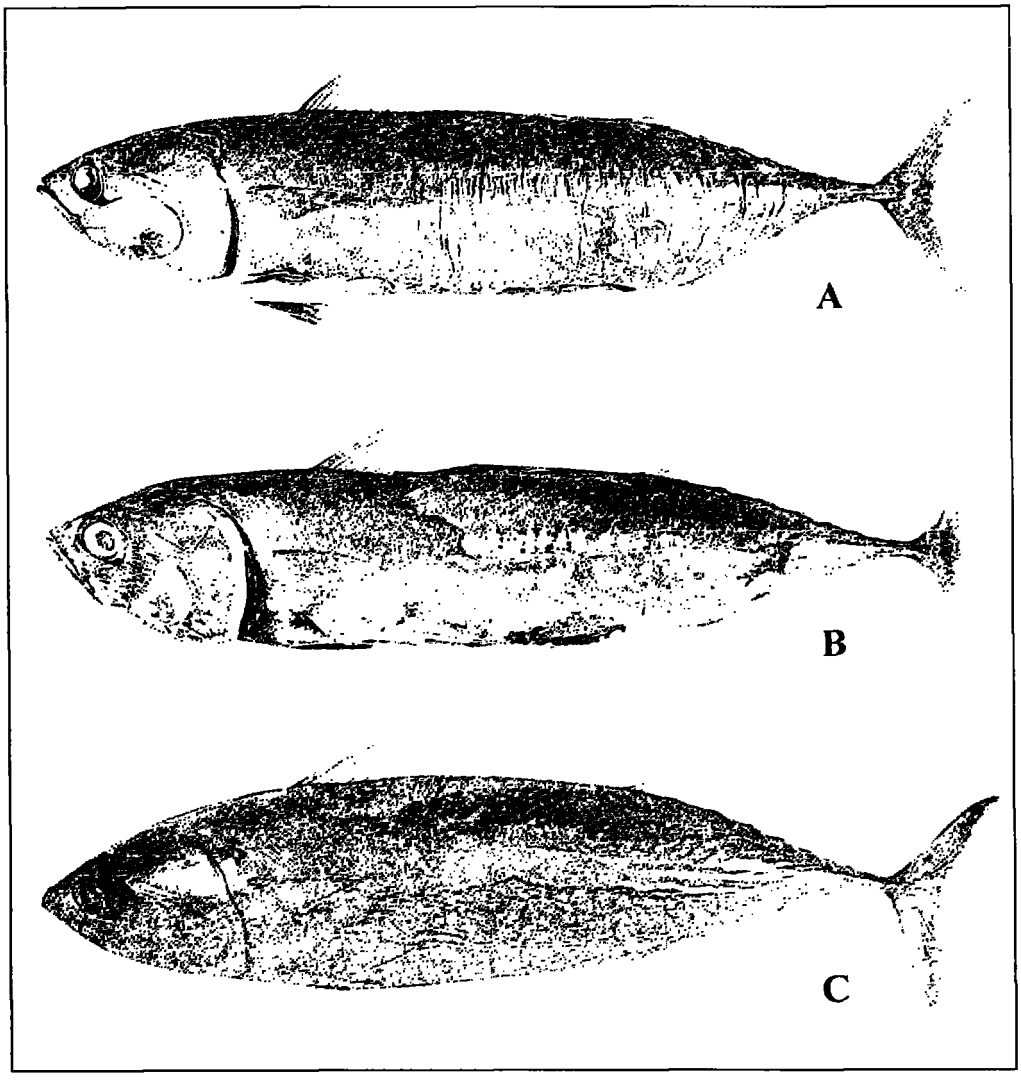


Figure 13

Type specimens of *Auxis rochei*. (**A**) Holotype of *Scomber rochei* Risso, 1810 and lectotype of *Auxis vulgaris* Cuvier, 1831; MNHN A.5808; 395 mm FL; Mediterranean Sea, Nice. (**B**) Holotype of *Auxis ramsayi* Castelnau, 1879; MNHN A.1241; 290 mm FL; Australia, Sydney. (**C**) Holotype of *Auxis rochei eudorax* n. ssp.; LACM 6712-1; 330 mm FL; California, 23 Fathom Bank.

173–174, fig. 1 (comparison of both species, Hawaii). Jones and Silas, 1961:378, fig. 4; 1963:1782–1786 (India). Jones, 1963:782–810 (species synopsis). Jones and Silas, 1964:23–24 (India).

Auxis Ramsayi Castelnau, 1879: 382 (original description, Port Jackson (Sydney), New South Wales, Australia); holotype MNHN A.1241.

Auxis rochei: Goode, 1880:808–810 and 1881:532–535 (first New England records). Fitch and Roedel, 1963:1331–1339, fig. 2 (generic review). Richards and Randall, 1967:245–247 (comparison with western Atlantic *A. thazard*). Chi and Yang 1972, (osteology, morphology, Taiwan). Richards and Klawe, 1972:67–68 (references to eggs and young). Gorbunova, 1974:50–52 (description, larvae, Pacific and Indian oceans, fig. 13). Rodríguez-Roda, 1980:169–176 (description, Spain). Uchida, 1981 (species synopsis). Collette and Nauen, 1983:29–30 (synonymy, description, distribution, fig.). Rodríguez-Roda, 1983 (age and growth, Spain). Richards, 1989:30–31 (description, larvae, western central Atlantic, figs. of 6 larvae, 3.5 mm NL to 39.0 mm SL).

Auxis thazard (*non* Lacepède, 1800): Dresslar and Fesler, 1889:434 (description, synonymy, in part), pl. 3 (USNM 25757, Rhode Island). Jordan and Evermann, 1896:867–868 (synonymy, in part). Fraser-Brunner, 1950: in part:152 (description; synonymy, in part). Rodríguez-Roda, 1966:279–291 (biology, eastern Atlantic).

Auxis maru Kishinouye, 1915:24 (original description, Japan); no type specimens known. Kishinouye, 1923:463464, pl. 31, fig. 56 (anatomy).

Diagnosis *Auxis rochei rochei* has fewer corselet scales, 5–24 (usually 6–19, Table 1), under the second dorsal-fin origin than *A. rochei eudorax,* 14–30 (usually 20–25).

Description Gill rakers 39–49, usually 41–47 in the Mediterranean, Gulf of Guinea, and Indo-West Pacific (Table 2); 39–46, usually 40–44 in the western Atlantic. The western Atlantic population has a narrower corselet (usually 6–9 scales wide under the second dorsal-fin origin compared with 8–19 in the eastern Atlantic and Indo-Pacific, Table 1) but appears best referred to as *A. r. rochei.* Corselet width under second dorsal-fin origin (Fig. 3) 2.0–10.0 mm, usually 3.0–7.0 mm, except in the western Atlantic where corselet width is only 1.0–4.0 mm, usually 1.5–3.5 mm. Dorsal scaleless area fails to reach pectoral-fin tip (Fig. 1) by up to 23.0 mm (Fig. 5); usually 3.0–17.0 mm in the Mediterranean, Gulf of Guinea, and Indo-West Pacific; may extend a little anterior to the pectoral-fin tip in the western Atlantic (Fig. 8).

Types

Scomber rochei Risso, 1810. Holotype MNHN A.5808 (395 mm FL), Mediterranean, Nice. Pectoral fin 50.1 mm; anterior extent of dorsal scaleless area extends 10.3 mm posterior to tip of pectoral fin; width of corselet under second dorsal-fin origin 3.7 mm; 12 scales in corselet under second dorsal-fin origin; gill rakers 9 + 33 = 42. Fig. 13A.

Auxis vulgaris Cuvier, 1831. Lectotype MNHN A.5808, herein selected. This specimen is also the holotype of *A. rochei*; thus *A. vulgaris* is an objective synonym of *A. rochei.*

Auxis thynnoides Bleeker, 1855. Holotype RMNH 6049 (260 mm FL), Indonesia, Ternate; C.F. Goldman. Pectoral fin broken, 27.2+ mm; dorsal scaleless area extends does not reach tip of pectoral fin; 5 scales in corselet under second dorsal-fin origin; gill rakers 11 + 36 = 47. Photograph of holotype in Boeseman (1964, pl. 3, fig. 9).

Auxis Ramsayi Castelnau, 1879. Holotype MNHN A.1241 (290 mm FL), Australia, New South Wales, Sydney. Pectoral fin 34.7 mm; anterior extent of dorsal scaleless area 12.7 mm posterior to tip of pectoral fin; width of corselet under second dorsal-fin origin 5.7 mm; 15 scales in corselet under second dorsal-fin origin; gill rakers 10 + 33 = 43. Fig. 13B.

Material examined 261 specimens (58.7–443 mm FL) from 102 collections.

Western Atlantic 37 specimens (96.4–442 mm FL) from 21 collections.

ROM 22066 (1, 292); off Nova Scotia, 41°06'N, 64°12'W; Jul 1955; Atlantic Bio Station. ROM 25064 (1, 350); Canada, Grand Bank; Aug 1967; E.O. Grandy. MCZ 39682 (1, 315); MA, Barnstable trap; 1 Aug 1954; F. Mather. USNM 35136 (1, 332); MA, Woods Hole; S.F. Baird. USNM 105002 (1, 285); MA, Woods Hole; 3 Jul 1936; H.M. Smith. ANSP 11335 (1, 283); RI, Newport; S. Powell. USNM 43717 (4, 322–340); RI, Newport; USFC. MCZ 26483 (1, 350); RI, Block I.; A. Agassiz. MCZ 40897 (1, 310); 20 mi S by E of No Man's Land; 30 Sep 1935; F.K. Schwomen. MCZ 123011 (1, 340); 40°05'N, 70°05'W; 29 Jun 1952; MV *Blue Dolphin.* USNM 50546 (1, 335); RI, off Block I.; H.C. Johnson. USNM 25973 (6, 420–442); RI, Newport; S.F. Baird. ANSP 119968 (1, 335); NJ, 29 mi ESE of Monasquain Inlet; 25 Jun 1966. ANSP 91791 (1, 340); NJ, Ventnor; 1946; C.B. Atkinson. USNM 127147 (9, 304–343); NJ. USNM 76694 (1, 324); MD, Ocean City; B.A. Bean. AMNH 3686 (1, 252); NC, Cape Lookout; summer 1910; R.J. Coles. USNM 325227 (1, 447); NC, Oregon Inlet. UF 38840 (1, 309); FL, Key Largo; A. Pflueger. USNM 325229 (1, 302); Florida; 20 Feb 1968. TU 6922 (1, 96.4); Gulf of Mexico, 28°27'N, 89°25'W; 9 Aug 1952; RV *Oregon,* R.D. Suttkus 2333.

Mediterranean 43 specimens (106–443 mm FL) from 22 collections.

USNM 266916 (1, 218); Israel, Haifa; 7 Jul 1960. HUJ 17073 (3, 318–328), Israel, purchased in Jaffa market; 17

June 1993; D. Golani. HUJ 17826 (1, 300); Haifa Bay; 8 Feb 1995; D. Golani. USNM 324234 (4, 134–147); Lebanon, St. George Bay; 10 Aug 1964; C. George. USNM 214659 (10, 119–155); Lebanon, St. George Bay; 28 Jul 1965; C. George. BMNH 1967.2.272–274 (3, 106–122); Lebanon, Antelias; C. George. NMW 14534 (1, 405); Yugoslavia, Fiume; 1881–1882; Steindachner. NMW 14531 (1, 443); Italy, Trieste; 12 Jun 1907; Steindachner. NMW 14532 (1, 408); Yugoslavia, Fiume; 1882; Steindachner. NMW 14533 (1, 399); Yugoslavia, Fiume; 1882; Steindachner. MNHN A.5808 (1, 395); Nice; Laurillard; holotype of *Auxis rochei* Risso. NMW 14537 (1, 335); France, Nizza; 1889. NMW 14538 (1, 395); France, Nizza; 1881. NMW 14527 (2, 297–303); Sicily; 9 Apr 1837. NMW 14536 (2, 149–228); France, Nizza; 1884.I.100; Steindachner. NMW 14535 (2, 108–113); France, Nizza; 1883; Steindachner. NMW 14551 (1, 435); Lissabon Dez; 1864; Steindachner. LACM 6707-1 (3, 377–410); Mediterranean Sea. MNHN A.5815 (1, 393); eastern Mediterrranean; Bory St. Vincent; paralectotype of *Auxis vulgaris* Cuvier. MCZ 58517 (1, 235); Straits of Messina; 10 Nov 1959; G. Arena. AMNH 5041 (1, 395); Italy, Naples; received Jun 1913. USNM 198207 (1, 362); Italy, Genoa; 1964; E. Tortonese.

Eastern Atlantic 69 specimens (212–399 mm FL) from 10 collections.

BMNH 1983.9.8.203 (1, 287); Azore Is.; Stonehouse. ISH 173/64 (2, 345–390); Cape Verde Is., 16°05'N, 22°45'W; RV *Walther Herwig* 81/64; 14 Mar 1964. USNM 325217 (15, 343–399); Gulf of Guinea; 15 Oct 1967; MV *Caribbean*, set 1. USNM 325955 (1, 212); Ghana; 5 Oct 1967. BMNH 1932.2.27.17 (1, 297); Ghana, Accra; Irvine. USNM 189004 (1, 279); Liberia; 27–29 Oct 1952; G.C. Miller 1789. USNM 218954 (1, 330); Angola, Baia Farta, 12°36'S, 13°12'E; 5 Apr 1968; RV *Undaunted* 68-279. USNM 325218 (32, 278–307); Angola, Benguela, 12°36'N, 13°12'E; 29 Mar 1968; RV *Undaunted* 68-273. USNM 325219 (14, 271–334); Angola, Baia Farta, 12°36'S, 13°12'E; 5 Apr 1968; RV *Undaunted* 68-279. BMNH 1868.6.15.11 (1, 390); St. Helena; Melliss.

Indian Ocean 9 specimens (175–273 mm FL) from 6 collections.

CMFRI uncat (1, 273); India, Cochin Harbor; 2 Oct 1979. CMFRI uncat (2, 198–267); India. CMFRI uncat (1, 198); India, Cochin Harbor; Oct 1979. CMFRI uncat (1, 175); India, Vellayil, Calicut; 31 Aug 1979. CMFRI uncat (1, 181); India, Cochin Harbor; 11 Sep 1979. USNM 215024 (3, 241–243); Ceylon; P.C. Heemstra.

Western Pacific 90 specimens (58.7–335 mm FL) from 41 collections.

MCZ 32422 (3, 295); Russia, Vladivostok market, Peter-the-Great Bay; 1925; Pacific Fisheries Institute. CAS SU 24121 (1, 262); Japan, Tokyo; 21 Oct 1932; D.S. Jordan. CAS SU 11763 (1, 213); Japan; 1895; K. Otaki. CAS SU 23788 (1, 235); Japan, Etcha; 1922; Ishikawa and Wakiya. MCZ 58514 (1, 173); Japan, near Tokyo; T. Abe. MCZ 58516 (1, 167); Japan, near Tokyo; T. Abe. AMNH 34877 (1, 240); Japan, Tokyo market; 31 Oct 1922; D.S. Jordan. AMNH 26893 (1, 216); Japan, Misaki; 1922; K. Aoki. AMNH 13025 (1, 250); Japan, Kyoto market; 1922; D.S. Jordan. UMMZ 142722 (1, 252); Japan, Tokyo market; 31 Oct 1922; D.S. Jordan. ZUMT 16380 (1, 270); Japan, Miyagi Pref., off Ishinomaki City; 10 Sep 1925. ZUMT 13758 (1, 311); Japan, Hokkaido, Muroran City; Sep 1924. ZUMT 20200 (1, 237); Japan, Wakayama Pref.; Jan 1920. ZUMT 46643 (1, 331); Japan, Niigata Pref.; Aug 1923. ZUMT 51365 (1, 250); Japan, Fukuoka fish market; 10 Dec 1959. ZUMT 41208 (1, 214), 41213 (1, 215), 41220-24 (5, 201–219), 41228 (1, 210), 41249-57 (9, 200–225), and 41282-84 (3, 206–216); Japan, Toyama Pref., Namerikawa. ZUMT 54922 (1, 214); Japan, Shizuoka Pref., Izu Peninsula; 12 Sep 1981; M. Aizawa. ZUMT 50407 (1, 243); Japan, Nagasaki Pref.; Motoura, Ikitsuki I.; 25 Oct 1953. CAS SU 49371 (1, 270); Taiwan; Chu. CAS SU 14524 (3, 230–240); Philippine Is., Luzon; 1934; Herre. CAS SU 28284 (1, 235); Philippine Is., Culion; Apr 1931; Herre. USNM 325236 (5, 227–233); Philippine Is., N. Palawan; 17 Sep 1963; I. Ronquillo. USNM 325233 (3, 217–236); Philippine Is., Almahon Bato; 17 Sep 1963. USNM 326677 (1, 209); Philippine Is., Manila Bay; 27 May 1962. USNM 339044 (6, 256–285); Philippine Is., Manila markets; 1–10 Oct 1995; B.B. Collette. LACM 45781-1 (17, 58.7–93.8); Philippine Is., Luzon, Batangas Bay, Bauan; 27 Mar 1949; M.A. Sabalo and Leonicio. SIO 75–149 (1, 156); 9°51.4'N, 117°32.5'W; 16 Nov 1970; F. Williams. SIO 61–736 (4, 173–179); Gulf of Thailand, 41 mi from Ban Laehn Pho, Pattani; 16 Nov 1960; RV *Stranger*. AMNH 15865 (2, 270–275); Java, Batavia; 5 Dec 1941; Inst. Zoevisch. RMNH 6049 (1, 260), East Indies, Ternate; C.F. Goldman; holotype of *Auxis thynnoides* Bleeker. MNHN A.1241 (1, 290); Australia, New South Wales, Sydney; F. Castelnau; holotype of *Auxis ramsayi*. AMS IB 4015 (1, 335); Australia, New South Wales, Sydney; G.P. Whitley. AMS IB 3227 (1, 325); Australia, New South Wales, Newcastle district; A. D'Ombrain. AMS IB 3535 (1, 318); Australia, New South Wales, off Port Stephens; A. D'Ombrain. AMS IB 1804 (1, 300); Australia, New South Wales, Shoal Bay. AMS I 15313 (1, 284); Australia, New South Wales, Shoal Harbor.

Central Pacific 13 specimens (50.5–283 mm FL) from 2 collections.

BPBM 27044 (6, 260–283); Hawaii, Cape Kaea, Lanai; 30 Nov 1957; RV *John R. Manning*, cr. 38. LACM 45779-1 (7, 50.5–59.2); Hawaiian Is., RV *Townsend Cromwell*, cr. 43, sta. 30; 17 May 1969.

Auxis rochei eudorax Collette and Aadland, new subspecies

Fig. 13C

Diagnosis *Auxis rochei eudorax* has more corselet scales under the second dorsal-fin origin (Table 1), 14–30 (usually 20–25) than *A. rochei rochei*, 5–24 (usually 6–19).

Description Gill rakers 43–48, usually 44–47 (Table 2). Corselet width under second dorsal-fin origin 5.0–11.0 mm, usually 7.0–10.0 mm (Fig. 3).

Etymology We use the name that Fitch and Roedel used in their manuscript, *eudorax* from the Greek

eu (well) and *dora* (hide) in reference to the wide or well-developed corselet. Carl L. Hubbs suggested this name in a memo dated 1 Feb 1951 to W.I. Follett, concerning an edition of their California fish list, with copies to Fitch and Roedel.

Material examined 30 specimens (300–365 mm FL) from 17 collections.

Holotype LACM 6712-1 (330 mm FL); CA, 23 Fathom Bank; 13 Jan 1955; R.D. Collyer; field number SSY 1-2. Pectoral fin 41.7 mm; anterior extent of dorsal scaleless area extends 8.1 mm posterior to tip of pectoral fin; width of corselet under second dorsal-fin origin 10.2 mm; 25 scales in corselet under second dorsal-fin origin; gill rakers 11 + 36 = 47. See Fig. 13C.

Paratypes from the eastern Pacific 29 specimens (300–365 mm FL) from 17 collections.

LACM 6711-5 (1, 350); CA, Balboa Pier; 17 Sep 1960; J.P. Reed. LACM 6711-6 (1, 312); CA, off Newport Beach; 13 Dec 1961; A. Gronsky. LACM 6711-3 (1, 338); CA, outside of Newport Beach; 13 Dec 1961; A. Gronsky. LACM 6711-4 (1, 322); CA, off San Clemente; 15 Sep 1960. LACM 6711-1 (1, 355); CA, Los Coronados Is.; 4 Nov 1957; MV *Lo-An*. LACM 34069-2 (1, 318); CA, between Oceanside and San Clemente; 30 Sep 1972. CAS 56944 (1, 363); CA, between Half Moon and San Francisco bays; 29 Oct 1984; MV *Aries*. CAS 54921 (1, 335); CA, San Luis Obispo Co., 30 mi N of Morro Rock, 7 Sep 1983; MV *Mary Beth*. LACM 6711-11 (1, 340); California; Jun–Jul 1951; MV *Courageous*. LACM 6712-2 (6, 300–325); CA, 23 Fathom Bank; 13 Jan 1955; R.D. Collyer; field number SSY 1-2. LACM 6711-10 (1, 316); California. LACM 6711-7 (3, 320–340); Baja Calif., Cape San Lucas; May 1950; MV *Nancy Rose*. LACM 39621-1 (1, 308); Mexico, Pta. Pequera, San Juanico; 24 Nov 1953; J.E. Fitch. CAS 56978 (1, 365); Baja California, below Holcombe Pt.; 25 Jul 1958; Walker and Connolly. LACM 6708-2 (3, 313–338); Gulf of California, 450 Fathom Bank; 24 Mar 1950; MV *Nancy Rose*. LACM 6709-1 (3, 309–331); Panama Bay, N of Isla Chepillo, 8°58'N, 79°10'W; 27 Feb 1954; MV *Mayflower*. ANSP 89082 (2, 340–343); Galapagos, James I., Sullivan Bay; 4 Jul 1941; Fifth Vanderbilt Expedition.

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Age, growth, and mortality of bonefish, *Albula vulpes*, from the waters of the Florida Keys

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Abstract.—We examined 528 bonefish ranging from 21 to 702 mm FL collected in South Florida waters from 1989 to 1995. Ages of 451 bonefish ranging from 228 to 702 mm FL were estimated from thin-sectioned otoliths (sagittae). Examination of OTC-marked otoliths from five fish held in a pond in the Florida Keys for periods ranging from 14 to 29 months suggested that a single annulus was formed each year. Marginal-increment analysis also showed that a single annulus was formed each year during March–June. Bonefish reach a maximum age of at least 19 years. Growth of the bonefish in our study was rapid until an age of about six years and then slowed considerably. The von Bertalanffy growth equation for females was $FL=680.9(1-e^{(-0.279(Age+0.934))})$ and for males was $FL=670.7(1-e^{(-0.242(Age+1.318))})$. The overall growth models for males and females were significantly different, but estimates of individual growth parameters L_∞, K, and t_0 were not. Predicted lengths of females were greater than those of males for all ages greater than 1 year. Catch-curve estimates of instantaneous rates of total mortality (Z) were 0.21 (95% confidence interval 0.167–0.303) for females and 0.25 (95% confidence interval 0.098–0.406) for males. Empirically derived estimates of natural mortality were similar to total mortality estimates, suggesting that fishing mortality is low.

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Bonefish, *Albula vulpes*, are moderate-size elopomorph fish that frequent coastal and inshore waters of tropical seas worldwide. In the western Atlantic, bonefish regularly occur in the Florida Keys, the Bahama Islands, and throughout the Caribbean Sea (Hildebrand, 1963). In many areas of the species' range, including the waters off the Florida Keys, bonefish are the basis of economically important recreational fisheries. Bonefish are renowned by anglers for their wariness and fighting abilities and are often caught in water as shallow as 0.3 m. In the Florida Keys, fishing for bonefish is a year-round activity and provides an important source of income for professional fishing guides. The commercial sale of bonefish in Florida is prohibited; the limits placed upon the recreational fishery for bonefish are a bag limit of one fish per angler per day and a minimum fish size of 457 mm total length. Bonefish are not considered a food fish in Florida, and most bonefish caught are released.

Bonefish life history has not been adequately described. Bruger (1974) described the age and growth of bonefish from an examination of scales of 205 bonefish from South Florida waters. He estimated the age of the oldest bonefish in his study to be 12 years and suggested that greater ages may be attained. His attempt to validate annulus formation on scales using the marginal-increment technique was inconclusive, perhaps because annulus formation in scales often occurs over a prolonged period and because annuli are often closely spaced in older fish, making validation of scale-derived ages by the marginal-increment technique difficult (Lowerre-Barbieri et al., 1994). In addition, Bruger's sample sizes for many months were small.

Since Bruger's work, studies on a variety of species have shown that scales are not reliable for ageing long-lived fishes and that scale-derived age estimates are typically lower than validated estimates derived from sectioned otoliths (Beamish and McFarlane, 1983; Casselman, 1983; Lowerre-Barbieri et al., 1994). Ageing of bonefish with a validated method is needed to assess Bruger's estimates of longevity. In addition, sex-specific differences in growth rates have not been evaluated and growth-model parameters have not been estimated for Florida bonefish. The only published growth-model parameters for bonefish are those by Morales-Nin (1994), who used length-frequency analyses to estimate von Bertalanffy growth parameters for a small sample of bonefish from Mexico's Pacific coast. In this article, we describe the age and

growth of bonefish from the waters off the Florida Keys and estimate mortality rates from a sample of fish whose ages were determined from an examination of sectioned otoliths.

Methods

We examined 528 bonefish collected from South Florida waters from February 1989 to April 1995. Most of these bonefish were caught with hook-and-line gear either by biologists or by a single professional bonefish guide and his anglers from waters off the Florida Keys and in Florida and Biscayne Bays. Five bonefish caught with hook-and-line gear were obtained from taxidermists in Fort Lauderdale and five others from tournaments in waters off the Keys. Supplemental collections of small bonefish (<425 mm) were made with various-size seines and gill nets in waters off the Keys. We collected young-of-the-year (YOY) bonefish using 21.4-m seines constructed with 6.35-mm mesh. These collections were made from shallow (<1 m) sand- and grass-bottom areas on the ocean (Florida Straits) side of Key West, Bahia Honda Key, and Lower Matecumbe Key and from the Indian River Lagoon on Florida's Atlantic coast.

Standard length (SL), fork length (FL), and total length (TL) were measured to the nearest millimeter (mm) and fish were weighed to the nearest gram. All lengths reported are fork lengths. Otoliths (sagittae) were removed, cleaned with bleach (5.25% sodium hypochlorite), and rinsed first in water and then in 95% ethanol. Otoliths were stored dry until sectioned. Sex of all fish, except that of YOY (age 0), was recorded and confirmed histologically.

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 cutting three or four thin sections approximately 0.5 mm thick, one of which was through the otolith core, using a Buehler Isomet low-speed saw with a diamond blade. 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 grits per sheet) 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; therefore, this technique was adopted as our standard protocol.

Annuli were counted three times by each of two independent readers who used a dissection microscope equipped with reflected light at magnifications of 8–25×. After the readers completed counting annuli on all the otoliths, we re-examined the otoliths for which different counts had been given. Most disagreements in counts concerned the presence or absence of an annulus on the otolith's margin. We were usually able to reconcile these disagreements and to assign an age to the otolith. A few otoliths had irregular and poorly defined annuli (n=20, 4.2%); these were discarded from the analysis.

Measurements for marginal-increment analysis were made with a digital image-processing system along an axis extending from the otolith's core to the ventral proximal margin of the section (Fig. 1). 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 bonefish, 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,

$$\frac{\sum_{i=1}^{n}\left((r_2 - r_1)/r_1\right)_i}{n} = 0.406 \qquad (\mathrm{SE} = 0.0081).$$

We then estimated the expected distance between the first and second annulus for each age-1 bonefish 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 $(MI/(0.406 \times r_1))\cdot 100$, where MI = the marginal increment. We then plotted the median percent marginal increment as a function of capture month for the 36-month period during which we made regular monthly bonefish collections. We also plotted marginal increments for individual age classes 4–9 for all study years pooled. Our monthly sample sizes for other individual age classes were insufficient for marginal-increment analysis.

Bonefish were captured with hook-and-line gear from the waters off the Florida Keys for age-valida-

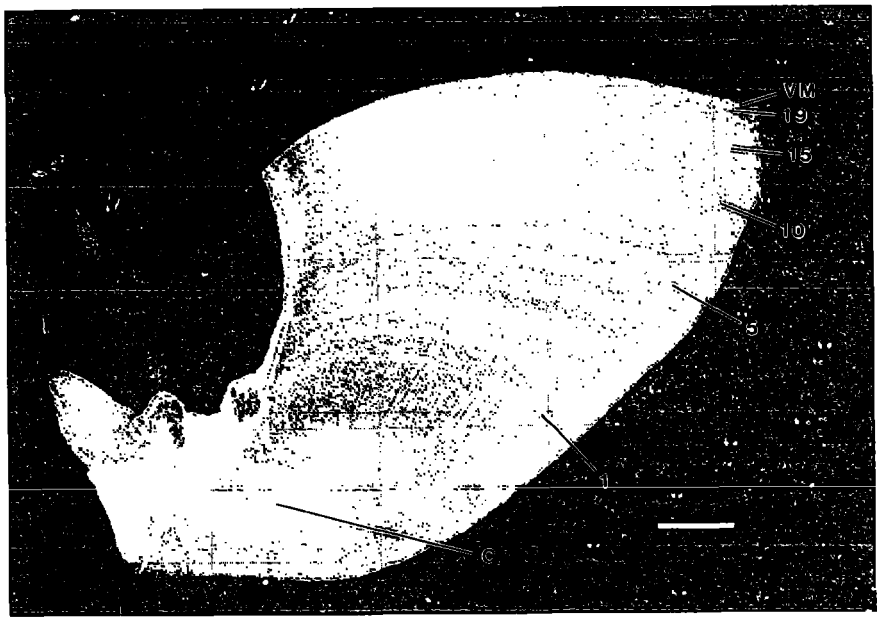

Figure 1

Transverse section from a 19-year-old (641-mm-FL) bonefish, *Albula vulpes*, otolith viewed with reflected light showing the annuli counted for age estimation. Measurements for marginal-increment analysis were made along an axis extending from the otolith core (c) to the ventral margin (vm) of the section. Scale bar = 1 mm.

tion experiments (Table 1). After capture, fish were measured for fork length and tagged with dart-type tags. Bonefish were then injected with Liquamycin LA-200 (200-mg oxytetracycline [OTC]/mL) in the dorsal musculature at a dosage of 100-mg OTC per kg fish weight. Fish weight was estimated with a length-weight regression. Bonefish were then transported to a 33.5-m by 5.5-m by 0.75-m deep pond at the Keys Marine Laboratory in Long Key, where they were held for 14 to 29 months. Water at ambient temperatures was pumped continuously from Florida Bay through the pond. Fish were fed at least three times a week with as much frozen fish or shrimp as they would consume. Sections from OTC-marked otoliths were examined with a compound microscope (40–100×) equipped with ultraviolet light so that the fluorescent OTC marks could be detected.

The von Bertalanffy (1957) growth equation $FL_t = L_\infty(1-e^{-K(t-t_0)})$ was fitted to observed age-length data with nonlinear regression procedures. Likelihood-

Table 1

Data for oxytetracycline (OTC)-injected bonefish, *Albula vulpes*. Otolith measurements were made along an axis extending from the otolith core to the OTC mark, annuli, and ventral margin of the section (Fig. 1). Measurements were made to the annulus at or just before the OTC mark and all subsequent annuli.

Injected		Sacrificed				Distance from core (mm)				
Date	Fork length (mm)	Date	Fork length (mm)	Months held	Age (years)	OTC mark	Annulus	Annulus	Annulus	Otolith edge
Nov 91	546	Oct 93	583	24	5	4.85	4.89	5.44		5.81
April 92	660	Nov 93	661	20	18	7.61	7.57	7.73		7.94
Oct 92	465	Nov 93	511	14	4	5.34	5.39			5.98
Oct 92	360	March 94	465	18	4	4.82	4.84	5.68		5.77
Dec 91	—	April 94	645	29	15	6.83	6.84	7.10	7.28	7.31

ratio tests were used to compare parameter estimates for males and females (Kimura, 1980; Cerrato, 1990). We used the outlier detection methods described by Sokal and Rohlf (1995) to test the significance of two perceived outliers from the age-length and otolith weight-age relations. Dixon's test statistic for outliers was used for sample sizes ≤25, and Grubb's test statistic for outliers was used for larger sample sizes. Outliers were considered significant at the $P<0.05$ significance level. Because we could not sex YOY bonefish, they were not included in growth models, but they were included in length-length regressions and pooled length-weight regressions. Sex-specific length-weight regressions were calculated by linear regression of $\log_{10}$-transformed data, and we compared the slopes and elevations using a t-test (Zar, 1984).

We used a catch curve to estimate the instantaneous total mortality rate (Z) from age-frequency data (Robson and Chapman, 1961). The age of full recruitment to the fishery for the catch-curve analysis was assumed to be 5 years, and year classes represented by fewer than five individuals were eliminated from the analysis. We estimated the instantaneous rate of natural mortality (M) using Pauly's (1980) formula $\ln M = -0.0152 - 0.0279\ln L_\infty + 0.6543\ln K + 0.463\ln T$, where L_∞ and K are parameters from the von Bertalanffy growth equation, and T is the average annual surface temperature. An average annual temperature of 25.9°C (SD=0.13) was calculated from daily temperature measurements made from 1992 to 1994 at the Keys Marine Laboratory's water intake pump in Florida Bay. Pauly (1983) suggested that for schooling species, such as bonefish, the estimate of natural mortality derived from the above equation should be reduced by 20%. We used Pauly's formula and the 20% correction to suggest a possible range of values for natural mortality.

Undamaged otoliths were weighed to the nearest 0.01 mg in order to evaluate the use of otolith weight as a predictor of age. If both left and right otolith weights were available for an individual fish, the mean of the two weights was calculated. Sex-specific linear regressions were fitted to $\log_{10}$-transformed otolith weight and age data, and we compared the slopes and elevations of the regressions using a t-test (Zar, 1984).

Results

The 528 bonefish we examined ranged from 21 to 702 mm in length; 56 (10.6%) of these fish were YOY (21–116 mm). Fish caught on hook-and-line gear ranged in length from 228 to 702 mm (median=591 mm, interquartile range=111 mm, n=452) and most (80%) were from 500 to 700 mm (Fig. 2). Among all bonefish that we sexed, females ranged from 228 to 702 mm in length (median=601 mm, interquartile range=110 mm, n=274) and males ranged from 290 to 700 mm (median=566 mm, interquartile range=146 mm, n=192). The size-frequency distributions of males and females were significantly different (Kolmogorov-Smirnov two-sample test, D=0.231, $P<0.001$); females were significantly larger than males (Mann-Whitney U-test, $P<0.001$). Females were also more abundant than males. In our sample there were 192 males and 274 females, and the sex ratio was significantly different from 1:1 (χ^2=14.43, df=1, $P<0.001$).

Neither slopes (t-test, df=453, t=0.474, P=0.318) nor elevations (t-test, df=454, t=0.084, P=0.467) of the length-weight regressions for male and female bonefish were significantly different. The pooled length-weight equation for sexed and unsexed fish and the relations between SL, FL, and TL are presented in Table 2.

Bonefish otoliths when viewed with reflected light have clear and easily counted narrow, opaque (bright) annuli that alternate with broad translucent (dark) zones (Fig. 1). 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 portion of the otolith

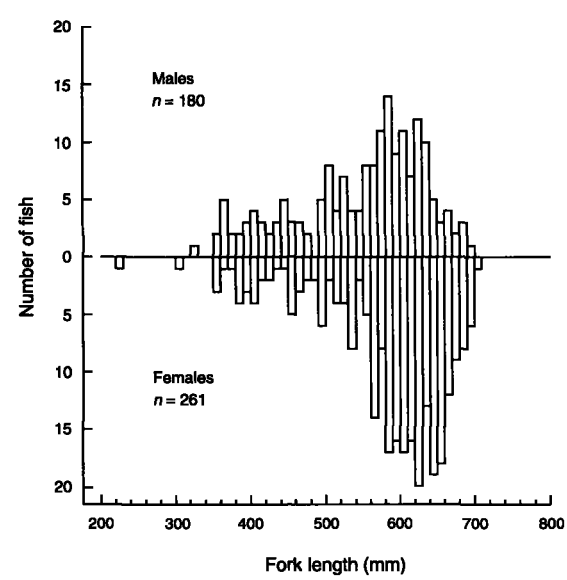

Figure 2
Length-frequency distributions for Florida Keys bonefish, *Albula vulpes*, caught with hook-and-line gear.

Table 2

Length-length, length-weight, and otolith weight-age regressions for bonefish, *Albula vulpes*, from the waters of the Florida Keys. TL = total length (mm), FL = fork length (mm), SL = standard length (mm), WT = weight (g), OWT = otolith weight (g), and AGE = age in years. Sample fork-length range for all length-length and length-weight regressions was 21–702 mm. Age range for the otolith weight-age regression was 1–19 years. Values in parentheses are standard errors.

			$Y = a+bX$		
Y	X	n	a (1 SE)	b (1SE)	r^2
FL	SL	521	4.5538 (1.0819)	1.0284 (0.0021)	0.998
FL	TL	516	–5.3384 (1.0297)	0.8652 (0.0017)	0.998
SL	FL	521	–3.3737 (1.0584)	0.9703 (0.0020)	0.998
SL	TL	516	–8.5152 (1.4894)	0.8394 (0.0024)	0.996
TL	FL	516	7.2580 (1.1770)	1.1537 (0.0022)	0.998
TL	SL	516	12.5401 (1.7404)	1.1864 (0.0034)	0.996
$\log_{10}$WT	$\log_{10}$FL	518	–5.3240 (0.0142)	3.1871 (0.0054)	0.999
$\log_{10}$OWT	$\log_{10}$AGE	427	–0.7161 (0.0107)	0.6489 (0.0133)	0.849

formed after about age 4, the dark translucent zones are narrow and only apparent in the region immediately adjacent to the annuli. The broad opaque zones in the outer portions of the otolith section are separate and distinct from the narrow opaque annuli, which are still visible at higher magnifications (30–50×) within the translucent zones in older fish, especially along the ventral ridge of the sulcus acusticus and the ventral margin of the otolith section.

We examined OTC-marked otoliths from five bonefish ranging from 465 to 661 mm in length and from 4 to 18 years in age (Table 1). All otoliths showed the expected pattern of otolith growth; one annulus had been formed per year. Marginal-increment analysis of otoliths also suggested that one annulus had been formed during March–June each year (Fig. 3). Median marginal increments had a consistent seasonal minimum during April–June and a maximum in October–February from 1992 to 1994. When median marginal increments were plotted for individual age classes 4–9, a similar pattern was seen (Fig. 4).

Of 471 otoliths processed for age estimation, only 20 (4.2%) were rejected because of disagreements among readings. The length-frequency distribution of fish whose otoliths were rejected because they were unsuitable for age estimation was not significantly different from that of all fish whose otoliths were examined (Kolmogorov-Smirnov two-sample test, D=0.234, P=0.22). The oldest bonefish examined were a 650-mm female estimated to be 19 years old and a 641-mm male also estimated to be 19 years old (Table 3). Bonefish growth was rapid until an age of about 6 years and then slowed considerably (Fig. 5). Results of likelihood-ratio tests showed a significant difference in the overall von Bertalanffy growth models for males and females (χ^2=26.15, df=3, P<0.001, Table 4). Estimates of L_∞(χ^2=0.406, df=1, P=0.52), K (χ^2=1.54, df=1, P=0.21), and t_0 (χ^2=1.28, df=1, P=0.26) were not significantly different between sexes. Lengths at age predicted by the von Bertalanffy equation agreed with the observed lengths of both female and male bonefish (Fig. 5). Predicted lengths at age of females were greater than those of males for all ages greater than 1 year, and observed lengths at age of females were greater than those of males for all ages except 1 and 18 (Table 3). The age-frequency distributions of males and females were significantly different (Kolmogorov-Smirnov two-sample test, D=0.265, P<0.001); females (median age=7 yr, interquartile range=4 yr, n=262) in our sample were significantly older than males (median age=6 yr, interquartile range=4 yr, n=181; Mann-Whitney U-test,

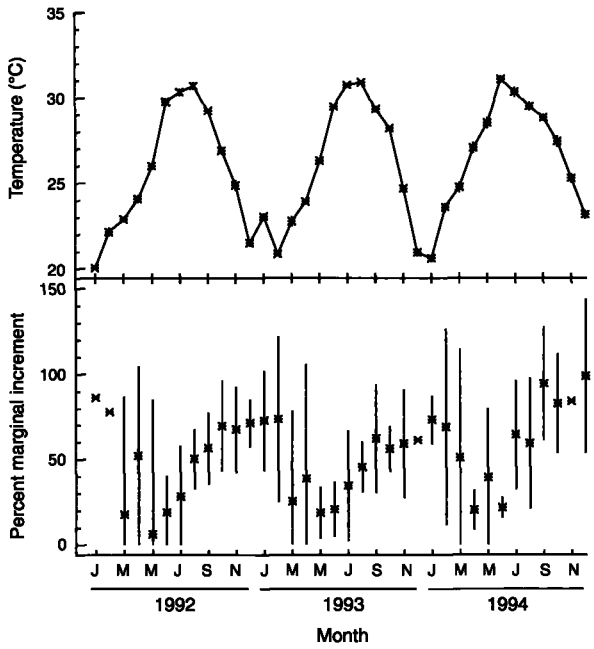

Figure 3

Mean monthly water temperatures (°C) calculated from daily temperature measurements at the water intake pump in Florida Bay adjacent to the Keys Marine Laboratory, and monthly median percent marginal increment and interquartile range for bonefish, *Albula vulpes*, otoliths.

P=0.012). Most bonefish (86%) in our sample that were caught with hook-and-line gear were from 3 to 10 years old (Fig. 6). On the basis of visual inspection of the age-frequency distributions, bonefish were not fully recruited to the fishery until an age of about 5 years.

The instantaneous rate of total mortality (Z) estimated by our catch-curve analysis was 0.25 (95% confidence interval 0.098–0.406, r^2=0.805, n=7, P<0.001) for males and 0.21 (95% confidence interval 0.167–0.303, r^2=0.922, n=9, P<0.001) for females. The instantaneous rate of natural mortality (M) estimated with Pauly's formula was 0.29 for males and 0.31 for females. The 20% reduction of this estimate recommended by Pauly (1983) for schooling species suggests a range of 0.2–0.3 for natural mortality.

Otolith weight was significantly related to age (Fig. 7). The slopes (t-test, df=417, t=1.34, P=0.09) and intercepts (t-test, df=418, t=0.49, P=0.31) of the otolith weight-age equations for males and females were not significantly different (Table 2).

Two of the bonefish that we aged were exceptionally small for their estimated ages and the weights of their otoliths were exceptionally light. One was a 351-mm female that was 7 years old and the other was a 458-mm female that was 18 years old. These two fish were statistically significant outliers, and we excluded them from growth models, age-frequency distributions, and otolith weight-age regressions. Both fish were caught with hook-and-line gear on the ocean (Florida Straits) side of North Key Largo, and they were the smallest females examined with active vitellogenic ovaries.

Discussion

We obtained bonefish from a variety of fishery-dependent and fishery-independent sources, but all fish larger than 405 mm that we examined were caught with hook-and-line gear. The size-frequency distribution of the hook-and-line-caught fish in our sample is probably similar to that of the fish caught in the fishery. Most of the hook-and-line-caught fish we examined were killed without regard to size, but a few fish included in our analysis were received from private anglers, tournaments, and taxidermists, sources that were presumably biased towards larger fish. Bonefish were not fully recruited to the hook-and-line gear until they reached a length of 550–600 mm and an age of about 5 years. We assume that our sample was representative of the Keys bonefish population beyond this size and age, but it is possible that hook-and-line gear introduced unknown biases that affected our mortality rates and growth-parameter estimates. We have no basis to evaluate the extent of these potential biases.

Age-validation experiments with OTC-marked otoliths supported our hypothesis that bonefish otoliths formed annual marks, and marginal-increment analysis suggested that annuli formed during March–June. Although sample sizes were insufficient to reveal trends for some individual age classes, age classes 4–9 showed marginal-increment patterns consistent with our hypothesis that annuli formed during March–June. Annulus formation appears to take place shortly after the season of minimal water temperatures in the Keys (Fig. 3). Monthly mean temperatures in Florida Bay at the Keys Marine Laboratory's water intake pump varied seasonally from a low of about 21°C during mid-December–February to a high of about 31°C during June–September (Fig. 3). These temperatures were probably similar to those of typical Keys bonefish habitat, and indeed on several occasions we collected bonefish on the flats adjacent to the pump. It is possible that holding fish under captive conditions and an artificial feeding regime affected the periodicity of annulus formation. However, we saw no change in the appearance or widths of the alternating translucent

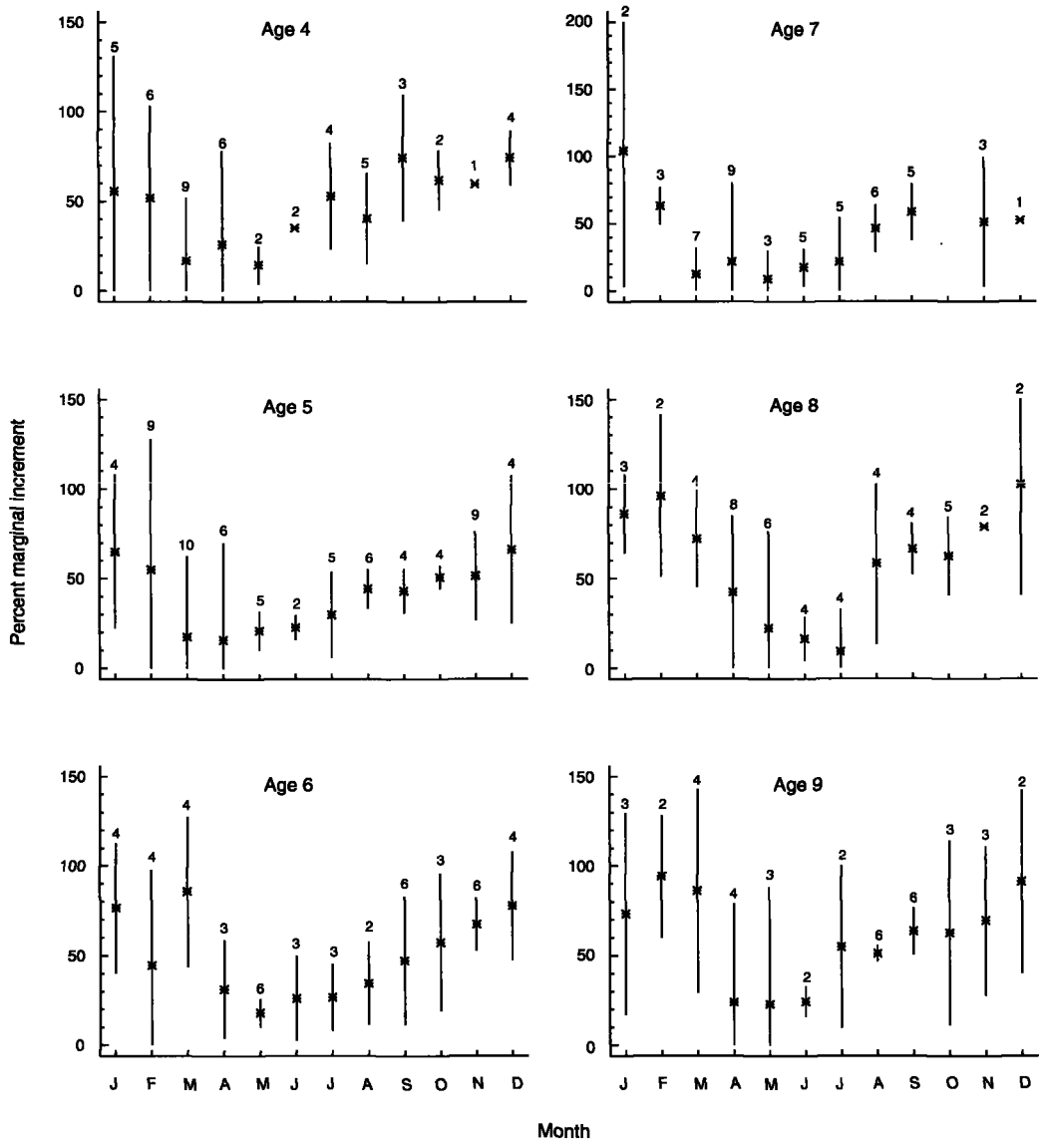

Figure 4

Monthly median percent marginal increment and interquartile range for bonefish otoliths for individual bonefish, *Albula vulpes*, age classes 4–9.

and opaque zones on otolith sections distal to the OTC mark to suggest that otolith growth had been fundamentally altered.

Our findings suggest that scales may not be suitable for ageing bonefish older than 6–9 years, the point at which our length-at-age data reached an asymptote. Scale-derived estimates of bonefish longevity by Bruger (1974) are lower than our otolith-derived estimate of 19 years. The oldest fish Bruger reported was estimated to be 12 years old, but he presented age-at-length data for only 140 bonefish ages 1–9. The number of fish in Bruger's sample declined quickly after age 6, and he apparently found only one fish older than age 9. In contrast, we found bonefish ages 3–9 to be abundant, and small numbers of fish were present in each age class from ages 10 to 19 yr (Fig. 6). The truncated age structure of Bruger's sample is probably an artifact of his ageing technique, but because we did not directly compare scale-derived and otolith-derived ages, we cannot rule out the possibility that Bruger's sample contained only one fish older than age 9.

Table 3

Average observed and predicted fork lengths (mm) for male and female bonefish, *Albula vulpes*, and average observed fork lengths for unsexed bonefish. Values in parentheses are standard error and sample size.

	Male		Female		Unsexed
Age (yr)	Average observed	Predicted	Average observed	Predicted	Average observed
1	320 (8.8; 7)	288	311 (13.4; 9)	284	
2	362 (4.7; 5)	370	374 (19.5; 8)	381	
3	401 (9.2; 19)	435	403 (10.9; 11)	454	399 (7.0; 2)
4	493 (11.6; 22)	486	499 (12.7; 27)	509	437 (37.0; 2)
5	531 (10.1; 33)	525	567 (8.1; 38)	551	538 (1)
6	559 (13.6; 20)	557	585 (7.2; 31)	583	608 (1)
7	588 (8.4; 17)	581	605 (6.3; 33)	606	597 (1)
8	619 (7.0; 19)	600	633 (4.2; 31)	625	635 (1)
9	608 (7.0; 17)	615	641 (7.4; 25)	638	
10	614 (7.6; 6)	627	651 (8.1; 16)	649	
11	618 (10.8; 7)	637	638 (25.0; 7)	657	
12	637 (17.0; 3)	644	672 (6.9; 5)	662	668 (1)
13	660 (1)	650	670 (29.0; 2)	667	
14		654	635 (18.0; 2)	670	
15	672 (1)	658	674 (13.6; 3)	673	
16		661	654 (3.0; 3)	675	
17	644 (1)	663	679 (5.7; 5)	676	
18	659 (22.0; 2)	664	642 (1.2; 3)	677	
19	641 (1)	666	650 (1)	678	

Table 4

Parameter estimates for the von Bertalanffy growth model for bonefish, *Albula vulpes*, collected from the waters of the Florida Keys. Values in parentheses are standard errors.

Sex	n	L_∞ (mm)	K	t_0	r^2
Males	181	670.7 (14.74)	0.242 (0.0256)	−1.318 (0.3205)	0.770
Females	260	680.9 (8.55)	0.279 (0.0195)	−0.934 (0.2031)	0.792

Although our growth models for male and female bonefish were significantly different, the differences were small. This is reflected in our findings that individual growth parameters were not significantly different, that the two growth curves appeared similar (Fig. 5), and that the maximum sizes attained by both sexes were similar. Observed lengths at age for females were larger than those for males in all but two age classes, which is consistent with the higher growth rates for females. The median length of the

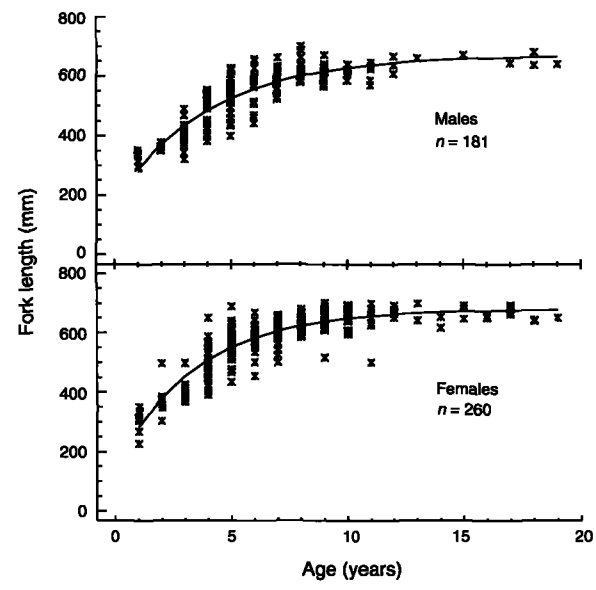

Figure 5

Observed and predicted lengths from the von Bertalanffy growth model for male and female bonefish, *Albula vulpes*.

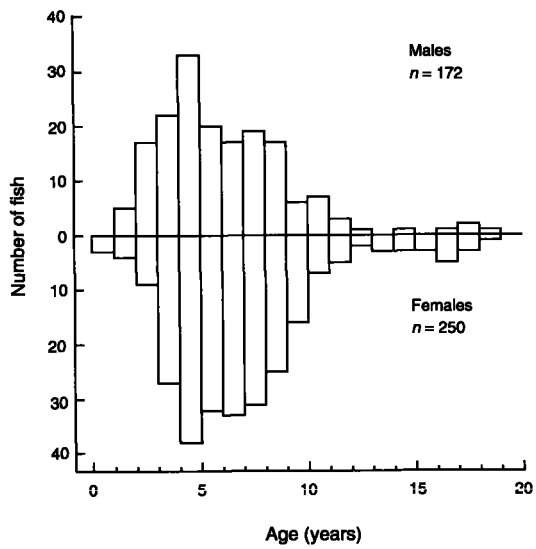

Figure 6

Age-frequency distributions for male and female Florida Keys bonefish, *Albula vulpes*, caught with hook-and-line gear.

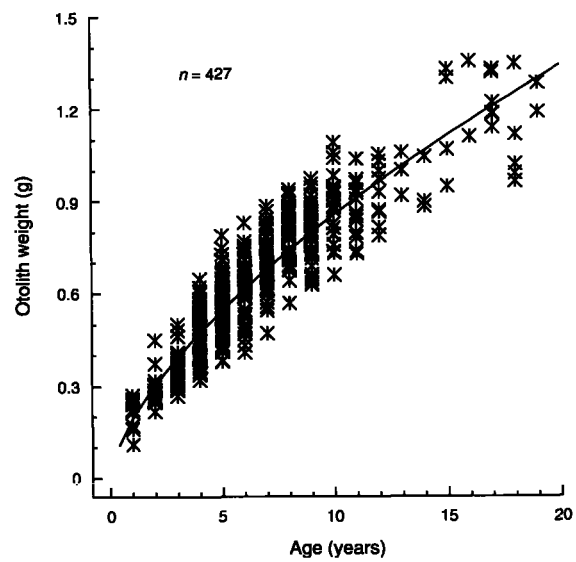

Figure 7

Growth of otoliths (g) of male and female bonefish, *Albula vulpes*. The equation for the regression of $\log_{10}$-transformed data is presented in Table 2.

females in our sample was slightly but significantly larger than that of males. This is also consistent with a small but significant difference in sex-specific growth rates; however, this finding is confounded by the significantly older median age of females, which would also contribute to the observed difference in the sex-specific size-frequency distributions. There is no readily apparent biological explanation for the slightly older age-frequency distribution of females in relation to males.

The only other estimates of von Bertalanffy growth parameters for bonefish are by Morales-Nin (1994) for 31 fish caught off Mexico's Pacific coast. She used a length-frequency analysis to estimate K=0.275 and L_∞ = 473 mm; her estimate of K is close to our Florida estimates, but her estimate of L_∞ is much less. Her small sample size could have seriously biased her parameter estimates. Furthermore, Pfeiler (1996) presented allozyme data that suggested that an undescribed species of *Albula* occurs off Mexico in the Gulf of California. It is unclear whether *A. vulpes* actually occurs off Mexico's Pacific coast or whether Morales-Nin's growth parameter estimates apply to *A. vulpes* or to Pfeiler's undescribed species.

The estimated instantaneous total mortality rate for bonefish was low. Our estimated range for natural mortality (0.2–0.3) included our total mortality estimates, suggesting that there is little fishing mortality. This was expected because the commercial harvest of bonefish from Florida waters is prohibited and most bonefish caught by recreational anglers are released. The low estimate for total mortality suggests that the mortality rate of bonefish caught with hook-and-line gear and then released was low, and that there was little mortality of bonefish as bycatch in commercial net fisheries operating in Florida Keys waters.

Otolith weight is not a precise estimator of bonefish age, but it could be used to approximate age distributions in situations where annulus counts are not available. Otolith weight accounted for more of the variability in age (84.9%) than fish length (77.0% for males and 79.2% for females). The Florida Keys are on the northern edge of the range of bonefish in the western North Atlantic. In specimens from the more tropical and less seasonal portions of the species' range, annuli may be more difficult to count and thus be less useful in age determination. This has been observed in other elopomorph species. Crabtree et al. (in press) reported that estimating age by sectioned otoliths was more difficult with tarpon from Costa Rican waters than it was with those from Florida waters; they rejected as unreadable more than twice as many otoliths from Costa Rican tarpon as those from Florida tarpon.

We cannot explain the presence of the two exceptionally small, old, and sexually mature female bonefish in our sample. Variable growth rates and stunting of some early maturing females is a possible ex-

planation. We cannot eliminate the possible existence of a cryptic species in the Keys, but the one specimen retained in our collection has no obvious morphometric or meristic characters to support this idea. Bruger (1974) also reported the occurrence of small bonefish from 221 to 352 mm FL with mature ovaries in the Florida Keys, but he found no morphometric or meristic evidence to suggest the presence of a second species. Additional specimens are needed to resolve this issue.

Acknowledgments

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Marine stock-enhancement potential in nursery habitats of striped mullet, *Mugil cephalus*, in Hawaii

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Abstract.—Declines in world fishery landings have prompted new interest in the use of cultured fishes to help replenish depleted fish populations. The hypothesis that hatchery releases can increase population size has at least two corollaries that need to be tested: 1) released cultured fish survive, grow, and contribute to recruitment; and 2) cultured fish do not displace wild stocks. The former corollary is considered here for striped mullet, *Mugil cephalus* L., in nursery habitats.

Results from pilot experiments were used to modify release strategies to test marine stock enhancement potential in Kaneohe Bay, Hawaii. Of 80,507 native, cultured, striped mullet fingerlings tagged with coded wire and released during spring and summer, 2,642 fish were recovered by cast-net sampling during 11 months. Recapture rate increased 600% compared with initial studies in Kaneohe Bay. This increase was the result of confining releases to the vicinity of fresh-water streams and of imposing a minimum size of 70 mm TL during summer releases. After 11 months, cultured fish represented 50% of the striped mullet in collections at the release site, 20% in a nursery habitat 1 km to the north, and 10% in a nursery 3 km north. The location of releases (stream mouth vs. upstream lagoon) significantly affected dispersal patterns but did not affect growth or recapture rate. This study corroborated earlier results which showed that the smallest fish released (45–60 mm) could survive relatively well if released in spring. At least three measures were needed to describe hatchery effect: 1) hatchery contribution (% cultured fish in samples), 2) catch per unit of effort for cultured and wild striped mullet, and 3) recovery rate (no. captured/no. released). This study documents that survival of cultured fish in coastal nurseries can be significantly improved by using information from pilot release experiments to revise release parameters.

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Fishery Bulletin 94:452–471 (1996).

The need for improved understanding and management of coastal fisheries is clear (New, 1991; NMFS, 1991, 1992; Anthony, 1993; Sissenwine and Rosenberg, 1993; Schnute and Richards, 1994). In 1990, growth in annual world fishery production peaked at 100 million metric tons (t) (FAO, 1992). Without more effective control of marine fisheries, seafood availability and recreational fishing opportunities are likely to decline at a rapid pace as demand increasingly outweighs supply during the next century (New, 1991; FAO, 1992). Ricker (1969) estimated maximum sustainable annual production levels of wild fisheries may be limited to 160 million t. More recently, the Food and Agriculture Organization of the United Nations (FAO) revised the estimate to 100 million t (WRI, 1990). Larkin (1993) suggests that sea farming could increase annual yields several fold over this level.

One form of sea farming, supplementing wild stocks with releases of cultured organisms (hatchery-based stock enhancement), may have considerable potential in marine and estuarine environments. Whether stock enhancement can help significantly increase world production levels of seafood is unclear (Schnute and Richards, 1994; Smedstad et al., 1994). Increased emphasis on quantitative evaluation is needed to determine the actual potential of stock enhancement. Norway and the United States first conducted large-scale hatchery releases of yolk-sac larvae of marine fishes at the end of the last century (Solemdal et al., 1984; Grimes, 1995); Japan followed with releases of hatched larvae of cod, herring, and king crab in the early 1900's (called "sea farming" in Japan; Kitada et al., 1992; Honma, 1993). A century later, the central issue remains largely unresolved—can propagation and release of cultured marine organisms into the wild increase coastal fish populations?

Although marine stocking programs in the USA were abandoned earlier this century for lack of a clear impact on fisheries landings, the potential for using hatchery releases to increase populations of coastal fishes was never critically tested (Richards and Edwards, 1986). Now, modern marking methods and new aquaculture capabili-

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ties provide the technologies required to quantify and evaluate marine stock enhancement (Jefferts et al., 1963; Buckley and Blankenship, 1990; and see Honma, 1993, for examples of growth in marine aquaculture). There is an emerging optimism that carefully implemented marine stock enhancement might be a useful fisheries management tool (e.g. Grimes, 1995). Use of cultured marine organisms to help replenish depleted coastal stocks has finally begun to receive empirical evaluation (Tsukamoto et al. 1989; Svåsand and Kristiansen, 1990; Svåsand et al., 1990, 1991; Bannister and Howard, 1991; Barlow and Gregg, 1991; Kitada et al., 1992, 1994; Iglesias and Rodríguez-Ojea, 1994; Jørstad et al., 1994, a and b; Nordeide et al., 1994; Smedstad et al., 1994; Stoner, 1994; Støttrup et al., 1994; Kent et al., 1995; Leber, 1995; Leber et al., 1995; Willis et al., 1995).

The hypothesis that hatchery releases can help increase marine fish populations has at least two corollaries that need to be tested. One is that cultured fishes released into coastal waters actually survive, grow, and contribute to recruitment. The other corollary is that cultured fish do indeed increase abundance rather than displace wild stocks. These two postulates are basic assumptions of stock-enhancement theory, yet both remain largely untested in coastal ecosystems (i.e. with organisms that reproduce in marine environments). The former corollary is the focus of this study, the latter is considered elsewhere (Leber et al., 1995).

A series of workshops was held to select species for immediate stock-enhancement research in Hawaii. The species given priority was Pacific threadfin, *Polydactylus sexfilis*, an inshore carnivore. An inshore herbivore, striped mullet, *Mugil cephalus*, ranked second in this semi-quantitative selection process (Leber[1]). We chose to begin field experiments with striped mullet because it ranked high in the selection process and culture techniques were available. We expected to apply lessons learned about stock enhancement to Pacific threadfin once culture techniques became available.

To design a rigorous test, data would be needed from pilot releases to define effective release strategies. Fish size-at-release (SAR) and the timing of releases were important choices that needed to be made, as Hager and Noble (1976) and Bilton et al. (1982) had already shown with coho salmon released into streams in the Pacific northwest. Releasing fish into coastal environments would also require careful consideration of release habitat. If any of these three variables affected survival of released fish, they would also affect the power of any test of stock-enhancement potential. In Hawaii, a series of pilot release experiments were conducted to identify effects of release magnitude, SAR, release habitat, and release season on survival and contribution of cultured striped mullet to wild stock abundance (Leber, 1995; Oceanic Institute[2]; Leber et al.[3]). The results of those pilot releases were used to design the present study, which is to test the first corollary—that cultured fish make a substantial contribution to a marine fish population in Hawaii.

As pilot release-recapture experiments began in Hawaii, Tsukamoto et al. (1989) published results that indicated that SAR affected survival of red sea bream, *Pagrus major*, juveniles released into News Bay, Japan. In 1990, Svåsand and Kristiansen (1990) showed similar results with cod, *Gadus morhua*, released into Norwegian fjords. In 1990, a similar pattern was observed in Hawaii following summer releases of about 40,000 tagged striped mullet into each of two embayments on Oahu, Maunalua Bay and Kaneohe Bay (Leber, 1995). Work with striped mullet revealed that recapture rates approached zero when cultured fish smaller than 60-mm total length (TL) were released in summer or fall months. These results ruled out the alternative of stocking newly hatched fry or postlarvae in an experimental test of the stock-enhancement concept in Hawaii. Pilot releases in Hawaii also revealed that survival of cultured mullet was strongly affected by release habitat and release season (Leber, 1995; Leber and Arce, in press; Leber et al.[3]). Hatchery release studies with marine fishes in Norway, Florida, and California (Svåsand and Kristiansen, 1990; Drawbridge et al., 1995; Willis et al., 1995) and with cultured conch released in the Caribbean (Stoner, 1994) have shown substantial effects of release strategies on survival in coastal environments.

Based on the results of pilot hatchery releases in Kaneohe Bay, an experiment was designed to incorporate improved release strategies and to evaluate the potential of using hatchery releases to increase significantly juvenile striped mullet recruitment in Kaneohe Bay, the largest estuary in Hawaii. Criteria for success were the following: 1) cultured fish released in this study represented a substantial pro-

[1] Leber, K. M. 1994. Prioritizing marine fishes for stock enhancement in Hawaii. The Oceanic Institute, Honolulu, HI, 46 p.

[2] Oceanic Institute. 1990. Stock enhancement of marine fish in the State of Hawaii (SEMFISH, Phase II). Annual report to NMFS, February 1989–June 1990, Waimanalo, Hawaii, 106 p.

[3] Leber, K. M., S. M. Arce, H. L. Blankenship, and N. P. Brennan. 1996. Influence of release season on size-dependent survival of cultured striped mullet, *Mugil cephalus*, in a Hawaiian estuary. In review.

portion (at least 20%) of the juvenile striped mullet in net samples 4 months after release; 2) there was a persistence of cultured fish in net samples throughout the study; and 3) growth was comparable to measured rates in wild juveniles. If these criteria were met, it would be reasonable to assume that cultured fish had substantially affected juvenile recruitment at the study site.

This study was conducted in and around fresh water tributaries, the preferred nursery habitat for striped mullet. Striped mullet are catadromous and begin to move out of their nursery habitats as they approach maturity (Blaber, 1987). In Hawaii, yearling juveniles begin to move out of the intertidal zone and out of shallow shore zones of streams by about February or March (Major, 1978; Leber, 1995; Oceanic Institute[4]). Striped mullet reach advanced sexual development in fresh water but must migrate to the sea to spawn (Blaber, 1987). Annual recruitment into inshore nursery habitats of young-of-the-year wild mullet occurs in spring in Hawaii (Major, 1978).

Methods

Hatchery releases

Striped mullet were spawned from wild broodstock at The Oceanic Institute and reared to fingerling size for spring and summer releases. Batches of striped mullet eggs were hatched about every six weeks over a five-month period. Larval striped mullet from each batch were hatched and cultured in 5,000-L cylindrical tanks with conical bottoms for 45 days. Stage-1 juveniles (45 days old, 20 mm TL) were transferred to 8,000-L circular tanks and nursed for 40 days to stage-2 juveniles (85 days old, 40 mm TL). Stage-2 juveniles were transferred to 30,000-L circular tanks and nursed to tagging size (45–130 mm TL). In culture tanks, growth rates averaged 0.5 mm TL/day.

A release-recapture experiment was performed to evaluate recapture rates of cultured striped mullet. Release magnitude, release location, release season, and size of fish released were determined from results of 1990 and 1991 pilot studies in Kaneohe Bay (Leber, 1995; Leber et al.[3]). During 4 May through 29 May 1992, and again from 13 July through 7 August 1992, juveniles were harvested from culture tanks, graded into five different length groups (ranging from 45 mm to 130 mm TL) by using commercial bar graders and tagged with binary coded-wire tags (CWT) (Northwest Marine Technology, Inc., Olympia, WA). Prior to tagging, fish were provided a 2-day period to recover from stress of harvesting and size grading. About 80,500 tagged fish were released into Kaneohe Bay.

Tags identified year and season of release, SAR, release habitat, release lot (date), and number of fish released per treatment condition. Fish were tagged in batches, with a different code for each season-SAR-site-lot combination. Tags were implanted in the snout area with an automatic injector with head molds designed specifically for striped mullet.

For each release season and SAR combination, the experiment was replicated with three release lots at each of two release locations in Kahaluu Stream (Fig. 1), where the greatest recruitment of wild mullet in Kaneohe Bay had been reported (Leber, 1995; Oceanic Institute[4]). In May, fish of all five size intervals were released in each lot (45–60 mm; 60–70 mm; 70–85 mm; 85–110 mm; and 110–130 mm). Only fish of

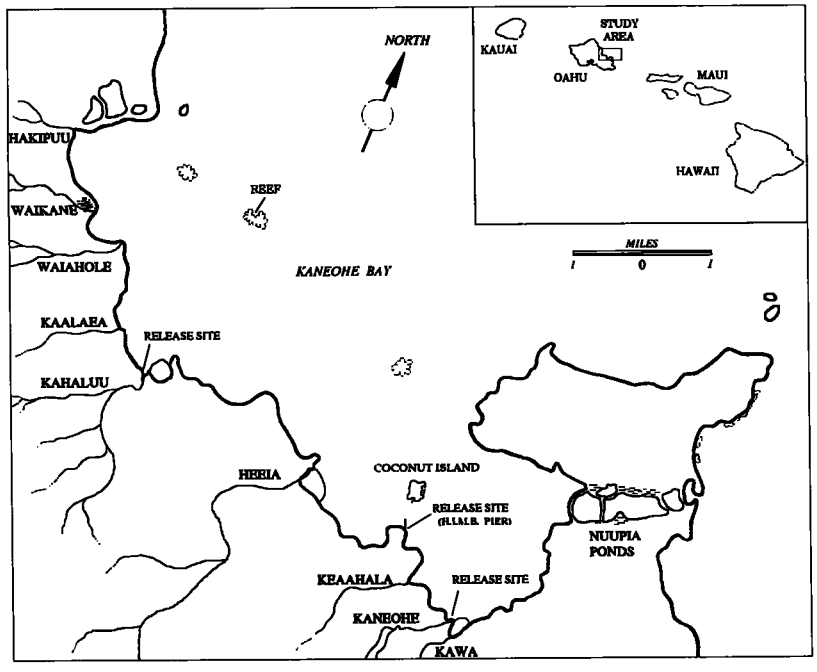

Figure 1

Map of Kaneohe Bay showing pilot study release sites and nursery habitats where monthly cast-net collections were conducted. In this study, all releases were made at Kahaluu Stream, a principal nursery habitat for striped mullet in Kaneohe Bay.

[4] Oceanic Institute. 1991. Stock enhancement of marine fish in the State of Hawaii (SEMFISH Phase III). Annual report to NMFS, June 1990–June 1991. Waimanalo, Hawaii, 107 p.

the three largest size intervals were released in summer (none <70 mm TL). There was size variation in all batches of mullet reared for this study. However, the primary difference among the five size intervals of fish released was fish age.

Replicate release lots were introduced biweekly for a 3- to 4-week period in both spring and summer. Fish were transported and then released simultaneously at the stream inlet and 300 m upstream in a 10-ha lagoon. Numbers of tagged and released fish varied between seasons and among size intervals released but were held nearly constant among release lots and between release sites (Table 1). Between 10,200 and 15,100 tagged fish were released in each of six release lots. Releases were conducted around mid-day or early afternoon. Bottom salinities at release sites ranged from 12 to 25 ppt. All releases were made near the shoreline in water from 0.5 to 1.5 m deep.

Previous studies revealed a CWT retention rate of 97% for striped mullet during 12 months following tagging (Oceanic Institute[4]). To verify tag-retention rates in this study, at least 5% of fish tagged for each release lot were randomly subsampled prior to each release. These subsamples, totalling 4,264 tagged fish, were retained in 12 tanks for up to 4 months; fish were checked monthly to verify when % tag retention stabilized (Blankenship, 1990).

Tagged fish from the 1991 study were also recovered in this study. Methods in that study were essentially identical to those here, with two exceptions: 1) in 1991, fish of all five size intervals were released in both spring and summer; 2) 1991 release sites included Kahaluu Stream mouth and Kaneohe Stream mouth (Leber et al.[3]). The mouth of Kaneohe Stream lies 11.6 km south of Kahaluu Stream mouth.

Monitoring

To evaluate the effect of releases on juvenile abundance, collections were made monthly with cast nets in four Kaneohe Bay nursery habitats, except for July (when summer releases were conducted). We began to monitor abundances of released and wild striped mullet in Kaneohe Bay on 8 June 1992 and continued to do so for 10 months. Each field collection was conducted during a 1-wk period. Collections were made during the day during an 8-h period at each nursery site (sampling station). Stations were established in the vicinity of documented striped mullet nursery habitats at various tributaries throughout the bay (Oceanic Institute[4]).

To standardize collection effort, two substations were established at each station—one 200 to 300 m upstream, the other in the bay seaward of the stream mouth and on subtidal reef flats running along the bay shore on both sides of the stream mouth. Within substations, 15 cast-net throws were made. A total of 120 cast-net samples were taken each month. To broaden the range of microhabitats and fish size-

Table 1

Summary statistics for 80,507 fish tagged and released in 1992 to evaluate hatchery releases in Kaneohe Bay. Unique batch codes were used to identify fish from each cell in the matrix. Spring release lot 1 occurred on 4 May, lot 2 on 15 May, and lot 3 on 29 May. Summer release lot 1 occurred on 13 July, lot 2 on 24 July, and lot 3 on 7 August.

		Release season								
		Spring release lot				Summer release lot				
Release site	Size at release	1	2	3	Total	1	2	3	Total	Grand total
Kahaluu (upstream at lagoon)	45–60 mm	2,356	2,368	2,277	7,001	0	0	0	0	7,001
	60–70 mm	2,372	2,375	2,371	7,118	0	0	0	0	7,118
	70–85 mm	1,595	1,594	1,591	4,780	2,867	2,497	4,063	9,427	14,207
	85–110 mm	807	807	805	2,419	2,863	2,493	2,540	7,896	10,315
	110–130 mm	398	399	399	1,196	250	125	72	447	1,643
	Subtotal	7,528	7,543	7,443	22,514	5,980	5,115	6,675	17,770	40,284
Kahaluu Stream (mouth)	45–60 mm	2,356	2,369	2,321	7,046	0	0	0	0	7,046
	60–70 mm	2,361	2,370	2,344	7,075	0	0	0	0	7,075
	70–85 mm	1,596	1,593	1,599	4,788	2,878	2,494	4,069	9,441	14,229
	85–110 mm	806	806	805	2,417	2,848	2,500	2,540	7,888	10,305
	110–130 mm	396	399	399	1,194	249	125	0	374	1,568
	Subtotal	7,515	7,537	7,468	22,520	5,975	5,119	6,609	17,703	40,223
Grand total		15,043	15,080	14,911	45,034	11,955	10,234	13,284	35,473	80,507

ranges sampled, two different-size cast nets were used. Of the 15 casts per substation, 10 were made with a 5-m diameter, 10-mm mesh net, and five casts were made with a 3-m diameter, 6-mm mesh net. The smaller net was more effective in narrow upstream habitats.

We used stratified-random sampling; cast nets were thrown over schools of mullet juveniles, rather than thrown randomly. Random sampling yielded few wild mullet and very few tagged individuals. Cultured and wild striped mullet schooled together in fairly low densities within these clear-water nursery habitats, and our collections targeted these schools. Nevertheless, data used to determine recapture rates and proportions of tagged mullet in samples were randomly distributed because there was no a-priori indication that schools, once sighted, contained tagged individuals.

Mullet sampled in these collections were measured and checked for tags with a portable tag detector (Northwest Marine Technology, Inc.). All tagged mullet were placed on ice and returned to the laboratory for size measurement and tag analysis. Wild fish were counted, measured, and released at the sample site. After extraction, the binary codes were read by a technician with a binocular microscope (40×). All tag codes were verified with a second (blind) reading by a another technician.

Data were analyzed with SYSTAT software (Wilkinson, 1990). A randomized-block design ANOVA was used to compare means. Treatments (SAR, release microhabitat) were blocked over time (3 release lots) within season (spring and summer). Proportions were arcsine transformed. Orthogonal contrasts were used to compare means (Sokal and Rohlf, 1981). SYSTAT Basic was used to write tag decoding algorithms. For each recaptured fish, the algorithms identified SAR, release microhabitat, release date, release lot, and number of fish released per treatment-lot combination on the basis of the binary tag codes. An error-check algorithm was also written. Variance estimates are expressed throughout as standard errors.

Results

Recapture summary

A total of 2,985 tagged cultured mullet were recaptured during the 11-month period of this study (Table 2). Of these, 2,642 were cultured fish from the present study (1992 releases). None of the fish released in 1992 were recaptured at Kaneohe Stream. From the tag codes it was determined that 304 (10.2%) of the 2,985 tagged fish collected had been released in

Table 2

Numbers of tagged cultured striped mullet recovered in cast-net samples made in Kaneohe Bay. 304 of the 2,985 cultured fish recaptured were released in 1991, the remainder in 1992. None of the fish released in 1992 were captured at Kaneohe Stream. Sites are arranged from north (Waiahole Stream) to south (Kaneohe Stream). 30 cast-net throws were made at each station monthly.

Collection site	Source	Jun	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	Total	Mean	SE
Waiahole Stream	Wild	126	169	141	121	10	65	54	13	47	26	772	77.2	18.2
	Cultured	29	26	27	64	15	47	32	8	7	3	258	25.8	6.0
	%Cultured	18.7	13.3	16.1	34.6	60.0	42.0	37.2	38.1	13.0	10.3	25.0	28.3	5.2
Kaalaea Stream	Wild	84	154	66	172	85	58	48	34	24	20	745	74.5	16.4
	Cultured	111	221	83	58	128	74	60	46	22	5	808	80.8	19.5
	%Cultured	56.9	58.9	55.7	25.2	60.0	56.1	55.6	57.5	47.8	20.0	52.0	49.4	4.6
Kahaluu Stream (1991 and 1992 release site in N. Kaneohe Bay)	Wild	258	99	82	69	65	49	34	64	32	28	780	78.0	24.7
	Cultured	231	376	237	188	164	111	136	132	37	28	1640	164.0	32.4
	% Cultured	47.2	79.2	73.7	73.2	71.6	69.4	80.0	67.4	53.6	50.0	67.8	66.5	3.8
Kaneohe Stream (1991 release site in S. Kaneohe Bay)	Wild	58	36	55	56	50	45	35	27	48	40	450	45.0	3.3
	Cultured	41	29	42	42	33	21	33	11	19	8	279	27.9	4.0
	%Cultured	41.4	44.6	43.3	42.9	39.8	31.8	48.5	29.0	28.4	16.7	38.3	36.6	3.1
All streams	Wild	526	458	344	418	210	217	171	138	151	114	2747	274.7	47.2
	Cultured	412	652	389	352	340	253	261	197	85	44	2985	298.5	55.2
	%Cultured	43.9	58.7	53.1	45.7	61.8	53.8	60.4	58.8	36.0	27.8	52.1	50.0	3.5

Kaneohe Bay in 1991 as part of a previous pilot study (Leber et al.[3]). Tags from 39 (1.3%) of the recaptured fish were lost during the extraction process. These 39 cultured fish were released either in 1991 or 1992 but could not be further identified and were excluded from our analyses. Thus, the decoded tag data are based on 2,946 tags.

Tag retention in the subsampled fish held for 4 months averaged 97.9% (±0.6 SE, n=12 tanks). With one exception (92.6%, lot 1, lagoon release), all tag retention rates within release lots exceeded 97%. After capture data were adjusted for the 2.1% tag loss, a total of about 2,697 cultured fish from the 1992 releases were actually captured (3.3% of the 80,507 fish released in this study).

Tagged cultured fish represented about 50% of the 5,732 wild and cultured mullet collected from the four study sites (Table 2). Proportions of cultured mullet in Kahaluu samples remained >50% of the total (wild and cultured) mullet sampled in collections throughout the study and were ≥70% in six of ten collections (Table 2). Proportions of hatchery fish were also high at two streams north of the release site.

Recovery of yearlings released in 1991

Sampling periods in the present study ranged from 47 weeks to 100 weeks after the 1991 releases. Most (86%) fish from 1991 releases were collected at Kaneohe Stream, where they represented a high proportion of 1-yr-old mullet at that site throughout their second year in the wild (Table 3). Only 42 of the 304 fish from the 1991 release were collected outside Kaneohe Stream. These 42 fish accounted for <3% of the cultured fish collected at any other site. Thus, some fish from 1991 releases continued to occupy juvenile mullet nursery habitats well into their second year.

Marine enhancement impact: 1992 releases

Release impact in nursery habitats About 90% of the 2,946 tags recovered and decoded were from striped mullet released at Kahaluu in 1992. These fish made a substantial contribution to juvenile recruitment in three nursery habitats in the north end of the bay: Kahaluu Stream, Kaalaea Stream, and Waiahole Stream (Table 2).

Impact of the test release was greatest at the release site, Kahaluu Stream; there was a trend towards reduced impact with shoreline distance away from that site. Cultured fish consistently outnumbered wild fish at the release site and averaged 66% of the mullet in monthly collections at Kahaluu. After 11 months in the wild, cultured fish still represented 50% of the mullet sampled at Kahaluu. Greatest impact outside of the release site was seen at Kaalaea, 1 km north of Kahaluu Stream, where cultured fish averaged about 50% of the mullet sampled. A substantial effect was also apparent in Waiahole Stream, a mullet nursery habitat 3 km north of Kahaluu Stream, where cultured fish averaged 28% of the mullet sampled. Proportions of cultured mullet in collections were stable through time at all four nursery habitats sampled until spring, when annual recruitment of wild mullet began. Numbers of both wild and cultured fish from the 1992 year class declined in samples in spring at all nursery sites (Table 2).

Table 3

Movement patterns following 1991 releases of 91,245 tagged cultured mullet in Kaneohe Bay (half at Kahaluu Stream, half at Kaneohe Stream.) Release season and release site are identified for 304 tagged fish recovered at the various collection (recapture) sites throughout the Bay. Recapture sites (and distances travelled) are ordered geographically within collection dates, from the northernmost site (Waiahole Stream) to the southernmost site (Kaneohe Stream) at which tagged fish were collected (see Fig. 1). Data are totals (n) recaptured in 300 cast-net samples per site taken over the 10-mo. study period.

Collection date (weeks after release)	Recapture site	Kahaluu release n	Kahaluu release Distance (km)	Kaneohe release n	Kaneohe release Distance (km)	Collection date (weeks after release)	Recapture site	Kahaluu release n	Kahaluu release Distance (km)	Kaneohe release n	Kaneohe release Distance (km)
Spring release						**Summer release**					
Weeks 57–100	Waiahole	—	3.05	3	15.00	Weeks 47–91	Waiahole	1	3.05	3	15.00
	Kaalaea	3	0.98	—	12.59		Kaalaea	—	0.98	—	12.59
	Kahaluu	26	0	—	12.04		Kahaluu	6	0	—	12.04
	Kaneohe	—	11.58	111	0		Kaneohe	1	11.58	150	0
	Total	29		114			Total	8		153	

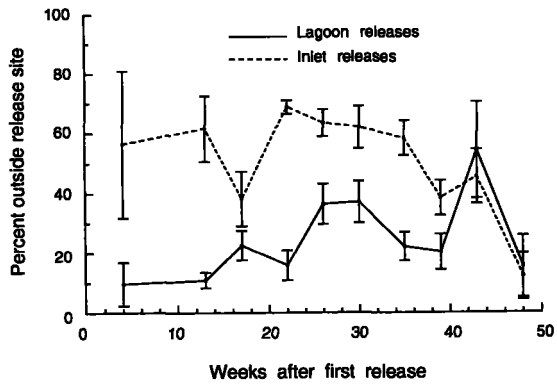

Figure 2

Release microhabitat effect on dispersal of released cultured fish. Proportions (± SEM, n=6 lots) of cultured striped mullet recaptured outside of the release habitat, Kahaluu Stream, following downstream (inlet) releases at the shore next to the stream mouth, and releases 300 m upstream (lagoon).

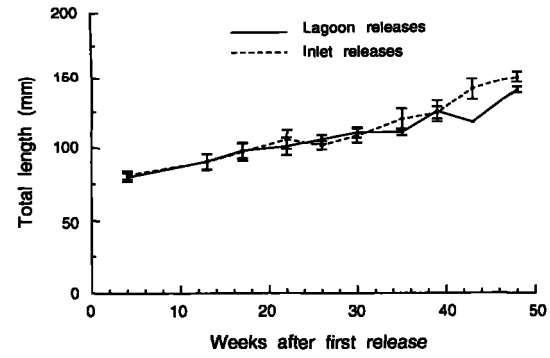

Figure 3

Mean length (TL [±SEM, n=6]) of cultured striped mullet recovered in net samples made over the course of the study, for individuals that were 70–85 mm TL when released.

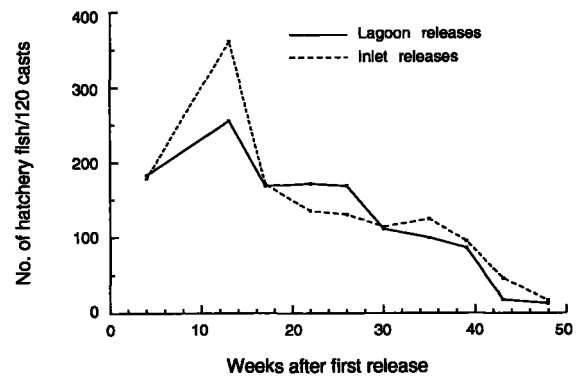

Figure 4

Catch per unit of effort (CPUE) for cultured striped mullet from collections made at four nursery habitats (combined data) in Kaneohe Bay, including the release site. Total number of tagged fish recaptured in 120 cast-net samples taken monthly (30 samples per month at each nursery habitat) compared with those taken over the 11-mo study period.

Release microhabitat effect on enhancement impact Initial habitat selection was strongly affected by release microhabitat. There was greater dispersal away from the release site by fish released next to the inlet of Kahaluu Stream than by fish released about 300 m upstream in the lagoon (Fig. 2.) This pattern was similar following both spring and summer releases (Table 4). Most fish released upstream remained in Kahaluu Stream throughout the study, whereas most fish from the inlet releases moved to other nursery sites in the bay. This difference in dispersal patterns was statistically significant by the second collection date (P<0.003, n=6 release lots per treatment [3 spring + 3 summer]) and was observed through mid February 1993 (P<0.01 in collections Aug, Oct, and Jan; P<0.05 in Nov, Dec, and Feb; not significant in Jun, Sep, Mar, and Apr).

Recapture rates and growth rates were unaffected by release microhabitat. Growth curves for fish released at the inlet and lagoon were intermingled (Fig. 3) as were plots of numerical abundances of cultured fish in collections (Fig. 4). Statistical comparisons were nonsignificant (n=6, P>0.08) for all collection dates.

SAR and release-season effects on enhancement impact

Overall SAR effect on recapture rates Fish size-at-release affected survival of mullet released in this study. The smallest size group (45–60 mm TL) had significantly reduced survival in comparison with other sizes (Fig. 5). Fish <60 mm TL were recaptured at less than half the frequency of larger fish released (Fig. 5; P<0.001; P<0.002 in orthogonal contrast in a comparison of SAR-1 with SAR1-2, -3, and -4 combined; n=6 with recapture data from spring and summer releases combined). For the four SAR groups >60 mm TL (in the aggregate data set, spring and summer releases combined), there were no significant differences among recapture frequencies (P>0.30 for any comparison, spring and summer releases combined).

Table 4

Movement patterns following 1992 releases at Kahaluu Stream in Kaneohe Bay. Release season and release sites (inlet release was at the mouth of Kahaluu Stream and lagoon release was about 300 meters upstream in a 10-hectare lagoon) are identified for tagged fish recovered at the various collection (recapture) sites throughout the Bay. Recapture sites (and distances travelled) are ordered geographically within collection dates, from the northernmost site (Waiahole Stream) to the southernmost site (Kaneohe Stream) at which tagged fish were collected (see Fig. 1). Monthly data are totals (n) per 30 samples per site, organized by the average time (weeks after release) that fish had been in the wild prior to collection.

Collection date (weeks after release)	Recapture site	Inlet release n	Inlet release Distance (km)	Lagoon release n	Lagoon release Distance (km)
Spring release					
8–12 Jun 92	Waiahole	25	3.1	4	3.2
	Kaalaea	100	1.0	10	1.1
	Kahaluu	53	0	169	.1
3	Kaneohe	—	11.6	—	11.7
	Total	178		183	
17–21 Aug 92	Waiahole	18	3.1	—	3.2
	Kaalaea	131	1.0	10	1.1
	Kahaluu	25	0	67	.1
13	Kaneohe	—	11.6	—	11.7
	Total	174		77	
21–25 Sep 92	Waiahole	11	3.1	4	3.2
	Kaalaea	38	1.0	13	1.1
	Kahaluu	34	0	54	.1
18	Kaneohe	—	11.6	—	11.7
	Total	83		71	
19–23 Oct 92	Waiahole	14	3.1	3	3.2
	Kaalaea	28	1.0	5	1.1
	Kahaluu	20	0	81	.1
22	Kaneohe	—	11.6	—	11.7
	Total	62		89	
16–23 Nov 92	Waiahole	3	3.1	2	3.2
	Kaalaea	25	1.0	17	1.1
	Kahaluu	17	0	46	.1
26	Kaneohe	—	11.6	—	11.7
	Total	45		65	
14–18 Dec 92	Waiahole	5	3.1	5	3.2
	Kaalaea	17	1.0	8	1.1
	Kahaluu	19	0	37	.1
30	Kaneohe	—	11.6	—	11.7
	Total	41		50	
11–15 Jan 93	Waiahole	8	3.1	4	3.2
	Kaalaea	21	1.0	2	1.1
	Kahaluu	17	0	27	.1
34	Kaneohe	—	11.6	—	11.7
	Total	46		33	
Summer release					
17–21 Aug 92	Waiahole	6	3.1	1	3.2
	Kaalaea	67	1.0	12	1.1
	Kahaluu	114	0	165	.1
3	Kaneohe	—	11.6	—	11.7
	Total	187		178	
21–25 Sep 92	Waiahole	10	3.1	2	3.2
	Kaalaea	12	1.0	15	1.1
	Kahaluu	65	0	80	.1
8	Kaneohe	—	11.6	—	11.7
	Total	87		97	
19–23 Oct 92	Waiahole	32	3.1	14	3.2
	Kaalaea	20	1.0	5	1.1
	Kahaluu	21	0	63	.1
13	Kaneohe	—	11.6	—	11.7
	Total	73		82	
16–23 Nov 92	Waiahole	3	3.1	6	3.2
	Kaalaea	49	1.0	35	1.1
	Kahaluu	33	0	62	.1
16	Kaneohe	—	11.6	—	11.7
	Total	85		103	
14–18 Dec 92	Waiahole	18	3.1	18	3.2
	Kaalaea	35	1.0	13	1.1
	Kahaluu	20	0	30	.1
20	Kaneohe	—	11.6	—	11.7
	Total	73		61	
11–15 Jan 93	Waiahole	14	3.1	5	3.2
	Kaalaea	27	1.0	10	1.1
	Kahaluu	37	.1	51	.1
24	Kaneohe	—	11.6	—	11.7
	Total	78		66	
15–19 Feb 93	Waiahole	3	3.1	4	3.2
	Kaalaea	23	1.0	6	1.1
	Kahaluu	33	0	23	.1
29	Kaneohe	—	11.6	—	11.7
	Total	59		33	
15–19 Mar 93	Waiahole	2	3.1	4	3.2
	Kaalaea	11	1.0	2	1.1
	Kahaluu	16	0	4	.1
34	Kaneohe	—	11.6	—	11.7
	Total	29		10	

Table 4 (continued)

Collection date (weeks after release)	Recapture site	Inlet release n	Inlet release Distance (km)	Lagoon release n	Lagoon release Distance (km)	Collection date (weeks after release)	Recapture site	Inlet release n	Inlet release Distance (km)	Lagoon release n	Lagoon release Distance (km)
Spring release						**Summer release**					
16–19 Dec 93	Waiahole	—	3.1	1	3.2	12–16 Apr 93	Waiahole	—	3.1	2	3.2
	Kaalaea	13	1.0	4	1.1		Kaalaea	—	1.0	2	1.1
	Kahaluu	23	0	48	.1		Kahaluu	8	0	5	.1
39	Kaneohe	—	11.6	—	11.7	38	Kaneohe	—	11.6	—	11.7
	Total	36		53			Total	8		9	
15–19 Mar 93	Waiahole	—	3.1	1	3.2						
	Kaalaea	8	1.0	1	1.1						
	Kahaluu	9	0	6	.1						
43	Kaneohe	—	11.6	—	11.7						
	Total	17		8							
12–16 Apr 93	Waiahole	—	3.1	—	3.2						
	Kaalaea	3	1.0	—	1.1						
	Kahaluu	6	0	4	.1						
47	Kaneohe	—	11.6	—	11.7						
	Total	9		4							
Grand totals	Waiahole	84	3.1	23	3.2	Grand totals	Waiahole	88	3.1	56	3.2
through	Kaalaea	373	1.0	69	1.1	through	Kaalaea	244	1.0	100	1.1
Week 39	Kahaluu	208	0	529	.1	Week 38	Kahaluu	347	0	483	.1
	Kaneohe	—	11.6	—	11.7		Kaneohe	—	11.6	—	11.7
	Total	665		621			Total	679		639	

Effect of release season Although recapture rates among SAR groups >60 mm appeared similar in the aggregate data set, an SAR effect was apparent when data were collapsed within release seasons (Table 5). To clarify survival and the interactive effect of release season with SAR, only fish that survived at least 16 weeks are included in Figures 6, 7, and 8. This provides a picture of those cultured fish that remain in the population from 4 months on, having survived initial causes of mortality in the wild, and that have the potential to affect adult abundances.

All sizes released in spring and summer were prominent in cast-net collections (Table 5). As expected following spring releases (Leber et al.[3]), no direct relationship was apparent between SAR and recapture rates. However, recapture rates (from week 16 on) were significantly less for the smallest size group released than for SAR groups 2, 3, and 5 (Fig. 6, $P<0.02$).

Summer releases resulted in better recovery of the largest size group released (Fig. 7, 110–130 mm TL; $P<0.04$; marginally significant). There was also a trend (nonsignificant) towards better recovery of the three largest SAR groups when released in summer rather than in spring (Fig. 8).

Growth of fish released in spring was comparable with that of fish released in summer (Fig. 9). Data in Figure 9 are for fish from the median SAR group (70–85 mm TL), for which the greatest amount of data was available. This growth comparison is representative of the other sizes released in both seasons.

Comparison with 1990 and 1991 release impact There was substantially greater impact on juvenile abundances in Kaneohe Bay following 1992 releases than after pilot releases in 1990 (Leber, 1995) and in 1991 (Leber et al.[3]). Proportions of cultured fish at Kahaluu 10 months after releases increased from about 3% following 1990 releases to 10% after 1991 releases, to about 50% in the present study (Fig. 10).

The general pattern following releases was similar in all years—an initial increase in proportions of cultured fish in samples, followed by a decline over the next year. However, there were two principal differences in 1992: 1) July releases in 1992 caused a considerably greater increase in abundance than in

Table 5

Numbers of tagged fish released in 1992 and recovered from each treatment group by size at release within release season at Kahaluu Stream in Kaneohe Bay. Data are totals (n) recaptured and recapture frequencies (% recap. [n recaptured/n released]), organized by the average time (weeks after release) that fish had been in the wild prior to collection. Note that summer releases followed spring releases by 10 weeks.

Collection date (weeks after release)	Size at release	Total recap. n	% recapt.	Collection date (weeks after release)	Size at release	Total recap. n	% recapt.	Grand total	Grand total % recap.
Spring release				**Summer release**					
8–12 Jun 92	45–60 mm	14	0.10	17–21 Aug 92	45–60 mm	—	—	14	0.10
	60–70 mm	98	0.69		60–70 mm	—	—	98	0.69
	70–85 mm	131	1.37		70–85 mm	161	0.85	292	1.03
3	85–110– mm	89	1.84	3	85–110 mm	192	1.22	281	1.36
	110–130 mm	29	1.21		110–130 mm	12	1.46	41	1.28
	Total	361	0.80		Total	365	1.03	726	0.90
				21–25 Sep 92	45–60 mm	—	—	—	—
					70–85 mm	—	—	—	—
					70–85 mm	76	0.40	76	0.40
				8	85–110 mm	106	0.68	106	0.68
					110–130 mm	2	0.24	2	0.24
					Total	184	0.52	184	0.52
17–21 Aug 92	45–60 mm	30	0.21	19–23 Oct 92	45–60 mm	—	—	30	0.21
	60–70 mm	98	0.69		60–70 mm	—	—	98	0.69
	70–85 mm	77	0.80		70–85 mm	82	0.43	159	0.56
13	85–110 mm	37	0.77	13	85–110 mm	70	0.51	107	0.52
	110–130 mm	9	0.38		110–130 mm	3	0.37	12	0.37
	Total	251	0.56		Total	155	0.44	406	0.50
21–25 Sep 92	45–60 mm	20	0.14	16–23 Nov 92	45–60 mm	—	—	20	0.14
	60–70 mm	55	0.39		60–70 mm	—	—	55	0.39
	70–85 mm	49	0.51		70–85 mm	104	0.55	153	0.54
18	85–110 mm	18	0.37	16	85–110 mm	78	0.49	96	0.47
	110–130 mm	12	0.50		110–130 mm	6	0.73	18	0.56
	Total	154	0.34		Total	85	0.53	342	0.42
19–23 Oct 92	45–60 mm	44	0.31	14–18 Dec 92	45–60 mm	—	—	44	0.31
	60–70 mm	68	0.48		60–70 mm	—	—	68	0.48
	70–85 mm	25	0.26		70–85 mm	60	0.32	85	0.30
22	85–110 mm	6	0.12	20	85–110 mm	68	0.43	74	0.36
	110–130 mm	8	0.33		110–130 mm	6	0.73	14	0.44
	Total	151	0.34		Total	134	0.38	285	0.35
16–23 Nov 92	45–60 mm	29	0.21	11–15 Jan 93	45–60 mm	—	—	29	0.21
	60–70 mm	36	0.25		60–70 mm	—	—	36	0.25
	70–85 mm	28	0.29		70–85 mm	84	0.45	112	0.39
26	85–110 mm	10	0.21	24	85–110 mm	56	0.35	66	0.32
	110–130 mm	7	0.29		110–130 mm	4	0.49	11	0.34
	Total	110	0.24		Total	144	0.41	254	0.32
14–18 Dec 92	45–60 mm	15	0.11	15–19 Feb 93	45–60 mm	—	—	15	0.11
	60–70 mm	39	0.27		60–70 mm	—	—	39	0.27
	70–85 mm	20	0.21		70–85 mm	52	0.28	72	0.25
30	85–110 mm	13	0.27	29	85–110 mm	38	0.24	51	0.25
	110–130 mm	4	0.17		110–130 mm	2	0.24	6	0.19
	Total	91	0.20		Total	92	0.26	183	0.23
11–15 Jan 93	45–60 mm	24	0.17	15–19 Mar 93	45–60 mm	—	—	24	0.17
	60–70 mm	23	0.16		60–70 mm	—	—	23	0.16
	70–85 mm	20	0.21		70–85 mm	19	0.10	39	0.14
34	85–110 mm	6	0.12	34	85–110 mm	19	0.12	25	0.12
	110–130 mm	6	0.25		110–130 mm	1	0.12	7	0.22
	Total	79	0.18		Total	39	0.11	118	0.15

Table 5 (continued)

Collection date (weeks after release)	Size at release	Total recap. *n*	% recapt.	Collection date (weeks after release)	Size at release	Total recap. *n*	% recapt.	Grand total	Grand total % recap.
Spring release				**Summer release**					
15–19 Feb 93	45–60 mm	19	0.14	12–16 Apr 93	45–60 mm	—	—	19	0.14
	60–70 mm	36	0.25		60–70 mm	—	—	36	0.25
	70–85 mm	23	0.24		70–85 mm	12	0.06	35	0.12
39	85–110 mm	6	0.12	38	85–110 mm	4	0.03	10	0.05
	110–130 mm	5	0.21		110–130 mm	1	0.12	6	0.19
	Total	89	0.20		Total	17	0.05	106	0.13
15–19 Mar 93	45–60 mm	5	0.04						
	60–70 mm	13	0.09						
	70–85 mm	4	0.04						
45	85–110 mm	1	0.02						
	110–130 mm	2	0.08						
	Total	25	0.06						
12–16 Apr 93	45–60 mm	2	0.01						
	60–70 mm	8	0.06						
	70–85 mm	3	0.03						
47	85–110 mm	—	—						
	110–130 mm	—	—						
	Total	13	0.03						
Totals (weeks 3–39)	45–60 mm	195	1.39	Totals (weeks 3–38)	45–60 mm	—	—	195	1.39
	60–70 mm	453	3.19		60–70 mm	—	—	453	3.19
	70–85 mm	373	3.90		70–85 mm	650	3.44	1,023	3.60
	85–110 mm	185	3.83		85–110 mm	631	4.00	816	3.96
	110–130 mm	80	3.35		110–130 mm	37	4.51	117	3.64
Grand totals (through week 39)		1,286	2.86			1,318	3.72	2,604	3.23

earlier studies with July releases; and 2) the late-summer decline in abundance resulted in less reduction in release impact in 1992 than in other years.

Recapture rates were disproportionately higher in this study than after releases in 1990 and 1991 (Table 6). Number of fish released at Kahaluu Stream in 1992 exceeded the number released at that same site in 1990 and 1991 by 690% and 180%, respectively. Yet the total number of fish recaptured from week 16 on exceeded comparable data (similar sampling effort) from 1990 and 1991 by 1,560% and 420%, respectively (Table 6). Increase in the effectiveness of 1992 releases is revealed by comparing recapture frequencies (no. recaptured/no. released) and by including data from all release sites. From week 16 on, 1.65% of the cultured mullet released in 1992 were recaptured in cast-net samples. This recapture rate was 6 times that seen in the 1990 study (0.28%) and 1.7 times the rate in the 1991 study. Sampling frequency and number of cast-net samples were nearly identical among the three studies.

These differences among studies were statistically significant. Recapture rates after 1992 releases were significantly greater than expected in all pair-wise comparisons of 1992 data with data from 1990 and 1991 (Table 6; *G*-tests, $P<0.001$ in all cases). The 1991 study yielded significantly greater recapture rates than did the 1990 study, when fish released outside of the Kahaluu site in 1990 are included in the comparison (Table 6; all sites, $\chi^2 = 225$, $P<0.001$).

Discussion

Marine enhancement potential

Context of this study A rigorous test of marine stock-enhancement involves several phases of research. These are considered here to place the current study in perspective. Key research phases include 1) understanding both wild stock distribution

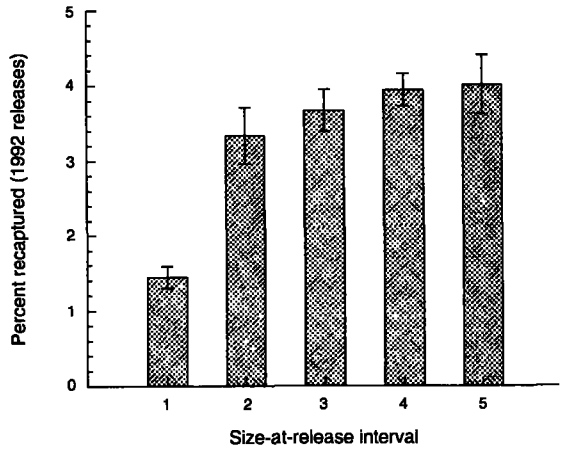

Figure 5

Recapture frequencies ([number recaptured/number released] × 100% [±SEM]) of cultured striped mullet juveniles released in 1992 and subsequently collected over 11 months at four nursery habitats in Kaneohe Bay. Combined data for fish from both spring and summer releases (n=6 lots) are presented and compared over the five size-at-release intervals: interval 1 = 45–60 mm, 2 = 60–70 mm, 3 = 70–85 mm, 4 = 85–110 mm, and 5 = 110–130 mm total length.

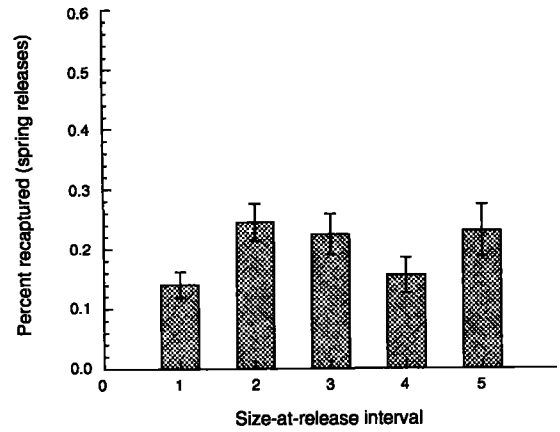

Figure 6

Recapture frequencies ([number recaptured/number released] × 100% [± SEM]) following spring releases (n=3 lots) of cultured striped mullet juveniles in 1992. These are combined data from four nursery habitats sampled in Kaneohe Bay. Data are plotted against size-at-release intervals, which are explained in the legend for Figure 5. Data are for the period from 16 weeks after release through the end of the study.

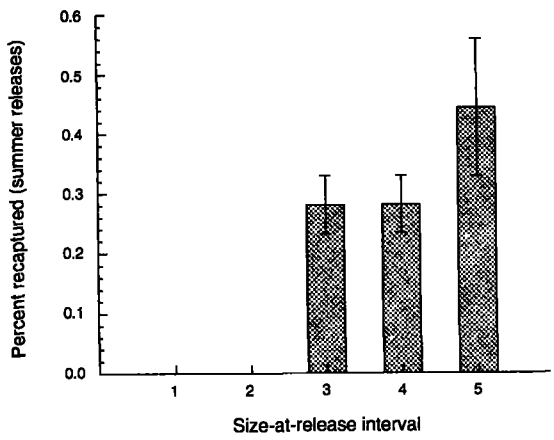

Figure 7

Recapture frequencies ([number recaptured/number released] × 100% [± SEM]) following summer releases (n=3 lots) of cultured striped mullet juveniles released in 1992. Size-at-release intervals are explained in Figure 5. No fish in the two smallest intervals were released in summer 1992. Data from the four nursery habitats are combined and are for the period from 16 weeks after release through the end of the study.

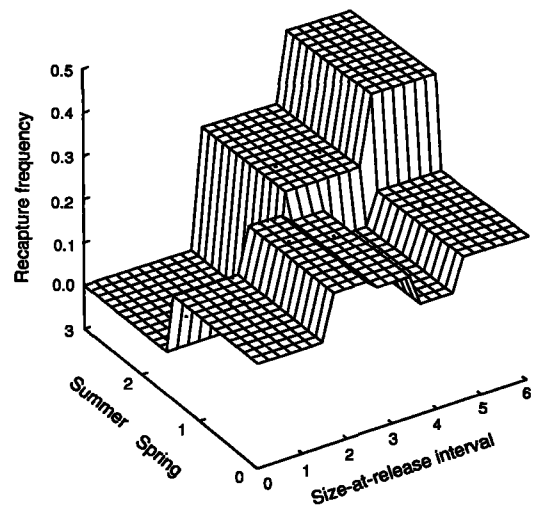

Figure 8

Comparison of spring and summer recapture frequencies of cultured striped mullet for the period from 16 weeks after release through the end of the study. No fish in the two smallest size intervals were released in summer. Data from the four nursery habitats are combined. Size-at-release intervals are explained in Figure 5.

and abundance patterns as well as behavior and ecological interactions; 2) conserving wild stock genetics and health; 3) developing reliable culture techniques; 4) establishing and testing a tagging method to identify hatchery fish; 5) evaluating optimal release strategies through experimentation; 6) assessing hatchery-release effect on population size and fishery landings; and 7) modeling economic costs and benefits (Richards and Edwards, 1986; Shaklee et al., 1993). These issues are interrelated to some degree (Blankenship and Leber, 1995).

That cultured fish will survive in the wild and contribute to stock abundance is a basic assumption that should be tested early in the development stage of planned hatchery-release programs (Richards and Edwards, 1986), notwithstanding the need to consider fish genetics and health, as well as economics of the fishery. In coastal ecosystems, understanding the potential of stock enhancement involves at least four levels of investigation in order to quantify growth

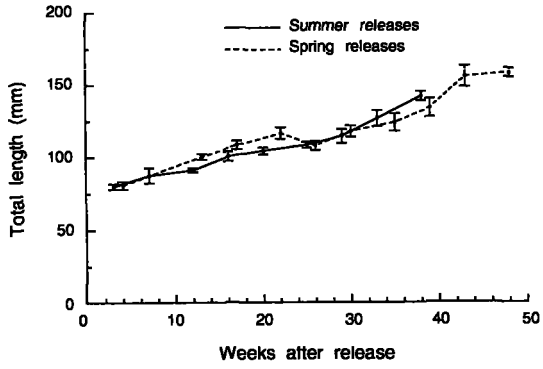

Figure 9

Mean total length (±SEM, n=3 lots) of cultured striped mullet released at 70–85 mm TL in spring and summer 1992 and retrieved in net samples over the next 10 to 11 months.

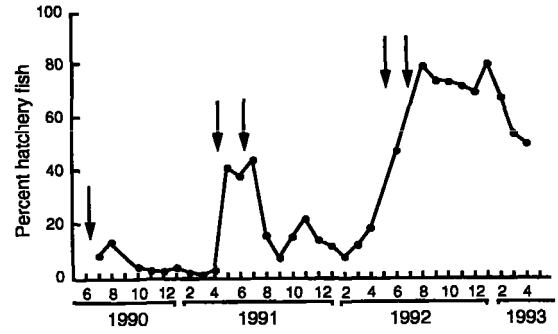

Figure 10

Percent contribution of cultured striped mullet to total abundance (wild and cultured striped mullet) in cast-net samples over a three-year study period in Kaneohe Bay (including this study). Data are from monthly cast-net collections at Kahaluu Stream. Arrows identify release periods. Spring and summer releases were conducted in 1991 and 1992. Releases in 1990 were made only in summer. Numbers on x-axis represent months of the year.

Table 6

Summary of numbers of cultured mullet released and recapture frequencies in Kaneohe Bay following hatchery releases in 1990, 1991, and 1992. Chi-square values (χ^2) and probablity levels (P) from G-tests are given for pair-wise comparisons of recapture frequencies (1990 vs. 1991 and 1991 vs. 1992). There were two release sites in Kaneohe Bay in 1990 and 1991.

	Kahaluu Stream			All sites combined		
	1990	1991	1992	1990	1991	1992
Released						
Total tagged	11,676	45,790	80,507	42,822	91,245	80,507
Recaptured						
Total	177	952	2,632	227	2,405	2,632
% recovered	1.52	2.08	3.27	0.62	2.64	3.27
χ^2		16.0	148		689	56
P		<0.001	<0.001		<0.001	<0.001
Total after 16 wk	85	315	1,326	118	890	1,326
% recovered	0.73	0.69	1.65	0.28	0.96	1.65
χ^2		0.021	225		225	147
P		>0.640	<0.001		<0.001	<0.001

and survival of cultured fish in the wild, each focused on different life stages:

Level 1 **Initial recapture rate:** A key issue is whether a release-recapture design is adequate to evaluate stocking effectiveness. Initial sampling of released fish after a pilot release (e.g. during the first couple of months) will establish whether monitoring is feasible under the chosen release strategies (e.g. release habitat, fish size at release) and with the condition of released fish and sampling design. An early look at recapture rates reveals a maximum expected recapture rate for a particular release (which will likely decrease over time because of mortality and dispersal) and can help determine whether release strategy or sampling strategy needs to be redesigned.

Level 2 ***Growth, survival and impact on abundance through the nursery stage of the life cycle:*** Assessing comparative effectiveness of release strategies in increasing juvenile recruitment can provide an early indication of enhancement potential. Two corollaries of the enhancement concept should be considered here: the first—cultured fish survive, grow, and contribute to population size—cannot be evaluated meaningfully without information on how chosen release strategies affect postrelease survival; the second corollary—cultured fish do not displace wild stocks—can be evaluated experimentally, once dispersal patterns are understood (Leber et al., 1995).

Level 3 **Growth, survival, and release impact through asymptotic growth:** involves assessment of release impact on adult population size and fishery landings. Recapture rates and growth can also be modeled to evaluate enhancement potential (Polovina, 1990, 1991). Results gained at level 2 on release-strategy impacts on survival may need to be confirmed at this level (e.g. a collecting gear bias favoring smaller fish can mask a size-at-release impact on survival at level 2; Leber et al., in press; Leber and Arce, in press).

Level 4 **Impact on reproduction and recruitment in subsequent generations:** With genetic markers to track hatchery impact across generations, an assessment can be made of hatchery impact on production of the next generation (Jørstad et al., 1994a).

Criteria for success need to be specified as testable hypotheses in enhancement programs (Larkin, 1979; Peterman, 1991; Blankenship and Leber, 1995). Percent increase in fish population size needed for success will depend on fish species and enhancement objectives. Cost-benefit evaluations can help determine yields required to break even. But value can be subjective and difficult to quantify when the objective is to enhance a recreational fishery or a threatened or endangered species. We evaluated success in terms of impact on recruitment and improvement in recapture rate in this study compared with our earlier studies. Our data reveal how information from pilot studies can be used to identify effective release strategies. Break-even costs for striped mullet enhancement are considered elsewhere (Leber and Cantrell[5]).

Enhancement concept with striped mullet In this paper, we address level 2 above and reveal a substantial hatchery contribution in nursery habitats following releases of cultured mullet. Results of this study corroborate the first corollary of the marine stock enhancement concept, that released fish can survive, grow, and contribute to recruitment. Released juveniles integrated with wild mullet at primary nursery habitats in Kaneohe Bay. Cultured mullet were abundant in samples on every collection date over the 11 months. Cultured fish showed linear growth; those released in May 1992 doubled in size within 48 weeks, with growth rates similar to wild striped mullet (Leber et al., in press). The second corollary, that cultured mullet are not displacing wild mullet at the Kahaluu Stream release site, was experimentally evaluated and corroborated in a follow-up field experiment (Leber et al., 1995).

Hatchery effect on abundances in nursery habitats was remarkable after adjusting release strategy to incorporate findings from pilot releases in Kaneohe Bay. Except for anadromous fishes, there are very few examples where hatchery releases have revealed the potential to double juvenile recruitment success with a marine organism (e.g. Kristiansen and Svåsand, 1990, for cod; Kitada et al., 1992, for flounder; Honma, 1993, for scallops). Cultured fish released in this study increased recruitment of juvenile striped mullet at the release site in 1992 by at least 100%. This large effect was partly a function of a poor recruitment year for wild fish and was partly due to higher survival following summer releases, compared with survival in earlier studies (Leber, 1995; Leber et al.[3]). Release impact on abundance

[5] Leber, K. M., and R. N. Cantrell. 1996. Effect of fish size-at-release on the relative cost to enhance striped mullet in Hawaii. In review.

was also considerable in streams 3 km away from the release site. Decrease in proportions of cultured fish in samples after 8 months coincided with the seasonal period (March) when yearlings begin to move out of nursery habitats into deeper water and when new recruits begin to arrive (Major, 1978; Leber, 1995; Oceanic Institute[4]).

The striped mullet collected in this study that were released in 1991 (Leber et al.[3]) represented a large portion (28%) of the total striped mullet caught in net samples at Kaneohe Stream. These data document that a portion of the cultured striped mullet released in Kaneohe Bay can be found in their nursery habitats up to two years after release.

It is evident from this study and from follow-up creel interviews in which fishery landings were surveyed that there is significant potential to increase the striped mullet population in Kaneohe Bay with relatively small-scale hatchery releases. Cultured mullet released in spring 1992 were first detected in the commercial fishery in Kaneohe Bay in October 1993, when a 367-mm-TL fish was recovered during contact interviews with commercial fishermen (Leber and Arce, in press). By the seasonal closure of the fishery in December 1994, 119 of the mullet released in 1992 had been recovered through contact interviews with commercial fishermen. According to tag data from interviewing fishermen in Kaneohe Bay, fish released in this study accounted for 9% of the commercial catch during fall 1994, at which time the proportion of cultured fish to wild fish was increasing logarithmically. Ninety-four of the cultured fish caught were checked for maturity; 44 males were ripe with milt and 2 females were gravid with mature eggs (Leber and Arce, in press).

Survival and hatchery impact on abundance The best gauge of the immediate effect of the 1992 hatchery releases on mullet population size is actual abundance of released fish in the wild. But actual number of survivors after 11 months is unknown. The >50% hatchery contribution to abundance at the release site is impressive, but from an economic viewpoint, data on actual increases in yields and population size are needed to compare the benefits of enhancement with costs. An estimate of survival would be a better gauge of stock-enhancement impact than would the proportion of hatchery fish in the population.

However, it is logistically difficult to quantify actual survival of released cultured fishes in open coastal environments. There is substantial literature on evaluating animal survival, much of which is based on change in relative abundance (catch per unit of effort [CPUE]) over time in mark-release-recapture experiments. The analysis theory for release-recapture experiments dates back to Ricker's (1945, 1948) relative recovery-rate method. A more general theory based on maximum likelihood was developed independently by Seber (1970) and Youngs and Robson (1975). Brownie et al. (1985) and Burnham et al. (1987) have provided a detailed discussion of maximum-likelihood methods. These methods for estimating survival are based on change in abundance in samples over time and are confounded in open environments by dispersal into and out of the population (Connor et al., 1983; MacCall, 1990; Nichols and Pollock, 1990; Frank, 1992) and by gear bias, as capture probabilities change with changes in fish size and habitat selection (e.g. Kjelson and Colby, 1976; MacLennan, 1992; Thompson, 1994; Acosta and Appeldoorn, 1995; Leber et al., in press). Without reliable estimates of immigration and emigration, one can use change in capture rate over time to measure loss from a population (i.e. the sum of mortality + emigration) but not to estimate mortality alone.

In this study, decrease in abundance over time in cast-net samples is a poor indicator of actual survival. Striped mullet move out of their nursery habitats as they approach maturity (Blaber, 1987), and juveniles move from shallow water to deeper water during their first year (Major, 1978; Leber et al.[3]). Overall decline in mullet abundance in samples over the 11-month study period was due to a combination of mortality, dispersal, and gear bias as mullet grew and moved into deeper water where cast nets are not effective sampling devices.

Postrelease mortality prior to initial sampling is also a source of error in estimating survival following hatchery releases. A key question is whether mortality of cultured fish is intense during the first day or so after a release (e.g. what percent of released individuals are consumed by predators?). Initial mortality could be an important factor in enhancement dynamics and should be accounted for in survival estimates, especially in open environments where mortality can be confused with emigration. But initial postrelease mortality has received little attention in "release-recapture" literature. There is evidence, however, that until cultured fish have been conditioned by exposure to predators in the wild, inadequate predator avoidance behavior can result in increased mortality (Parker, 1968; Healey, 1982; Olla and Davis, 1988; Olla and Davis, 1989; Tsukamoto, 1993; Olla et al., 1994). Initial mortality following hatchery releases of Pacific salmon can be severe and is most intense during the 48-h period following releases.[6] Ini-

[6] Blankenship, H. L. 1995. Washington Department of Fish and Wildlife, 600 Capitol Way North, Mail Stop 43149, Olympia, WA. Personal commun.

tial behavior of stocked fish can also be directly affected by handling stress and temperature change, either of which could cause an increase in susceptibility to predators shortly after release (Fuiman and Ottey, 1993).

The difficulty in quantifying initial mortality is in obtaining an unbiased early sample of abundance to establish a baseline recapture rate for comparison with recapture rates in later samples. Dispersal of striped mullet from the point of release is not an immediate event (Leber et al., personal observ.). The first few hours after a release should be the very time when released fish are most vulnerable to predators. However, immediate sampling in an open environment to determine initial abundance in samples violates assumptions of basic mark-recapture models (Ricker, 1975), primarily the assumption that marked fish mix randomly within the study area.

Without a reliable, unbiased method to estimate postrelease survival in open coastal ecosystems, how do we gauge benefits from hatchery releases? In effect, the best indicator of hatchery impact is total annual catch of cultured fish in a fishery. Thus, assessment of marine stock enhancement requires unbiased estimates of CPUE, total fishing effort, and proportion of cultured fish in the fishery. Accurate catch statistics for marine organisms are expensive and often lacking (e.g. Shomura[7]), as in Hawaii for striped mullet. The difficulty of assessing total hatchery impact is exacerbated when cultured fish are released unmarked, which has often been the case with marine fishes (discussed in Richards and Edwards, 1986).

Because a fishery on juveniles is lacking, some measures besides fishery landing statistics are needed to evaluate survival of cultured fish during the nursery phase. Consequently, researchers in coastal systems report recovery rates and percent cultured fish in samples of cultured and wild fish (hatchery contribution) as early indicators of enhancement effect. Percentage of cultured fish can be a good relative indicator of release impact but only when reported with CPUE for wild and cultured fish. Hatchery contribution is a function of abundance of wild fish, release magnitude, survival, dispersal, size of hatchery and wild fish, and environmental carrying capacity.

Hatchery contribution is sensitive to variation in any of the above six factors. Thus, alone, it has low information content as an indicator of success. In fact, year to year comparisons of hatchery contribution can be misleading. Three examples below illustrate the relationship among hatchery contribution (%C), CPUE of cultured (C) and wild fish (W) in samples, and actual hatchery effect on recruitment:

Example 1 %C in year 1 and year 2 are equal, but W is greater in year 2: hatchery effect on magnitude of recruitment actually increased; increase is not apparent from comparing %C but is when C and W are compared between years;

Example 2 %C is greater in year 2 but W is less: actual hatchery effect on abundance could be identical in years 1 and 2;

Example 3 %C and W are both greater in year 2: substantial increase in hatchery effect (i.e. greater hatchery impact than realized by merely comparing %C between years).

Lacking an unbiased indicator of actual survival following hatchery releases, we submit that recruitment, hatchery contribution, and recovery rate (no. captured/no. released) provide a good preliminary indication of enhancement effect if all three of these are presented. Each is needed to evaluate and control enhancement effectively.

Variation in fishery yields is driven largely by recruitment dynamics (see Frank and Leggett, 1994, for recent review). The CPUE of cultured and wild fish reflects the magnitude of recruitment, which should have a direct relevance to fishery yields, if food and habitat are available. Also, without CPUE data, there is no indication of how the whole population (cultured and wild individuals) is changing from year to year in response to natural recruitment processes, enhancement, and other management strategies.

Hatchery contribution from pilot studies can be used as an index to help in planning release magnitude at levels that would not swamp wild stocks with cultured fish. Hatchery contribution is easily computed from CPUE data (i.e. $\%C = [C \times 100\%] / [C + W]$).

Because cost effectiveness is directly related to survival of cultured fish in the wild, optimizing recovery rate should also be a key consideration in enhancement programs (Kitada et al., 1992). Recovery rate provides a relative measure of survival and is a good indicator (if standardized by sampling effort) for comparing performance of cultured fish. In comparisons of recovery rates from different years, differences in release magnitude are factored out.

The above three indicators can be used to evaluate release effects during the juvenile stage, before fish enter the fishery, to obtain a preliminary estimate of stock enhancement success. Thus, a way of

[7] Shomura, R. S. 1987. Hawaii's marine fishery resources: yesterday (1900) and today (1986). Honolulu Laboratory, Southwest Fisheries Center, Natl. Mar. Fish. Serv., Admin. Rep. H-87-21.

characterizing field data is needed that clearly reflects 1) recruitment (CPUE) of both cultured and wild fish, 2) hatchery contribution, and 3) standardized recovery rates for released fish. One way of illustrating these variables together is presented here.

All three indicators are used in Figure 11 to compare relative hatchery effect at Kahaluu in 1992 with data from three other years of pilot releases (Leber, 1995; Leber et al., 1995; Leber et al.[3]). Overall, CPUE of cultured juveniles was greatest after 1992 releases. However, recovery rate (and presumably survival) was greatest after 1993 releases. Thus, 1992 releases had greatest impact on recruitment, whereas yield per stocked juvenile was greatest from 1993 releases. Recovery rate improved in 1992 and again in 1993. The improvement was largely due to better survival after adjusting SAR protocol to avoid summer releases of fish <70 mm TL and to avoid release sites outside of habitat preferred by striped mullet. Although hatchery contribution was inflated in 1992 because of reduced recruitment of wild fish, overall effect from releasing cultured fish was greatest following 1992 releases, and recovery rate improved most in 1992.

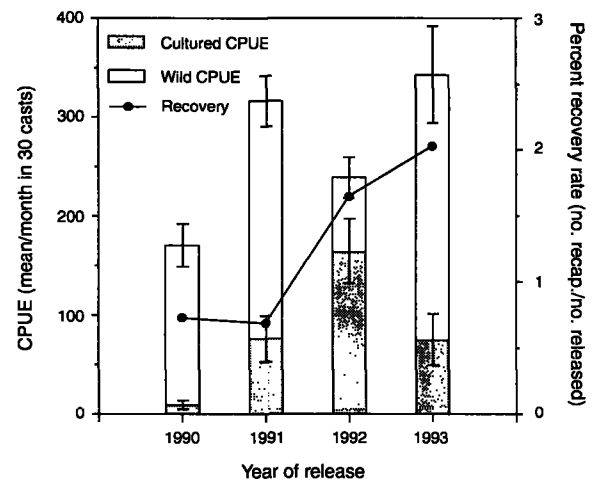

Figure 11

Stacked bar graph of release impact at Kahaluu Stream following releases conducted there from 1990 to 1993. CPUE is total number of cultured fish (gray bars) and wild fish (open bars) in 30 casts per month averaged over 10–11 monthly collections. Percent cultured fish (hatchery contribution) varied from monthly average of 4.4% (SEM =±1.3) of the striped mullet collected in 1990 to 20.6% (±4.1) in 1991, 65.2% (±5.2) in 1992, and 23.5% (±5.0) in 1993. Percent recovery rate of cultured fish (solid line with closed circles) is number recaptured/number released, × 100%.

Pilot releases

Whereas actual survival of cultured fish may be difficult to quantify in open ecosystems, relative survival can be quantified and compared across treatment groups in pilot release experiments (Burnham et al., 1987). Results from two previous years of pilot releases were used to identify optimal release strategies for this study. Discontinuing releases near the Hawaii Institute of Marine Biology (HIMB) pier after 1990 resulted in a >300% increase in recovery rate in the 1991 study; the increase in recovery rate was compounded in 1992 by modifying SAR protocol as well (Table 6; note the 1990 data in Fig. 11 are only for fish released at Kahaluu). By confining releases in this study to the vicinity of Kahaluu Stream and by adjusting minimum SAR upwards to include only fish >70 mm TL in summer, we achieved a 590% increase in recovery rate over the 1990 study and a 170% increase over the 1991 study (Table 6: after 16 weeks, all sites combined).

This study provided new information on effects of release site. Choice of release microhabitat at Kahaluu (inlet and upstream lagoon) affected dispersal north from Kahaluu into other streams but had no apparent impact on survival. The similar survival was surprising, given the poor survival in 1990 of fish released along the shoreline near HIMB pier, in comparison to fish released at streams (Leber, 1995; Leber and Arce, in press). We hypothesize that refuge from predators, afforded by mangroves and other shoreline vegetation in the north end of Kaneohe Bay, accounted for the higher survival of mullet that were released at Kahaluu Inlet and that dispersed along the shoreline.

Release microhabitat affected the extent of enhancement in Kaneohe Bay in this study by partially controlling colonization of nursery habitats north of Kahaluu. If a management objective for full-scale releases were to have a portion of fish from each release lot disperse into adjacent nursery sites in the bay (e.g. in order to maximize use of available nursery habitat), then releases at the inlet to Kahaluu Stream would achieve this. If stronger site fidelity were desired, releases farther upstream would result in lower dispersal during the nursery phase of the life cycle. The ability to affect which nursery habitats are selected by released fish, coupled with knowledge about recruitment success of wild fish, could be used to help prevent overstocking a particular nursery.

Implications

This study shows that information from pilot releases is critical for managing full-scale stock enhancement

in coastal environments. The use of results from pilot studies to modify release protocol caused a considerable increase in recovery rates and hatchery contributions to striped mullet abundance in their nursery habitats. Even before fish enter a fishery, data on relative survival of juveniles following pilot releases can be used to design effective release strategies.

The results of this study could be magnified if enhancement activities expanded to include other nursery sites in Kaneohe Bay, provided sufficient habitat is available. Leber et al. (1995), reported hatchery releases of cultured striped mullet at Kahaluu had an additive effect on population size. Kahaluu, Kaalaea, and Waiahole streams are primary mullet nursery habitats in Kaneohe Bay; including the latter two with Kahaluu as release sites would increase stock-enhancement effect.

According to this study, Leber et al. (1995), and Leber and Arce (in press), marine stock enhancement appears to have high potential as an additional fishery management tool for Hawaiian coastal fishes. Hatchery releases of striped mullet could be used in conjunction with fishing regulations and habitat protection, with the expectation that recruitment success of juveniles and subadults would increase significantly in Kaneohe Bay. To ensure that stocks are actually enhanced by hatchery-release activities, information from pilot studies needs to be coupled with additional management considerations to provide a controlled approach to stock enhancement (Peterman, 1991; Cowx, 1994; Blankenship and Leber, 1995).

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Aspects of the life histories of the kelp bass, *Paralabrax clathratus*, and barred sand bass, *P. nebulifer*, from the southern California Bight

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Abstract.—Kelp bass, *Paralabrax clathratus*, and barred sand bass, *P. nebulifer*, are major components of the nearshore marine environment in the southern California Bight. Both species are also very important parts of the marine recreational fishery. Surveys at King Harbor, Redondo Beach, California, have shown that kelp bass primarily recruit between August and December. In general, both kelp bass and barred sand bass numbers increased in King Harbor beginning in the late 1970's and continuing into the 1980's. Male and female kelp bass and barred sand bass grow at the same rates, and growth rates of both species are similar. The oldest kelp bass in our sample was 33 yr old, the oldest barred sand bass was 24 yr old. For kelp bass, 50% of males matured at 22.0 cm; for barred sand bass, 50% of males matured at 21.9 cm. For kelp bass, 50% of females matured at 22.6 cm; for barred sand bass, 50% of females matured at 23.9 cm. In both species, males matured between ages 2 and 4 years and females matured between ages 2 and 5 years.

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Kelp bass, *Paralabrax clathratus*, and barred sand bass, *P. nebulifer*, are major components of the nearshore marine environment in the southern California Bight.

Kelp bass grow to 72 cm total length (TL) and occur between the mouth of the Columbia River, Washington, and southern Baja California, most commonly from Point Conception, California, southward (Eschmeyer et al., 1983). Distributed from intertidal waters to 59 m (Quast, 1968), most fishes live in 3–25 m (Feder et al., 1974). Although usually associated with substrata, kelp bass will often rise into the water column, well away from structure.

Barred sand bass reach 65 cm (TL) and range from Santa Cruz, central California, to southern Baja California (abundant from Pt. Conception southward). This species is distributed from subtidal water to 183 m (Eschmeyer et al., 1983). Barred sand bass are benthic, relatively sedentary fish which, in contrast to kelp bass, are rarely found more than 3 m above the substratum (Turner et al., 1969; Feder et al., 1974; Larson and Demartini, 1984).

Both species are very important parts of the marine recreational fisheries of southern California and northern Baja California (Rodriguez Medrano, 1993; Ally et al.[1];

[1] 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 recommendations, based on analyses of catch and size composition data collected on board commercial passenger fishing vessels from 1985 through 1987. Mar. Res. Div., Calif. Department of Fish and Game, 330 Golden Shore, Suite 50, Long Beach, CA, 90802. Admin. Rep. 90-2, 376 p.

Love et al.[2]). Measured by catch per unit of effort, both species rank annually among the top three species in the commercial passenger fishing vessel catch (Love et al.[2]).

The life histories of these two species are poorly understood. While there is some information on habitat preferences, food habits, and reproduction, summarized in Read (1992) and Ono (1992), data on age and growth as well as size and age at first maturity and recruitment are limited. We describe the age and growth patterns and size and age at first maturity relationships for kelp bass and barred sand bass in the southern California Bight. In addition, we provide information on recruitment of kelp bass to a nearshore southern California reef.

Methods

Recruitment and annual abundance

Since 1974, we have used 5-min isobathic diver transects at 3-m depth intervals between 1.5 and 15 m at 8 stations along the breakwater in King Harbor, Redondo Beach, California (Fig. 1) to estimate fish abundance by life history stage. During these transects, divers swam along the vertical face and counted all fishes in a 3-m deep band (1.5 m above and below the diver). Outer harbor transects were 254 m in length, inner ones were 208 m long. Transects were swum monthly in 1974 and 1975 and quarterly after 1976. For the years after 1975, this survey yielded 96 transects per year (8 stations and 3 depths surveyed quarterly).

We obtained data on month of recruitment for kelp bass from 1986 to 1992 by conducting a monthly survey along the inner wall of the Redondo Beach breakwater and along a rock groin within the inner harbor. Three divers (at depths of 0–3, 4–6, and 7–10 m) swam parallel transects along approximately 500 m of rock and closely inspected bottom cover, crevices, and algae for newly settled fishes (Pondella and Stephens, 1994). The survey along the inner rock groin was similar, except that only two divers swam transects (one shallow, one deep), because of the shallower (1–4 m) location. Fishes ranging from 1.5 to 2.0 cm were considered newly recruited. Juveniles were considered to be those fish from 2.1 to 10.0 cm, and subadults ranged from 10.1 to 15.0 cm. Barred sand bass do not recruit from the plankton to the rocky substrate of King Harbor.[3]

Age and growth

Between 1978 and 1992, we collected kelp and sand bass throughout southern California waters by using hook and line as well as pole spear. These samples were supplemented by fish from commercial passenger fishing vessel (CPFV) catches, from kills at coastal power plant intakes (water heat treatments), from experimental gill-net studies, and from California Department of Fish and Game wardens. Data collected from all fishes included total length, sex, capture location, and collection date. We ascertained whether the fish were mature or not by an inspection of their gonads during spawning season. We also collected otoliths from each fish. In cases where standard lengths were recorded, we converted these to total lengths by using length conversions (Table 1).

Otoliths were embedded in plastic and sectioned prior to being read. We made an embedding mold from 3/4-inch pvc pipe with stoppered ends, cut in half longitudinally. A thin layer of resin (1/4 inch thick) was poured into the mold and allowed to harden. The otoliths were then placed into the mold with a label containing an identification code and

[2] Love, M. S., A. Brooks, and J. R. R. Ally. 1996. An analysis of the commercial passenger fishing vessel fisheries for kelp and barred sand basses (*Paralabrax clathratus* and *P. nebulifer*) in the southern California Bight. In review.

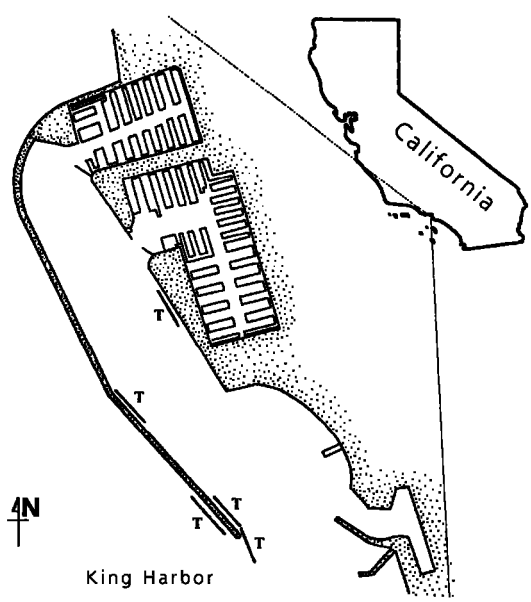

Figure 1
Location of underwater transect sites (marked with a "T"), King Harbor, Redondo Beach, California.

[3] Pondella, D. 1995. Department of Biology, Occidental College, 1600 Campus Rd., Los Angeles, CA 90041. Personal commun.

Table 1

Conversions between standard (SL), fork (FL), and total lengths (TL) for kelp bass (*Paralabrax clathratus*) and barred sand bass (*P. nebulifer*) (each species, n=100). [As an example, to calculate the total length of a kelp bass of 20.0 cm standard length: $TL = b + m(SL) = 1.41 + 1.20(20.0) = 24.1$ cm.] Maximum and minimum total lengths used in the these analyses were as follows: kelp bass, 12.7 and 48.5 cm; barred sand bass, 17.8 and 49.4 cm.

	r^2
Kelp bass	
FL = 2.38 + 1.10 SL	0.89
TL = 1.41 + 1.20 SL	0.96
TL = 0.83 + 1.01 FL	0.93
Barred sand bass	
FL = 1.11 + 1.17 SL	>0.995
TL = 0.70 + 1.22 SL	>0.995
TL = 0.46 + 1.05 FL	>0.995

covered by additional resin. After curing, the hardened resin bar was taken from the mold.

We used a Buehler Isomet saw with two low-density diamond blades separated by a thin (0.3–0.5 mm) metal shim to section each otolith. Otolith sections were placed in a 50% solution (by volume) of glycerol in water and cleaned in an ultrasonic bath for 2–3 minutes. After cleaning, sections were dried and stored in labelled plastic bags. Sections were later placed on a glass slide, cleaned with 2–3 drops of toluene, and mounted with enough cytoseal to cover the structures and ensure permanent storage.

Many fishes lay down annually an opaque and a hyaline (translucent) zone in their otoliths. Seasonal variations in calcium deposition may be responsible for this zonation (Irie, 1960). By calculating the percentage of fish with otoliths with opaque margins in our monthly samples, we attempted to validate that the bands were formed annually. It seems reasonable to assume that band deposition was seasonal if the bands were present during one part of the year. Kelp and sand bass do appear to lay down seasonal bands, beginning in spring and continuing into fall (Fig. 2). In both species, the first three annuli were usually readable. The fourth one was often more difficult to distinguish; however, bands subsequent to number four were clear.

Lengths at ages were estimated by direct observation of otolith annuli from 261 kelp bass and 137 barred sand bass. Growth was assumed to be described by the von Bertalanffy growth curve model (von Bertalanffy, 1938):

$$l_t = l_\infty\left(1 - e^{-k(t-t_0)}\right),$$

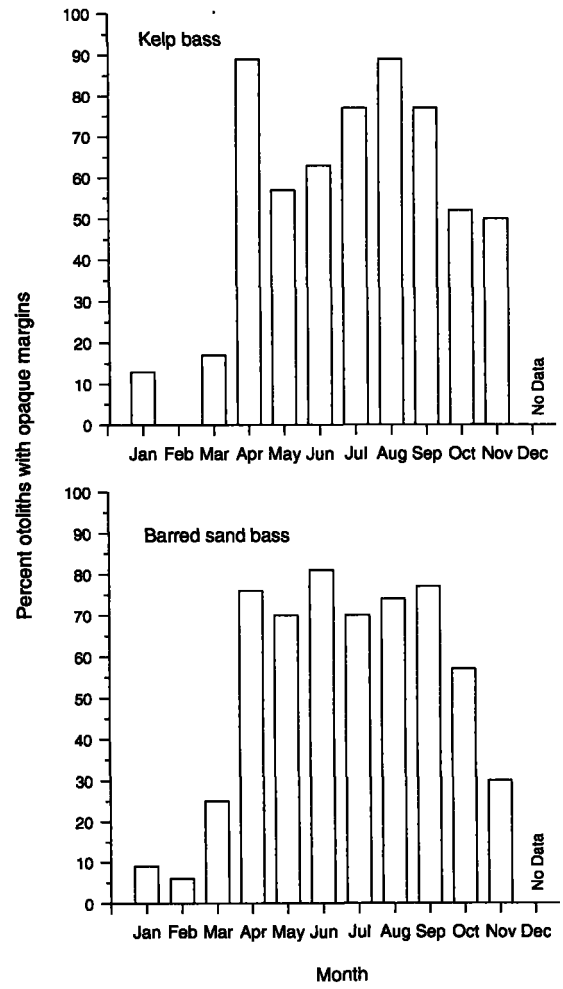

Figure 2

Seasonal deposition of opaque edges in kelp bass (*Paralabrax clathratus*) and barred sand bass (*P. nebulifer*) otoliths from southern California (kelp bass, n =204; barred sand bass, n=238).

where l_t = length at time t;
l_∞ = theoretical maximum length;
k = constant expressing the rate of approach to l_∞; and
t_0 = theoretical age at which $l_t = 0$.

Growth equation constants for the von Bertalanffy growth model were calculated from length-at-age data for each species by using the Marquardt method of iteration in a least-squares, nonlinear regression (SAS, 1988). We were unable to accurately fit these functions separately by sex for either species because of our relatively small sample sizes and, in particular, because of the absence of smaller-size fish that could be unambiguously sexed. We did test the hy-

pothesis that there was no difference between the growth rates of kelp bass and barred sand bass by constructing a "complete" least-squares, nonlinear regression model that fitted the three von Bertalanffy parameters t_0, l_∞, and k separately for each species. We then used an F-test to compare the amount of variance explained by this separate species model with that explained by a "combined-species model," fitting the data for both species to just one set of parameters. A nonsignificant F-value indicated that no significant additional variation was explained by assuming different values for the three von Bertalanffy parameters for each species.

Length and age at first maturity

We sampled kelp and sand bass in July–August 1988–89, July 1991, and June–August 1992. As we have noted previously in rockfishes (*Sebastes* spp., Love et al., 1990), white croaker (*Genyonemus lineatus*, Love et al., 1985), and California halibut (*Paralichthys californicus*, Love and Brooks, 1990), it is often difficult to distinguish immature from mature fishes during their nonreproductive seasons. Thus, we concentrated our sampling on the summer months, well within the spawning seasons of the two species. Most of the sand bass were taken by a 7.6-m semiballoon trawl, by hook and line, or by gill nets between Marina del Rey and San Diego. Kelp bass were taken by hook and line and gill nets between Redondo Beach and Newport Beach and at Santa Catalina and San Clemente islands. Fish were frozen until analyzed, when they were measured (TL) and both sagittal otoliths and gonads were removed. Gonads were examined without magnification to determine sex and gonad state. Annuli from otolith sections were counted under water with a dissection microscope. Sixty-eight male (16–36 cm TL) and 84 female (14–35 cm TL) kelp bass as well as 66 male (12–33 cm TL) and 85 female (13–35 cm TL) barred sand bass were examined.

The relationships between length and maturity and age and maturity were established by using a natural log transformation of the equation

$$p_x = \frac{1}{1+e^{ax+b}}$$

(Gunderson et al., 1980) to yield

$$\ln\frac{(1-1)}{p_x} = ax+b,$$

where p_x is the proportion mature at length or age x, and a and b are fitted parameters. We then plotted x against

$$\ln\frac{(1-1)}{p_x}$$

using simple linear regression (SAS, 1988) to estimate values for a and b. Fifty-percent maturity was calculated by using fitted values of a and b, and by using $p_x = 0.50$ to solve for x.

Results

Recruitment and annual abundance

Kelp bass showed considerable seasonal variation in recruitment at the King Harbor breakwater (Fig. 3). A few newly settled recruits were found in April, more in May, but most were observed during transects conducted in the fall and winter. Surveys of young of the year (YOY), subadult, and adult kelp bass in King Harbor showed a distinct temporal pattern (Fig. 4). Low in the mid-1970's, YOY abundance increased sharply from 1977 to 1979, decreased in the early 1980's, and

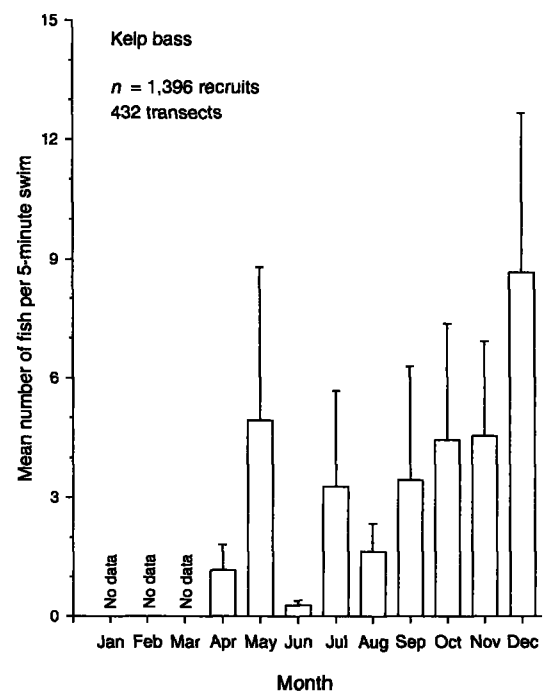

Figure 3

Monthly recruitment of kelp bass, *Paralabrax clathratus*, (1986–92) at the King Harbor (Redondo Beach, California) breakwater. We considered recruitment to any month to have occurred between the 16th day of the current month and the 15th of the next month. Means are based on monthly data from 1986 to 1990. Error bars represent ± one standard error.

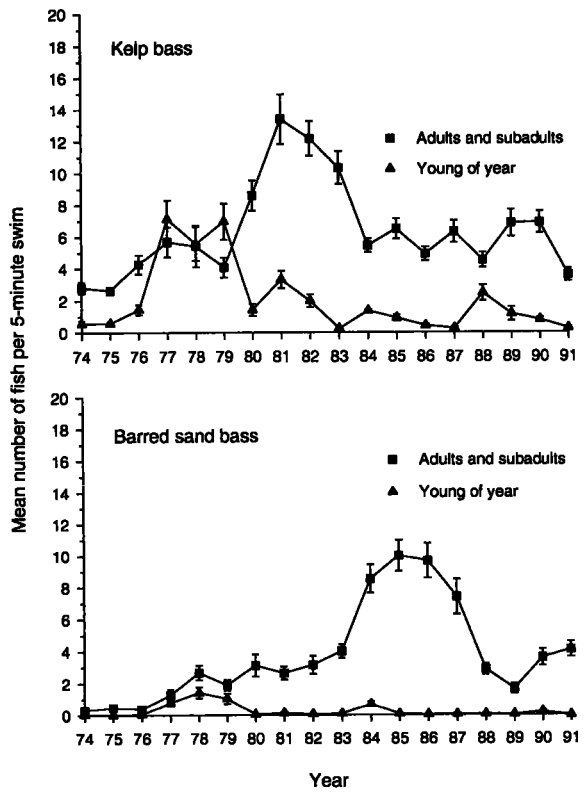

Figure 4

Mean abundance per transect of adults or subadults, or both, and young-of-the-year (YOY) kelp bass (*Paralabrax clathratus*) and barred sand bass (*P. nebulifer*) along the King Harbor (Redondo Beach, California) breakwater 1974–90. Error bars are ± one standard error. Each point represents mean of 96 five-minute diver surveys (8 stations and 3 depths surveyed quarterly).

remained low for the rest of the decade. The abundance of adults and subadults peaked from 1980 to 1983, probably reflecting the successful year classes of the previous few years, then declined somewhat in the mid-1980's. The abundances of barred sand bass at all life stages increased in the late 1970's (Fig. 4). Although the numbers of YOY declined soon after, the population of older fishes increased continuously, reaching a peak in 1985.

Age and growth

For each species, we combined age-at-length data for both sexes. We did this because we were unable to accurately fit the von Bertalanffy growth functions separately by sex because of our relatively small sample sizes and, in particular, because of the absence of smaller-size fish that could be unambiguously sexed. We do not feel that by combining this data undue bias was introduced into our results because the numbers of males and females comprising the combined samples were approximately equal (kelp bass, males = 86, females = 100; sand bass, males = 36, females = 55) and because the separate fits for each sex failed to show a significant difference in growth rates for either species (kelp bass, t=0.059, df=182, P>0.05; barred sand bass, t=0.004, df=87, P>0.05).

We tested the hypothesis that there was no difference between the growth rates of kelp bass and barred sand bass by constructing a "complete" least-squares, nonlinear regression model that fit the three von Bertalanffy parameters t_0, l_∞, and k, separately for each species. We then used an F-test to compare the amount of variance explained by this separate species model with that explained by a "combined-species model," fitting the data for both species to

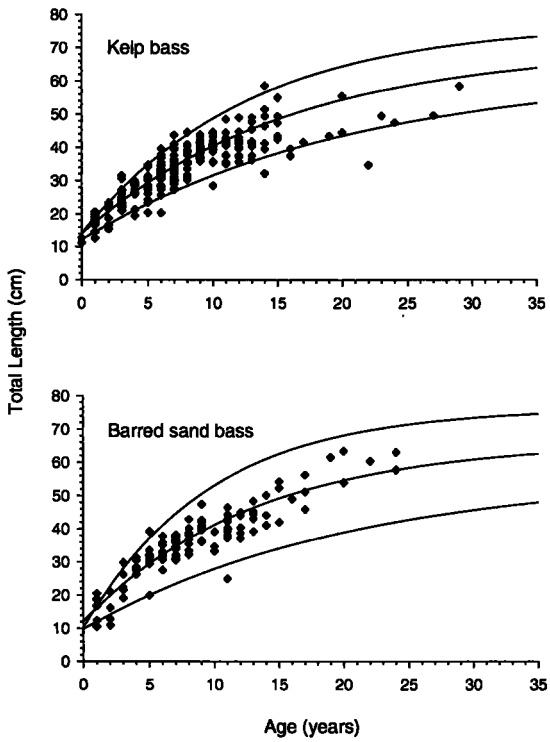

Figure 5

Von Bertalanffy growth curves for kelp bass (*Paralabrax clathratus*) and barred sand bass (*P. nebulifer*) from southern California. Dotted curves are the 95% prediction limits about the von Bertalanffy regression lines.

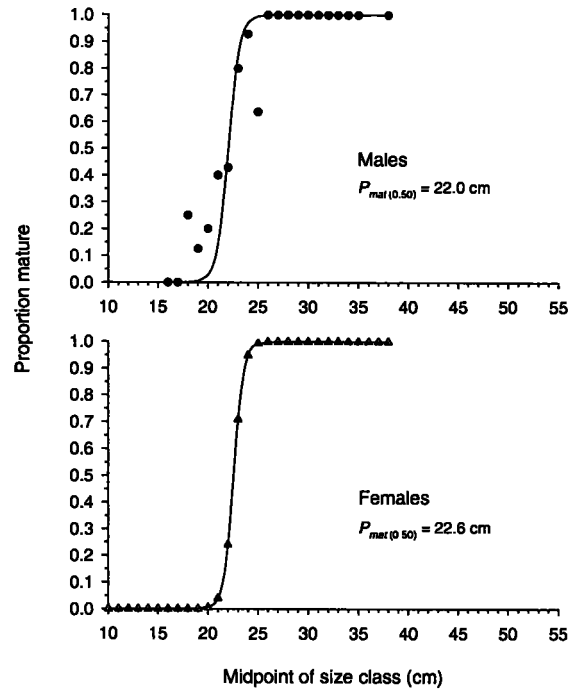

Figure 6

Length-maturity relationships for male (n=68) and female (n=84) kelp bass (*Paralabrax clathratus*) taken in the southern California Bight, including estimated lengths at which 50% of the bass were mature. Solid line represents predicted relationship.

just one set of parameters. A nonsignificant F-value ($F_{3,397}$=0.60, P>0.05) indicated that no significant additional variation was explained by assuming different values for the three von Bertalanffy parameters for each species.

In their early years, both species grew fairly quickly, a few reaching 20 cm TL in their first year (Fig. 5). Growth rates declined at around age 5. The von Bertalanffy parameters for all kelp bass (with standard errors in parentheses) were l_∞=69.8 (3.76), k=0.06 (0.008), t_0=–3.50 (0.48); those for all barred sand bass were l_∞=66.2 (5.08), k=0.08 (0.014), t_0=2.63 (0.63). The oldest kelp bass aged was 33 yr, and the oldest barred sand bass was 24 yr; however, most fish sampled were less than 15 yr old.

Length and age at first maturity

Both male and female kelp bass matured within a relatively narrow length range and at about the same age (Figs. 6 and 7). While a few males and females matured at 18 cm, 50% of males matured at 22.0 cm and 50% of females at 22.6 cm. All males were mature by 26 cm, all females by 27 cm. Males matured between the ages of 2 and 4 years; females between 2 and 5 years.

The smallest mature male barred sand bass that we found were 19 cm, the smallest females were 21 cm (Figs. 8 and 9; Table 2). All males were mature by 26 cm, all females by 27 cm. Length at 50% maturity was 21.9 cm for males and 23.9 cm for females. As with kelp bass, male barred sand bass matured between the ages of 2 and 4 years, and females between 2 and 5 years.

Discussion

Recruitment and annual abundance

In the annual recruitment pattern, kelp bass is a late spring to early fall spawner. Because this species has a pelagic larval phase lasting at least one month (Butler et al., 1982), most of this recruitment pattern would be expected. The peak of recruitment seen in December may represent an artifact of slower win-

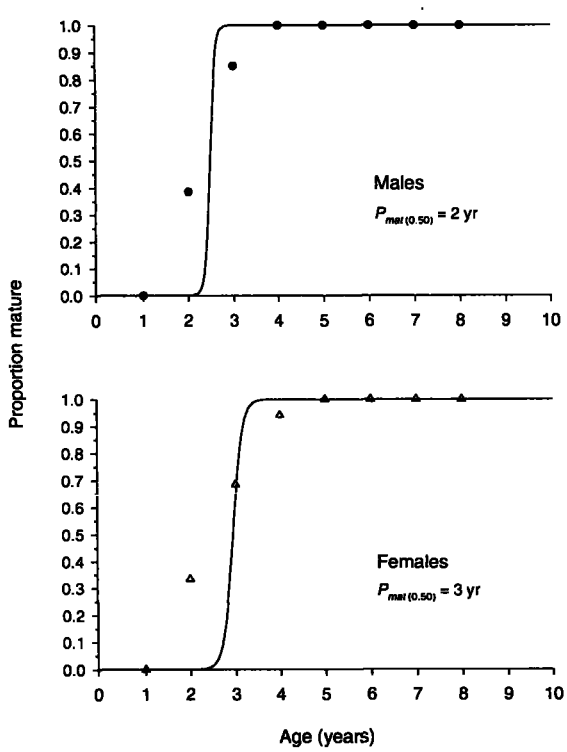

Figure 7

Age-maturity relationships for male (n=68) and female (n=84) kelp bass (*Paralabrax clathratus*) taken in the southern California Bight, including estimated ages at which 50% of the bass were mature. Solid line represents predicted relationship.

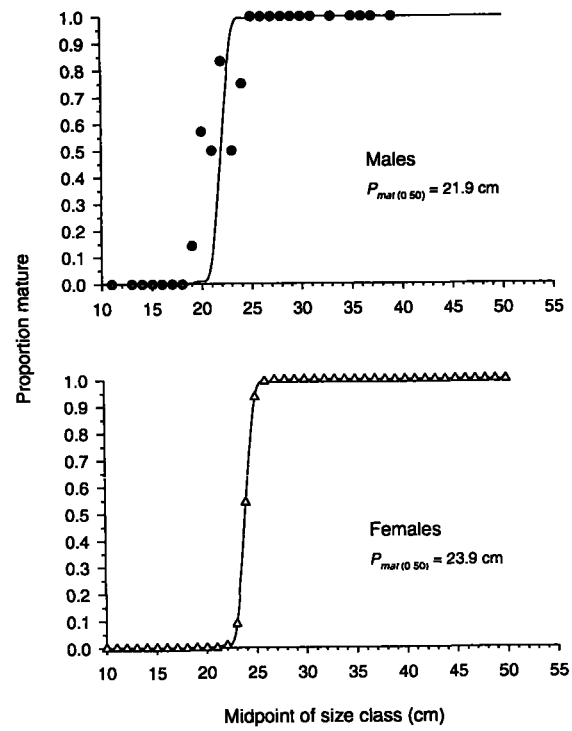

Figure 8

Length-maturity relationships for male (n=66) and female (n=85) barred sand bass (*Paralabrax nebulifer*) taken in the southern California Bight, including estimated lengths at which 50% of the bass were mature. Solid line represents predicted relationship.

ter growth rates. A fish recruited in October may not grow appreciably and, with only length as a criterion, would appear to be a new recruit in December. Barred sand bass recruitment in King Harbor was low throughout the 1980's; the large increase in numbers of older fish was probably due to immigration from outside the harbor.

We believe that the increase in abundance of kelp bass and barred sand bass in King Harbor during the late 1970's and 1980's may be related to a general warming trend of southern California waters during the period (Stephens et al., 1994). A significant increase in catches of both kelp and barred sand bass occurred then throughout the southern California Bight (Love et al.[2]). In fact, the increase in bass populations may have been part of a general alteration of nearshore fish populations, resulting from warming ocean waters. During this period, colder-water species (such as rockfishes) declined in abundance, whereas populations of warm-temperate and subtropical species (including labrids and pomacentrids) increased (Stephens et al., 1986). This trend has also been noted among nearshore pelagic species, such as chub mackerel (*Scomber japonicus*) and Pacific sardine (*Sardinops sagax*) (Barnes et al., 1992).

Age and growth

Although no other study of barred sand bass growth rates is available, some age-length data derived from scales, for kelp bass, have been reported in Young (1963). We compared our age-at-length estimates (from the von Bertalanffy equation) with the mean length at age calculated by Young (Table 3). Except for the very youngest and the very oldest fish, our data sets are similar, particularly at ages 4–7.

The results of our comparison of growth rates of the two species suggest that there is little difference between kelp bass and barred sand bass. We were unable to reject our "combined species" model by fitting the age and length data for both species to one growth curve in favor of our "separate" model which fits the three growth parameters separately for each species.

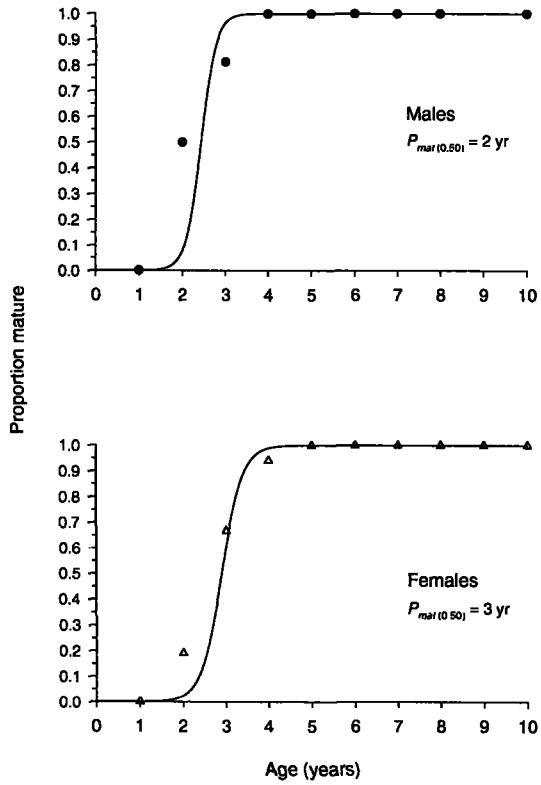

Figure 9

Age-maturity relationships for male (n=66) and female (n=85) barred sand bass (*Paralabrax nebulifer*) taken in the southern California Bight, including estimated lengths at which 50% of the bass were mature. Solid line represents predicted relationship.

Table 2

Maximum-likelihood estimates for the parameters of the logistic equation relating proportion mature to lengths and ages of kelp bass (*Paralabrax clathratus*) and barred sand bass (*P. nebulifer*). Predictive length ($l_{0.50}$) and age ($age_{0.50}$) at 50% maturity and correlation coefficients (r^2) are also presented.

	Length			
Kelp bass	a	b	$l_{0.50}$(cm)	r^2
Males	−1.77	38.88	22.0	0.65
Females	−2.04	46.03	22.6	0.59
	Age			
	a	b	$Age_{0.50}$	r^2
Males	−18.18	45.14	2.0	0.92
Females	−9.56	28.10	3.0	0.86
	Length			
Barred sand bass	a	b	$l_{0.50}$(cm)	r^2
Males	−2.48	54.49	21.9	0.67
Females	−2.50	59.82	23.9	0.68
	Age			
	a	b	$Age_{0.50}$(cm)	r^2
Males	−5.67	13.81	2.0	0.94
Females	−4.11	11.91	3.0	0.91

Table 3

A comparison of kelp bass (*Paralabrax clathratus*) age at length (to the nearest centimeter) up to age 9 in Young's study (1963) with age at length in the current study. Young's data are based on mean length at age for each year in inches and are converted to the nearest centimeter.

Age (yr)	Length (cm) Young's study (1963)	Length (cm) Current study
1	10	16
2	15	20
3	22	24
4	25	26
5	29	29
6	31	31
7	34	32
8	36	34
9	42	36

Since individuals of both species appear to be adequately described by a common age-length relationship, a comparison of size records for each species may provide some insight into their relative longevities. Eschmeyer et al. (1983) reported maximum lengths of 72 cm and 65 cm for kelp bass and barred sand bass, respectively. These lengths suggest that kelp bass may be the longer lived of the two species. Indeed, the oldest kelp bass we found was 33 yr (a new record), the oldest barred sand bass was 24 yr.

Length and age at first maturity

Clark (1933) reported on length at first maturity for kelp bass and barred sand bass taken in the commercial catch and landed at San Pedro. In that study, all kelp bass <25 cm were immature (note that she used fork length [FL]), and she assumed that the "average size at first maturity" was about 26 cm FL. We also found that there was little difference in length at first maturity for the two species. However, if we take "average size at first maturity" to mean length at which 50% of the individuals are mature,

our results are somewhat different. On average, our fish were two to four centimeters (depending on sex and species) shorter at maturity. Our results for kelp bass are very similar to those reported by Collyer and Young (1953). Clark also speculated from only a few fish that barred sand bass matured at about the same length as kelp bass.

Kelp bass and barred sand bass matured over an almost identical size and age range. In both species, sexual maturity was reached at a young age and small size, particularly when compared to many of the other large reef species in California. In the eastern Pacific Ocean, kelp and barred sand bass are the most northerly occurring Serranidae, which are typically tropical. In general, tropical fishes tend to mature at a fairly young age and these two subtropical-warm temperate species follow this pattern. The differences between these basses and some other co-occurring species, for instance the many rockfishes (Scorpaenidae) that share habitats with the two basses, is particularly pronounced. Rockfishes are typically cold-temperate species and tend to mature when older and larger, relative to maximum body length. For instance, olive rockfish (*Sebastes serranoides*), which superficially resembles kelp bass and co-occurs with it in the northern part of the southern California Bight, matures between 29 and 39 cm and between 3 and 8 years (Love and Westphal, 1981).

Conversely, the two species exhibit a typically temperate-fish growth pattern (Beverton, 1986); a relatively slow growth rate and fairly long life span. Research on a sympatric congener, the spotted sand bass, *P. maculatofasciatus*, implies that not all *Paralabrax* exhibit this pattern (Allen et al., 1995). Spotted sand bass inhabit backwaters from southern California into the Gulf of California and, compared with kelp bass and barred sand bass, exhibit a typically tropical-species pattern, with a faster growth rate and short (about 12 years) life span.

One possible explanation is that growth rate is more plastic in response to environmental conditions than is reproduction. This would lead to fishes growing more slowly, because of colder conditions in the southern California Bight, but conserving their tropically-derived reproductive schedule.

Acknowledgments

The research on kelp bass and barred sand bass age and growth, age and length at first maturity, and recreational fisheries was supported by Federal Aid for Sport Fish Restoration Program and the National Biological Service, contract number 1445-CA-0995-0386. Recruitment studies were funded through a grant from the Southern California Edison Company. Dan Pondella supplied data on abundance of kelp bass and barred sand bass recruits.

Larry Allen provided many of the specimens for this study and both he and Chuck Valle critically reviewed drafts of the manuscript. We would like to thank the crew of the RV *Yellowfin*, Jim Cvitanovich, Paul Irving, and Danny Warren, for their good-humored assistance. Michael Franklin, Tom Grothues, Tim Hovey, Ron Klaver, Loretta Roberson, Bob Scott, and Carrie Wolfe collected, prepared, and analyzed many of the fish.

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Marine distribution and origin of prerecruit chinook salmon, *Oncorhynchus tshawytscha*, in southeastern Alaska

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Abstract.—Chinook salmon, *Oncorhynchus tshawytscha*, <71 cm total length, are typically not retained in directed marine fisheries of southeastern Alaska because of size restrictions; consequently, little is known of the origin or temporal and spatial distribution of these prerecruits. To obtain such data, commercial power trollers were chartered to fish for small chinook salmon with small hooks and lures within the Alexander Archipelago (inside waters) and the adjacent coastal region (outside waters). During the 135-d study in February, May, and September 1986–87, a total of 5,838 prerecruit chinook salmon were caught, of which 539 contained coded-wire tags with information on stock origin. Age -.0 chinook salmon were caught in September during their first year at sea; they originated predominately from stream-type stocks of southeastern Alaska. Age -.1 chinook salmon in February and May were primarily from stream-type stocks of southeastern Alaska; however, by September most were from ocean-type stocks from British Columbia, Washington, and Oregon streams. Most age -.2 chinook salmon were from ocean-type stocks of southern origin. Average net marine migration rates of different chinook salmon age groups ranged from 0.1 to 6.9 km/d; the highest rates were for age 1.0 fish from Washington and Oregon. For coded-wire-tagged chinook salmon of the same ocean age group, growth rates of ocean-type fish were significantly ($P<0.05$) higher than growth rates of stream-type fish during most periods. Spatial distribution also differed by race: stream-type fish predominated in inside waters and ocean-type fish in outside waters. This study identifies the importance of marine waters of southeastern Alaska as a nursery area for an amalgam of prerecruit chinook salmon stocks originating between Oregon and southeastern Alaska, a range of 1,800 km.

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Fishery Bulletin 94:482–497 (1996).

Alaskan and non-Alaskan stocks of chinook salmon, *Oncorhynchus tshawytscha*, are harvested in southeastern Alaska waters predominately in hook-and-line marine fisheries; however, owing to a minimum size restriction of 71-cm total length, limited information exists on the temporal and spatial occurrence of smaller fish (prerecruits). Many North American stocks of chinook salmon embark on extensive marine migrations along the eastern Pacific Rim (Mason, 1965; Hartt and Dell, 1986). Some migrate across international or state boundaries and are intercepted in fisheries along migration corridors or in distant nursery areas. Consequently, many chinook salmon stocks have been overexploited, and rebuilding depressed runs is a major concern identified in the 1985 U.S.-Canada Pacific Salmon Treaty (Pacific Salmon Commission, 1986). A better understanding of the marine life history and distribution of chinook salmon populations will contribute to the development of management policies that are needed to restore the depressed stocks.

Not all chinook salmon migrate long distances. Some stocks in Oregon, Washington, British Columbia, and southeastern Alaska apparently do not migrate northward to any great extent (Mason, 1965; Nicholas and Hankin[1]), and many remain in inside waters all or much of their marine life (Hartt and Dell, 1986).

Two distinct races of chinook salmon have been identified: stream-type and ocean-type ("sea-type") (Gilbert, 1914; Healey, 1983). Stream-type fish are found throughout the geographic range of the species, whereas ocean-type fish occur primarily from British Columbia to California (Major et al., 1978; Healey, 1983). Stream-type chinook salmon remain in fresh water for one or more years before migrating to an estuary, whereas ocean-type chinook salmon migrate directly to an estuary as newly emerged fry or after 2–3 months of freshwater residence (Healey, 1983; Taylor, 1990). Prior to ocean entry, stream-type chinook salmon have a brief estuarine residence (Healey, 1983; Fisher and Pearcy, 1990) in contrast to ocean-type chinook salmon, which may reside in estuaries for up to three months (Healey, 1980; Myers and Horton, 1982; Nicholas and Hankin[1]; Reimers[2]).

[1] Nicholas, J. W., and D. J. Hankin. 1988. Chinook salmon populations in Oregon coastal river basins: description of life histories and assessment of recent trends in run strengths. Info. Rep. 88-1, Oregon Dep. Fish Wildl., Fish. Div., Res. and Develop. Section, Portland, OR 97207, 359 p.

[2] Reimers, P. E. 1973. The length of residence of juvenile fall chinook salmon in Sixes River, Oregon. Oregon Fish Comm. Res. Rep. 4(2), Oregon Dep. Fish Wildl., Portland OR 97201, 43 p.

In marine waters of southeastern Alaska, chinook salmon occur throughout the year (Cobb, 1910) and are harvested principally in a commercial troll fishery. Origins of stocks in this fishery are diverse, as documented by marine tagging studies, coded-wire tag (CWT) recoveries, and scale pattern analyses (Parker and Kirkness, 1956; Clark et al., 1985; Van Alen, 1988; Kissner[3]; Funk[4]). Throughout the history of this fishery, ocean-type chinook salmon of non-Alaskan origin have been the major harvest component (Parker and Kirkness, 1956; Van Alen and Wood, 1983; Olsen, 1992). Surprisingly, relatively little is known of the early marine distribution of prerecruit ocean-type fish after the initial summer at sea (Healey and Groot, 1987). In particular, it is not known whether prerecruit chinook salmon of different age groups within Alaskan marine waters are primarily of Alaskan or non-Alaskan origin.

Southeastern Alaska stocks of chinook salmon, which are primarily stream-type (Van Alen et al., 1986), migrate through inside marine waters of southeastern Alaska before their first marine winter (Orsi et al., 1987). In the summer and fall after their first marine winter, some portion of these stocks are recovered in southeastern Alaska waters (Hubartt and Kissner, 1987), whereas others migrate offshore to the North Pacific Ocean (Dahlberg et al.[5]). To identify the temporal and spatial distribution of prerecruit chinook salmon stocks in southeastern Alaska waters, we used commercial salmon trollers with small hooks and lures to sample prerecruits during February 1987 and May and September 1986 and 1987.

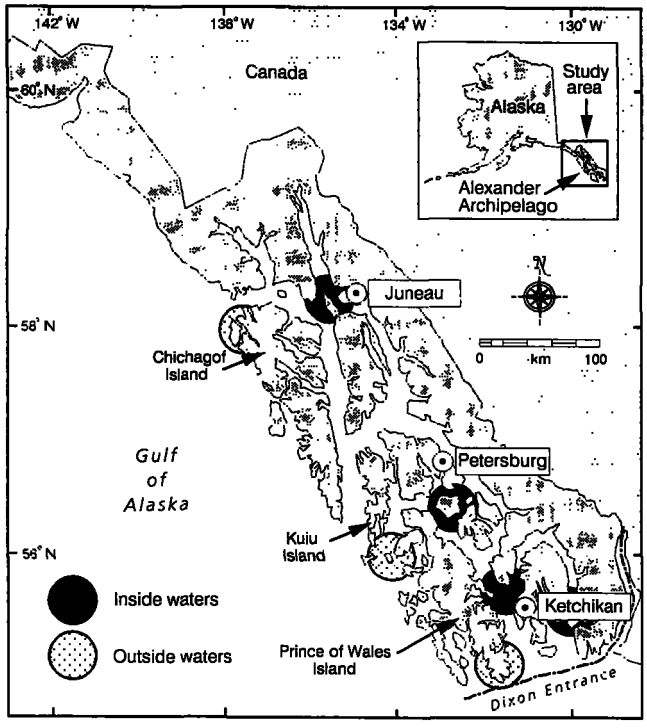

Figure 1

Inside and outside marine waters sampled in the northern, central, and southern regions of southeastern Alaska, 1986–87.

Methods

Sampling areas and times

Southeastern Alaska comprises the mainland coast and a large island group, the Alexander Archipelago, which covers about 100,000 km^2 (Fig. 1). Marine waters throughout this island group are a network of estuaries, fjords, and straits that lead into the Gulf of Alaska or Dixon Entrance. We sampled chinook salmon in "inside" and "outside" marine waters of the northern, central, and southern regions of the archipelago (Fig. 1). We defined "inside" waters as those within the Alexander Archipelago, typically adjacent to mainland southeastern Alaska, and "outside" waters as the coastal waters exposed to the Gulf of Alaska or Dixon Entrance near the outer coasts of Chichagof, Kuiu, and Prince of Wales Islands. Our selection criteria for sampling areas and times were influenced by the geographical localities of the major fishing ports in southeastern Alaska and by the availability of commercial trolling vessels during three off-season fishing periods separated by about four months.

We sampled chinook salmon from 11.0–16.2-m chartered commercial power troll vessels during May and September 1986 and February, May, and September 1987 for a total of 1,156 h of fishing effort over a 135-d period (Table 1). The vessels were operated by experienced commercial salmon trollers, accompanied by fishery biologists. Inside and outside waters were typically sampled in each region and season; however, the central region was sampled only in September 1986, and inclement weather precluded sampling the outside waters of the southern region in February 1987 (Table 1).

[3] Kissner, P. D. 1977. A study of chinook salmon in Southeast Alaska. Alaska Dep. Fish Game, Sport Fish Div. Completion Rep., Vol. 18, Project F-9-8, Study AFS-41-5, Juneau, AK, 63 p.

[4] Funk, F. 1981. Analysis of southeastern Alaska troll fisheries data. Final Report, Contract 79-4, North Pacific Fishery Management Council Document 17. Alaska Dep. Fish and Game, Juneau, 103 p. + appendix.

[5] Dahlberg, M., S. Fowler, N. Maloney, and R. Heintz. 1991. Incidence of coded-wire tagged salmonids in commercial and research catches in the North Pacific Ocean and Bering Sea, 1990–1991. (INPFC [International North Pacific Fisheries Commission] Doc.), Auke Bay Laboratory, Alaska Fish. Sci. Cent., NMFS, NOAA, 11305 Glacier Hwy., Juneau, AK 99801-8626, 17 p.

Table 1

Hours of sampling effort for chinook salmon, *Oncorhynchus tshawytscha*, in inside and outside marine waters of southeastern Alaska over a 135-d period in February, May, and September 1986–87.

	February		May		September	
Region	Inside waters	Outside waters	Inside waters	Outside waters	Inside waters	Outside waters
1986						
Southern	—	—	—	—	79	40
Central	—	—	—	—	68	69
Northern	—	—	121	47	63	45
1987						
Southern	106	—	128	19	118	12
Northern	50	43	84	64	—	—
Total	156	43	333	130	328	166

Trolling gear

We fished with reduced-size replicates of commercial trolling gear. These small hooks and lures have proven more selective than standard commercial trolling gear in catching smaller sizes and younger age groups of chinook salmon (Orsi, 1987). The hooks were single Mustad no. 9510X3S, size 2/0, barbed, gap 1.6 cm, throat 2.0 cm. All lures used were 6.0-cm hootchies (plastic imitation squid) fished behind 9 × 28-cm flashers at 0.5–1.5 m/s and typically at 7.3-m depth intervals (7.3 m, 14.6 m, 21.9 m, 29.3 m, and 36.6 m). Five flasher and hootchie combinations were used concurrently on each of four trolling lines weighted with 13.6–22.7-kg lead "cannonballs." Areas where the bottom depth was shallower than 37 m were not sampled. Additional information on trolling methods or gear is given in Browning (1980) and Orsi et al. (1987).

To test whether the catch and size distribution of the youngest age group of chinook salmon in our study were representative of the population, we compared the catch and length of prerecruit chinook salmon caught on our standard small gear versus the catch and length of prerecruit salmon caught on smaller hooks (Mustad no. 9321, size 6, gap 0.7 cm, throat 1.0 cm) and hootchies (4.0 cm). We tested this for two days during September 1987 in inside waters of the southern region, where chinook salmon are known to occur during their first summer at sea. Equal numbers of each gear size and color were used on opposing vessel sides at equivalent depths; sides of the vessel were alternated each day. A chi-square (χ^2) test was used to test for significant differences ($P<0.05$) in catch between gear sizes, and a one-tailed t-test was used to test for significant differences ($P<0.05$) in the mean fork length of chinook salmon caught between gear sizes.

Fish processing

Chinook salmon were sampled while immobilized in an electric basket (Orsi and Short, 1987). While in the basket and lifted from the water, fish were identified, measured from tip of snout to fork of tail (to the nearest cm), tagged with a 6.4-cm-long Floy anchor tag (to ensure that fish had not already been caught), and sampled for scales from the preferred area (INPFC, 1957). All chinook salmon were released after tagging, except adipose-clipped fish under the Alaska minimum size limit (66 cm fork length [FL]=71 cm total length; Reed, 1972), which were retained to recover previously implanted CWT's (Jefferts et al., 1963). Sex and weight (to the nearest 0.1 kg) were recorded for all retained CWT chinook salmon.

Because field identification between chinook salmon and coho salmon, *O. kisutch,* in their first ocean year is sometimes difficult, salmon identifications during the charters in September were confirmed later by a scale reader. Identifications that did not correspond to the determinations of species by the scale reader were reexamined and reassigned as appropriate. Salmon with CWT's were also used to corroborate species identifications.

Scale, age, and sex analysis

Scales of chinook salmon were aged according to the methods of Van Alen and Wood (1983) and designated with the nomenclature of Koo (1962). The end of the calendar year was used as a break point for ocean-age assignment. For example, a 1984-brood-year chinook salmon that entered saltwater in 1986 was designated to be age 1.0 until 31 December 1986 and age 1.1 from 1 January to 31 December 1987.[6] Distinguishable ocean-winter annuli were present in scales taken from fish in February.

Data on age -.3 chinook salmon were not presented because few were caught; the hooks used in this study

[6] Numeral preceding the decimal point denotes the number of freshwater winters and the numeral following the decimal point denotes the number of marine winters. A dash before the decimal point indicates freshwater ages of 0 and 1.

tend to bend or straighten when large fish strike (Orsi, 1987). The data were also limited because we did not retain CWT fish >66 cm FL, which are typically age -.3 fish (Wright et al., 1972).

Scale and CWT ages, when available for the same fish, were used to compare age-determination techniques each season. Although freshwater and marine age can be misinterpreted from reported CWT release information, we assumed that the release year reported for CWT chinook salmon (Johnson and Longwill[7]) was also the year of seawater entry unless specified otherwise. We rejected age determinations based on scale analysis for fish in time periods or regions where they were unlikely to occur and were not substantiated by CWT recoveries; examples of this were age 0.0 fish in September in the northern and central regions, age -.0 fish in February and May and age 0.1 fish in February and May in the northern region.

We used χ^2 tests to examine differences in the proportion of male and female CWT chinook salmon by ocean-age group for each period. In September, all three ocean-age groups were present (i.e. age -.0, -.1, and -.2), whereas in February and May, data were available for only the age -.1 and -.2 ocean-age groups.

Length analysis

Box-and-whisker plots (Tukey, 1977) were performed for length ranges of each age group of chinook salmon within each region and time stratum to ensure accurate ageing and length representation. Values over 1.5 times the inner quartile range (IQR) were examined to identify extreme cases in length within a given age group that may have resulted from errors (by misinterpreting scale position on a scale card or by transposing age values). After extreme values had been examined and age or length reassigned as appropriate, box-and-whisker plots were reconstructed and values >3.0 times the IQR were eliminated from the database unless substantiated by CWT fish. The eliminated values constituted less than 0.5% of the data.

To demonstrate temporal and regional differences in length-frequency distributions of chinook salmon, length data were plotted for the three sequential sampling periods (September 1986, February 1987, and May 1987) from fish in inside and outside waters (when possible) in the northern and southern regions. All age groups were pooled in each length-frequency distribution.

To demonstrate seasonal size structure, fork lengths of ocean- and stream-type chinook salmon were plotted by age group and period. Fork-length data were pooled across regions, years, and waters.

Stock composition

Coded-wire tag recoveries from chinook salmon and the expanded number of fish represented by each tag code were used to determine stock composition. Expanded numbers represent the total number of fish represented by a CWT, based on the proportion of tagged fish in a release group. Origin of chinook salmon stocks represented by CWT's were pooled into three geographic groups: southeastern Alaska, British Columbia, and Washington or Oregon. Washington and Oregon stocks were combined because most recoveries from these regions originated from the Columbia River basin.

Catch per unit of effort (CPUE) was used with CWT recoveries to determine the spatial and temporal distribution of stock groups. To determine CPUE, expanded numbers for a particular age and stock group of chinook salmon were divided by the number of hours fished. This CPUE was computed separately for inside and outside waters and pooled across regions. For examining spatial distribution of individual age groups of ocean- and stream-type fish in inside and outside waters, CPUE was plotted against age for each stock group. For examining seasonal distribution, CPUE was plotted against ocean age and season for each stock group.

Migration and growth

Net migration rates for each CWT chinook salmon were calculated by dividing the hypothetical "straight line" marine distance traveled between release and recovery points by the number of days since release. Because of limited information on precise freshwater release sites for many CWT fish, freshwater distance was not included in the determination of migration distance. Direction of travel of each fish from its marine entrance point to its recovery locality was recorded to the nearest 45° directional interval (e.g. N=337.6°–22.5°, NE = 22.6°–67.5°, etc.).

Growth rates were compared between ocean- and stream-type CWT chinook salmon recovered during seven seasonal periods after release: age -.0 fish in September; age -.1 fish in February, May, and September; and age -.2 fish in February, May, and September. Specific growth rates, G, were determined for CWT chinook salmon by dividing the difference

[7] Johnson, J. K., and J. R. Longwill. 1988. Pacific salmonid coded wire tag releases through 1987. Regional Mark Processing Center, Pacific Marine Fisheries Commission, Metro Center, Suite 170, 2000 S.W. First Ave., Portland, OR 97201-5346, 228 p.

of the natural logarithms of the recovery weight and of the release weight by the change in time (Weatherley and Rogers, 1978). Because of limited samples of CWT fish, growth rates for ocean- or stream-type fish were pooled between years, regions, waters, and stock groups for each growth period. Ocean- and stream-type fish in each growth period were then tested for significant differences ($P<0.05$) in growth rates with t-tests.

Results

Gear selectivity

For the 2-d gear comparison conducted in inside waters of the southern Alaska region in September 1987, both sizes of hooks and lures caught similar numbers and mean fork lengths of age -.0 chinook salmon. In this comparison, 68 age -.0 chinook salmon were caught on our "standard" small gear and 59 on the smaller gear; numbers caught did not differ significantly ($\chi^2, P > 0.10$) by gear size. Mean fork length (27.6 cm) of age -.0 chinook salmon caught on "standard" small gear also did not differ significantly from mean fork length (27.0 cm) of fish caught on smaller gear (t-test, P=0.36). However, age -.0 chinook salmon caught on the "standard" small gear were larger (range, 22–37 cm FL) than those caught on the smaller gear (range, 15–34 cm FL).

Age, length, and sex composition

Of the 539 CWT chinook salmon sampled, 486 had scales that could be aged. Agreement between scale- and CWT-age was highest in September (95%) and lowest in February (79%); overall agreement was 90% (Table 2). The most common disagreement of age designations was the assignment of ocean-type chinook salmon (as determined by CWT's) as stream-type. Of the 51 disagreements in chinook salmon age determinations, 43 (84%) were ocean-type fish assigned stream-type designations; some of these disagreements may have been a result of fish that were released as ocean-type but that overwintered in freshwater, and therefore bore a "stream-type" scale pattern.

Age data for 5,838 chinook salmon were obtained from scales and CWT's in all sampling periods and regions in 1986–87 (Table 3). CWT's were represented in 36 of the 39 age-group–time-period strata. Age -.0 chinook salmon were caught only during September, and most were stream type (age 1.0); only a few ocean-type (age 0.0) chinook salmon were caught, all in the southern region. In February and May, age -.1 chinook salmon were primarily stream type (age 1.1); a few ocean-type fish (age 0.1) were caught only in the southern region. In September, however, both stream- and ocean-type age -.1 chinook salmon were caught in all regions. Age -.2 chinook salmon of the ensuing year were also a mixture of ocean- (age 0.2) and stream-type (age 1.2) fish in each season and region. Only four age -.3 CWT chinook salmon were recovered and all were ocean type (age 0.3).

Chinook salmon were larger and older in the northern than in the southern region in each sampling period (Fig. 2; Table 3). Length modes of chinook salmon within each region generally increased between September and May. The proportion of small fish (<30 cm FL) was highest in inside waters of both regions in September.

Mean length of chinook salmon increased with each successive period; and for each ocean-age group, stream-type fish were consistently longer than ocean-type fish for each period (Fig. 3). Differences in mean length of ocean- and stream-type chinook salmon

Table 2

Percent accuracy of scale reading (in parentheses) based on coded-wire–tag (CWT) age determinations of chinook salmon, *Oncorhynchus tshawytscha*, during February, May, and September 1986–87. n = number of fish.

CWT age	February		May		September		Total	
	n	(%)	n	(%)	n	(%)	n	(%)
0.0	—	—	—	—	1	(100)	1	(100)
0.1	1	(0)	7	(0)	48	(81)	56	(70)
0.2	19	(16)	23	(60)	9	(89)	51	(49)
1.0	—	—	—	—	152	(100)	152	(100)
1.1	64	(98)	90	(97)	31	(94)	185	(95)
1.2	3	(100)	36	(97)	2	(50)	41	(95)
Total	87	(79)	156	(87)	243	(95)	486	(90)

Table 3

Number of chinook salmon, *Oncorhynchus tshawytscha*, of different age groups (based on scale samples and coded-wire tags) caught in marine waters of the northern, central, and southern regions of southeastern Alaska during February, May, and September 1986–87. The number of coded-wire tags recovered is shown in parentheses.

Month and Region	Year	Age -.0		Age -.1		Age -.2		Total
		0.0	1.0	0.1	1.1	0.2	1.2	
February								
Northern	1987	—	—	—	20	62	86	168
		—	—	—	(0)	(4)	(1)	(5)
Southern	1987	—	—	8	520	62	50	640
				(1)	(69)	(17)	(3)	(90)
May								
Northern	1986	—	—	—	88	114	149	351
		—	—	—	(13)	(10)	(17)	(40)
Northern	1987	—	—	—	162	92	254	508
		—	—	—	(7)	(9)	(18)	(34)
Southern	1987	—	—	110	639	39	69	857
		—	—	(8)	(83)	(7)	(1)	(99)
September								
Northern	1986	—	38	318	114	30	17	517
		—	(0)	(19)	(7)	(2)	(1)	(29)
Central	1986	—	112	141	157	42	10	462
		—	(7)	(10)	(8)	(1)	(1)	(27)
Southern	1986	2	450	149	64	14	1	680
		(1)	(32)	(9)	(14)	(2)	(0)	(58)
Southern	1987	21	1,283	168	126	45	12	1,655
		(1)	(125)	(14)	(11)	(5)	(1)	(157)
Total		23	1,883	894	1,890	500	648	5,838
		(2)	(164)	(61)	(212)	(57)	(43)	(539)

were not as great among age -.2 fish as among younger fish, especially in September. Some age -.2 fish were probably not caught effectively then, owing to the small gear used; therefore the lengths of age -.2 chinook salmon in September did not extend far above one standard deviation from the mean (Fig. 3). Conversely, the lengths of age 0.0 chinook salmon caught in September, which did not extend far below one standard deviation from the mean, suggest that fish <15 cm FL were too small for our gear or were absent.

The overall sex ratio of the 539 CWT chinook salmon was nearly equal to 1.0, namely 275 males to 264 females. There were, however, significant differences in proportion of males by ocean-age group in September (χ^2, $P<0.01$) and May (χ^2, $P=0.05$) but not in February (χ^2, $P=0.75$). Percentage of males for each ocean age by season were as follows: September, age -.0 (57%), age -.1 (41%), and age -.2 (23%); May, age -.1 (56%) and age -.2 (40%); and February, age -.1 (56%) and age -.2 (52%). Of the CWT chinook salmon examined, most were immature; only a few age -.1 and -.2 males sampled in May were qualitatively assessed as maturing on the basis of coloration, shape, or enlarged gonads.

Origin and distribution

According to CWT recoveries, prerecruit chinook salmon in southeastern Alaska were from 74 stocks originating from Oregon to the northern region of southeastern Alaska, a range of 1,800 km (Table 4; Table 5).

Most stream-type chinook salmon of Alaska origin were caught in inside waters, whereas ocean-type fish of non-Alaska origin were slightly more abundant in outside than in inside waters (Fig. 4; Table 6). Most age -.0 stream-type chinook salmon from Alaska and British Columbia stocks were caught in inside waters, whereas those from Washington and Oregon stocks were caught in both inside and outside waters (Fig. 4; Table 6). Only two CWT age -.0 ocean-type chinook salmon were sampled; both were experimental hatchery releases from Alaska stocks caught in inside waters. Age -.1 and -.2 stream-type chinook salmon were mainly from Alaska stocks and were caught at a higher rate in inside waters than

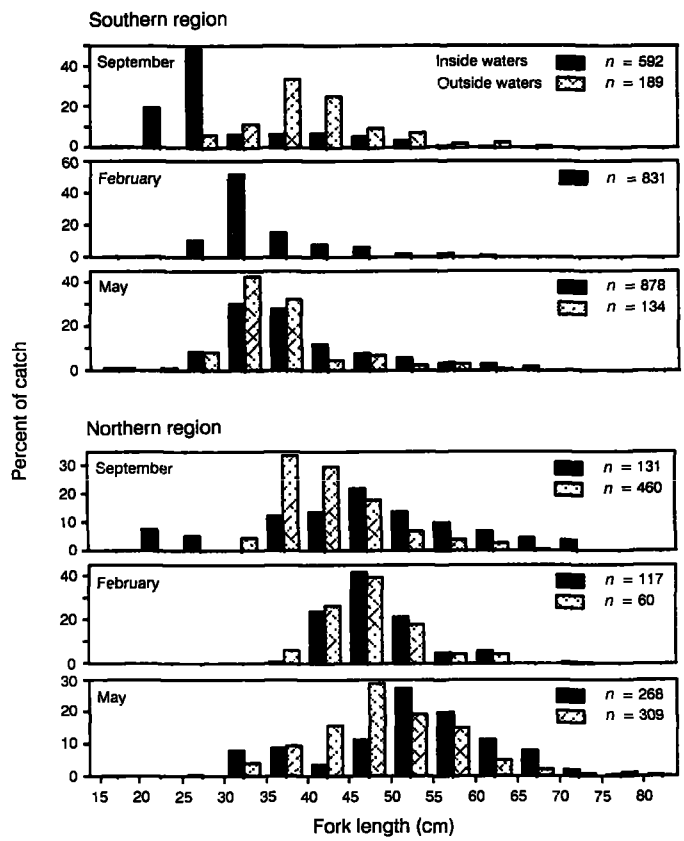

Figure 2

Length structure of chinook salmon, *Oncorhynchus tshawytscha*, sampled in inside and outside marine waters of the southern and northern regions of southeastern Alaska, September 1986 and February and May 1987.

Table 4

Major release localities of 539 coded-wire–tagged (CWT) chinook salmon, *Oncorhynchus tshawytscha*, recovered in marine waters of southeastern Alaska, February, May, and September 1986–87.

	CWT age at recovery						
Release locality	0.0	0.1	0.2	1.0	1.1	1.2	Total
Southeastern Alaska	2	4	—	127	204	40	377
Northern British Columbia	—	16	10	14	4	—	44
East coast Vancouver Island	—	12	14	—	—	—	26
West coast Vancouver Island	—	5	8	—	—	—	13
Fraser River drainage	—	2	—	—	—	—	2
Puget Sound	—	—	—	—	1	—	1
Strait of Juan de Fuca	—	—	1	—	—	—	1
Coastal Washington	—	8	12	—	—	—	20
Columbia River drainage	—	7	6	23	3	3	42
Coastal Oregon	—	7	6	—	—	—	13
Total	2	61	57	164	212	43	539

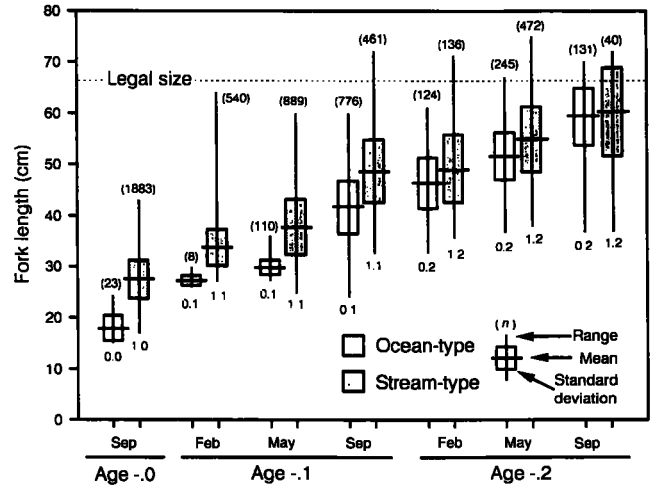

Figure 3

Length at age for ocean- and stream-type chinook salmon, *Oncorhynchus tshawytscha*, sampled in marine waters of southeastern Alaska during February 1987, May 1986–87, and September 1986–87. Sample sizes are in parentheses.

in outside waters; conversely, age -.1 and -.2 ocean-type fish were almost exclusively from British Columbia, Washington, or Oregon stocks and were caught at a slightly higher rate in outside waters (Fig. 4).

The CPUE of chinook salmon originating from each geographic region changed seasonally for each ocean-age group (Fig. 5). Age -.0 chinook salmon, which were caught only in September, were mainly of Alaska origin. All age -.1 chinook salmon in February were of Alaska origin except a few fish from British Columbia in inside waters (Fig. 5; Table 6). Among age -.1 fish caught in May, increasing numbers of fish from non-Alaska stocks were present; however, most of the fish were still of Alaska origin (Fig. 5). By September, an influx of age -.1 chinook salmon from British Columbia, Washington, or Oregon occurred, whereas the catches of age -.1 fish of Alaska origin diminished (Fig. 5). Most age -.2 chinook salmon were also from non-Alaska stocks for all periods.

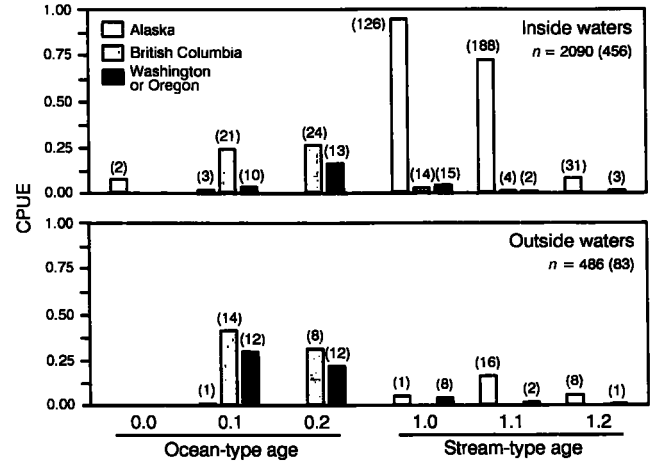

Figure 4

Catch rate by age and origin of ocean- and stream-type chinook salmon, *Oncorhynchus tshawytscha*, in inside and outside marine waters of southeastern Alaska, 1986–87. Catch rate is based on the expanded numbers of coded-wire–tagged fish caught per hour. Actual numbers of coded-wire–tagged fish are shown in parentheses.

Migration and growth

Assessment of migration direction and rates of the CWT chinook salmon was based on the origin and age of the stock group (Table 7). Stocks originating from British Columbia and Washington or Oregon generally traveled NW or N to reach our sampling localities, whereas stocks originating from within southeastern Alaska had no apparent directional tendency. Average net migration rates ranged from 0.1 to 6.9 km/d (Table 7). A decrease in average migration rates with increasing age occurred for all stock groups of ocean- and stream-type fish.

Table 5

Origin and age of 539 coded-wire–tagged chinook salmon, *Oncorhynchus tshawytscha*, recovered in marine waters of southeastern Alaska, February, May, and September 1986–87.

Origin		Number of chinook salmon					
		Age (yr)					
Locality	Latitude	0.0	0.1	0.2	1.0	1.1	1.2
Southeastern Alaska							
Speel Arm	58°04'N	—	—	—	—	3	3
Kasnyku Bay	57°13'N	—	—	—	—	2	3
Medvejie	57°01'N	—	—	—	—	4	1
Crystal Creek	56°53'N	—	—	—	—	—	2
Ohmer Creek	56°46'N	—	—	—	—	—	1
Osprey Lake	56°24'N	—	—	—	—	—	1
Little Port Walter	56°23'N	—	—	—	—	11	19
Earl West Cove	56°18'N	—	—	—	1	—	—
Unuk River	56°05'N	—	—	—	—	1	—
Chickamin River	55°47'N	—	—	—	2	4	—
Neets Bay	55°46'N	1	—	—	15	24	7
Carroll Inlet	55°39'N	1	1	—	63	67	—
Thomas Basin	55°21'N	—	3	—	—	—	—
Ketchikan Creek	55°21'N	—	—	—	6	23	—
Herring Cove	55°20'N	—	—	—	4	58	3
Whitman Lake	55°20'N	—	—	—	31	—	—
Tamgas Creek	55°01'N	—	—	—	5	7	—
Southeastern Alaska total		2	4	0	127	204	40
British Columbia							
Babine River	55°41'N	—	—	—	9	4	—
Upper Bulkley River	55°15'N	—	—	—	1	—	—
Hadenchild Creek	54°56'N	—	—	—	3	—	—
Cedar River	54°50'N	—	—	1	—	—	—
Copper River	54°32'N	—	—	2	—	—	—
Kitsumkalum River	54°31'N	—	3	—	—	—	—
Deep Creek	54°30'N	—	—	—	1	—	—
Hirsch Creek	54°05'N	—	4	—	—	—	—
Skeena River	54°01'N	—	2	2	—	—	—
Kitimat River	54°00'N	—	4	3	—	—	—
Kildala River	53°48'N	—	—	1	—	—	—
Snootli River	52°23'N	—	2	—	—	—	—
Atnarko River	52°22'N	—	1	—	—	—	—
Wannock River	51°40'N	—	—	1	—	—	—
Marble River	50°32'N	—	2	2	—	—	—
Tenderfoot Lake	50°25'N	—	1	—	—	—	-
Birkenhead River	50°19'N	—	1	—	—	—	—
Campbell Transit	50°02'N	—	—	2	—	—	—
Deepwater Bay	50°02'N	—	1	—	—	—	—
Quinsam River	50°02'N	—	6	8	—	—	—
Puntledge River	49°42'N	—	4	3	—	—	—
Big Qualicum	49°24'N	—	—	1	—	—	—
Little Qualicum	49°22'N	—	1	—	—	—	—
Robertson Creek	49°19'N	—	3	3	—	—	—
Thornton Creek	48°58'N	—	—	2	—	—	—
Nitinat River	48°40'N	—	—	1	—	—	—
British Columbia total		0	35	32	14	4	0
Washington or Oregon							
Kendall Creek	48°54'N	—	—	—	—	1	—
Elwha River	48°06'N	—	—	1	—	—	—
Soleduck River	48°03'N	—	3	2	—	—	—

Table 5 (continued)

Origin		Number of chinook salmon					
		Age (yr)					
Locality	Latitude	0.0	0.1	0.2	1.0	1.1	1.2
Washington or Oregon (continued)							
Wells Channel	47°55'N	—	—	—	2	—	—
Rocky Reach	47°32'N	—	—	—	5	—	—
Cook Creek	47°30'N	—	1	5	—	—	—
Fork Creek	46°33'N	—	—	2	—	—	—
Cowlitz River	46°31'N	—	—	1	—	—	—
N. Nemah River	46°30'N	—	1	1	—	—	—
Hanford	46°30'N	—	1	—	—	—	—
Naselle River	46°23'N	—	3	2	—	—	—
W. Fork Grays River	46°23'N	—	1	—	—	—	—
Columbia River	46°20'N	—	1	2	—	—	1
Lyons Ferry	46°15'N	—	—	—	4	—	—
N. Fork Lewis River	45°54'N	—	—	1	—	—	—
Wind River	45°51'N	—	—	—	1	—	—
Umitilla River	45°50'N	—	1	—	2	—	—
Spring Creek	45°42'N	—	—	1	—	—	—
Bonneville Dam	45°39'N	—	—	—	3	—	—
Washougal River	45°39'N	—	1	1	—	—	—
Tanner Creek	45°38'N	—	1	—	—	2	—
Trask River	45°25'N	—	1	2	—	—	—
Clackamas River	45°20'N	—	—	—	1	—	1
N. Santiam River	44°40'N	—	—	—	—	—	1
Yaquina Bay	44°37'N	—	2	—	—	—	—
Newport offshore	44°37'N	—	1	—	—	—	—
Deschutes River	44°36'N	—	—	—	2	—	—
McKenzie River	44°07'N	—	1	—	2	1	—
Willamette River	43°55'N	—	—	—	1	—	—
Coos Bay	43°20'N	—	—	2	—	—	—
Elk River	42°45'N	—	3	2	—	—	—
Washington or Oregon total		0	22	25	23	4	3

Growth rates were significantly higher (*t*-test, $P<0.05$) for ocean- than for stream-type CWT chinook salmon in four of the seven growth periods examined (Fig. 6). Sample sizes of certain age groups of fish in the three growth periods with no statistical significance were extremely limited (4 or less), although ocean-type chinook salmon in those cases also had higher growth rates than had stream-type fish. Mean growth rates generally declined as age increased and season progressed for ocean-type (2.35, 1.54, 1.20, 0.97, 0.71, 0.74, and 0.69% body wt/d) and stream-type (1.85, 0.99, 0.88, 0.78, 0.63, 0.64, and 0.58% body wt/d) chinook salmon (Fig. 6).

Discussion

This study has described the initial marine occurrence and distribution of ocean-type chinook salmon of non-Alaska origin in marine waters of southeastern Alaska. During earlier research on prerecruit chinook salmon in the central and northern regions of southeastern Alaska in May and September, Orsi et al. (1987) caught age 0.1 chinook salmon of non-Alaska origin in September, but not earlier. In our study, we caught age 0.1 non-Alaskan stocks of chinook salmon in the southern region in February, May, and September (Table 6). Consistent with Orsi et al. (1987), we also found an influx of non-Alaska age 0.1 chinook salmon by September in the central and northern regions (Table 6). We found age 0.2 chinook salmon of non-Alaska origin throughout marine waters of southeastern Alaska each season. Age 0.2 chinook salmon reach the minimum harvest size limit in the southeastern Alaska troll fishery in June and July (Olsen, 1992), and age 0.3 fish are the predominant harvest component (Van Alen and Olsen, 1986; Van Alen et al., 1986, 1987). Thus, non-

Table 6

Catch per hour of numbers represented by coded-wire–tagged (CWT) age groups of chinook salmon, *Oncorhynchus tshawytscha*, of southeastern Alaska (AK), British Columbia (BC), and Washington or Oregon (WO) origin recovered in inside and outside marine waters of the northern, central, and southern regions of southeastern Alaska in February, May, and September 1986–87. The actual number of CWT's is shown in parentheses.

	Inside waters						Outside waters					
Region	0.0	1.0	0.1	1.1	0.2	1.2	0.0	1.0	0.1	1.1	0.2	1.2
Southeastern Alaska origin												
February												
Northern	—	—	—	—	—	—	—	—	—	—	—	—
Southern	—	—	—	2.46	—	0.08	—	—	—	—	—	—
	—	—	—	(67)	—	(3)	—	—	—	—	—	—
May												
Northern	—	—	—	0.06	—	0.20	—	—	—	0.08	—	0.15
	—	—	—	(12)	—	(24)	—	—	—	(7)	—	(8)
Southern	—	—	0.03	1.96	—	0.01	—	—	0.09	0.98	—	—
	—	—	(2)	(78)	—	(1)	—	—	(1)	(2)	—	—
September												
Northern	—	—	—	0.08	—	0.09	—	—	—	0.35	—	—
	—	—	—	(2)	—	(1)	—	—	—	(4)	—	—
Central	—	0.87	—	0.43	—	0.05	—	—	—	—	—	—
	—	(4)	—	(8)	—	(1)	—	—	—	—	—	—
Southern	0.29	3.60	0.02	0.16	—	0.01	—	0.28	—	0.14	—	—
	(2)	(122)	(1)	(21)	—	(1)	—	(1)	—	(3)	—	—
AK total	(2)	(126)	(3)	(188)	—	(31)	—	(1)	(1)	(16)	—	(8)
British Columbia origin												
February												
Northern	—	—	—	—	0.87	—	—	—	—	—	0.57	—
	—	—	—	—	(2)	—	—	—	—	—	(2)	—
Southern	—	—	0.01	0.02	0.75	—	—	—	—	—	—	—
	—	—	(1)	(2)	(15)	—	—	—	—	—	—	—
May												
Northern	—	—	—	—	0.03	—	—	—	—	—	0.65	—
	—	—	—	—	(3)	—	—	—	—	—	(6)	—
Southern	—	—	0.25	0.02	0.52	—	—	—	—	—	—	—
	—	—	(4)	(2)	(3)	—	—	—	—	—	—	—
September												
Northern	—	—	0.89	—	—	—	—	—	1.87	—	—	—
	—	—	(3)	—	—	—	—	—	(6)	—	—	—
Central	—	—	0.36	—	—	—	—	—	0.59	—	—	—
	—	—	(1)	—	—	—	—	—	(6)	—	—	—
Southern	—	0.08	0.45	—	0.07	—	—	—	0.11	—	—	—
	—	(14)	(12)	—	(1)	—	—	—	(2)	—	—	—
BC total	—	(14)	(21)	(4)	(24)	—	—	—	(14)	—	(8)	—
Washington or Oregon origin												
February												
Northern	—	—	—	—	—	0.02	—	—	—	—	—	—
	—	—	—	—	—	(1)	—	—	—	—	—	—
Southern	—	—	—	—	0.02	—	—	—	—	—	—	—
	—	—	—	—	(2)	—	—	—	—	—	—	—
May												
Northern	—	—	—	—	0.04	0.02	—	—	—	0.02	0.47	0.01
	—	—	—	—	(1)	(2)	—	—	—	(1)	(9)	(1)
Southern	—	—	0.01	0.01	0.15	—	—	—	—	—	0.05	—
	—	—	(1)	(1)	(3)	—	—	—	—	—	(1)	—
September												
Northern	—	—	—	—	0.19	—	—	—	1.56	0.05	0.09	—
	—	—	—	—	(1)	—	—	—	(10)	(1)	(1)	—

Table 6 (continued)

	Inside waters						Outside waters					
Region	0.0	1.0	0.1	1.1	0.2	1.2	0.0	1.0	0.1	1.1	0.2	1.2
Washington or Oregon origin (continued)												
Central	—	—	0.07	—	0.18	—	—	0.07	—	—	—	—
	—	—	(3)	—	(1)	—	—	(3)	—	—	—	—
Southern	—	0.15	0.08	0.01	0.37	—	—	0.14	0.11	—	0.18	—
	—	(15)	(6)	(1)	(5)	—	—	(5)	(2)	—	(1)	—
WO total	—	(15)	(10)	(2)	(13)	(3)	—	(8)	(12)	(2)	(12)	(1)
Total	(2)	(155)	(34)	(194)	(37)	(34)	—	(9)	(27)	(18)	(20)	(9)

Alaska ocean-type chinook salmon of age 0.1 begin to arrive in the marine waters of southern region of southeastern Alaska in February and May, and by September, non-Alaska chinook salmon age 0.1, as well as those 0.2 and 0.3, are distributed throughout the marine waters of southeastern Alaska.

The temporal and spatial distribution of stream-type chinook salmon in southeastern Alaska appears more complex than that of ocean-type stocks. We found that age 1.0 chinook salmon in September originated from southeastern Alaska, British Columbia, Washington, and Oregon. Age 1.0 stocks from southeastern Alaska were almost exclusively found in inside waters of the southern and central regions; Orsi et al. (1987) also identified age 1.0 fish from these stocks in the northern region. Age 1.0 stocks from British Columbia were found exclusively in inside waters of the southern region. Age 1.0 chinook salmon from Washington and Oregon stocks were recovered in both inside and outside waters of the southern region and in outside waters of the central region. These recoveries corroborate the external tagging studies of Hartt and Dell (1986). Healey (1983, 1991) reported that the residence of stream-type chinook salmon in estuaries and sheltered coastal waters is generally brief and that fish move offshore during their first summer at sea, in contrast to ocean-type fish, which remain in sheltered coastal waters. Our data support his hypothesis with respect to stream-type chinook salmon from Washington and Oregon. However, our recoveries of Alaska and British Columbia stream-type chinook salmon in inside waters during September, and during the ensuing year in February and May, suggest a more protracted residence or limited marine migration for portions of stocks from these regions.

The limited marine migration of some Alaska stream-type stocks of chinook salmon could have a genetic basis. Although Alaska stocks of chinook salmon are almost exclusively stream-type, electrophoretic evidence suggests that southeastern Alaska stocks are genetically intermediate between stream-type stocks of western Alaska and ocean- and stream-type stocks of the Pacific Northwest (Gharrett et al., 1987). Therefore, following the Wisconsinan glacial age, some southeastern Alaska drainages were probably colonized by ocean-type stocks. These fish may have selected a stream-type freshwater life history trait as a result of low "growth opportunity" in northern lati-

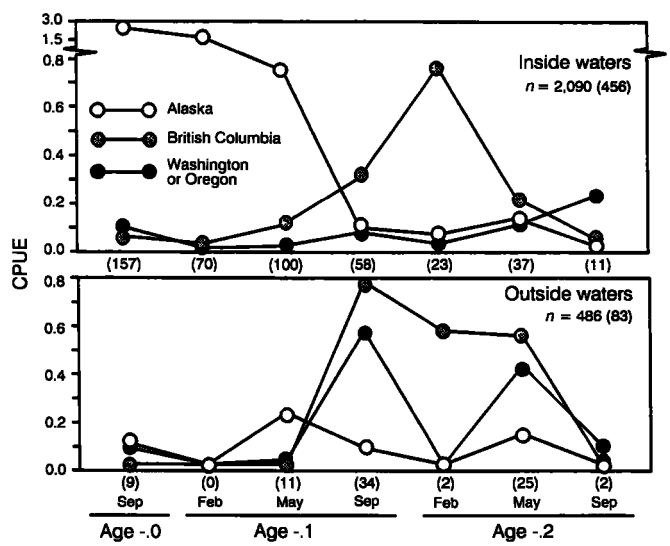

Figure 5

Catch rate of chinook salmon, *Oncorhynchus tshawytscha*, by ocean age and season in inside and outside marine waters of southeastern Alaska, 1986–87. Catch rate is based on the expanded numbers of coded-wire–tagged fish caught per hour. Actual numbers of coded-wire–tagged fish are shown in parentheses.

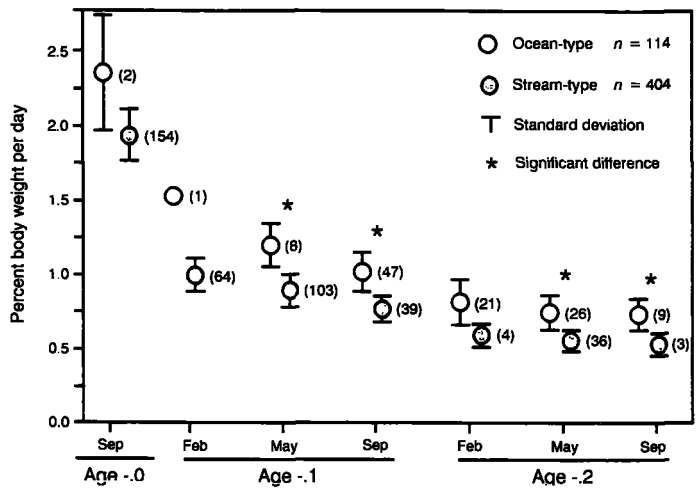

Figure 6

Growth rates of ocean- and stream-type chinook salmon, *Oncorhynchus tshawytscha*, by ocean age and season in marine waters of southeastern Alaska, 1986–87. Mean growth rates are based on coded-wire–tag recoveries shown in parentheses. Significant differences ($P<0.05$) in growth rates between ocean- and stream-type chinook salmon were denoted by an asterisk.

Table 7

Migration rate and direction of coded-wire–tagged ocean- and stream-type chinook salmon, *Oncorhynchus tshawytscha*, recovered in inside and outside marine waters of the northern, central, and southern regions of southeastern Alaska in February, May, and September 1986–87. Stock group designations: AK = Southeastern Alaska, BC = British Columbia, and WO = Washington or Oregon. *n* = number of fish.

			Average migration			Migration direction							
Stock group	Age	*n*	km	Days out	Rate km/d	N	NE	E	SE	S	SW	W	NW
Ocean-type													
AK	0.0	2	41	95	0.4	—	—	—	—	1	1	—	—
AK	0.1	4	37	345	0.1	—	—	1	1	—	1	1	—
AK	0.2	—	—	—	—	—	—	—	—	—	—	—	—
BC	0.0	—	—	—	—	—	—	—	—	—	—	—	—
BC	0.1	35	653	446	1.5	—	—	—	—	—	—	2	33
BC	0.2	32	741	642	1.2	—	—	—	—	—	—	—	32
WO	0.0	—	—	—	—	—	—	—	—	—	—	—	—
WO	0.1	22	1,430	397	3.6	6	—	—	—	—	—	—	16
WO	0.2	25	1,325	686	1.9	—	—	—	—	—	—	—	25
Stream-type													
AK	1.0	127	39	120	0.3	3	1	15	17	38	14	24	15
AK	1.1	204	64	354	0.2	9	4	19	37	70	15	17	33
AK	1.2	40	176	734	0.2	19	0	1	1	1	2	3	13
BC	1.0	14	183	197	0.9	—	—	—	—	—	—	—	14
BC	1.1	4	175	349	0.5	—	—	—	—	—	—	1	3
BC	1.2	—	—	—	—	—	—	—	—	—	—	—	—
WO	1.0	23	1,153	168	6.9	10	—	—	—	—	—	—	13
WO	1.1	4	1,354	486	2.8	—	—	—	—	—	—	—	4
WO	1.2	3	1,546	729	2.1	—	—	—	—	—	—	—	3

tudes owing to temperature and photoperiod regimes (Taylor, 1990) but retained the early ocean-distribution pattern characteristic of their ocean-type lineage.

Differences in length and spatial occurrence of prerecruit ocean- and stream-type chinook salmon in our study were similar to those found later in the commercial troll fishery of southeastern Alaska. Our stream-type chinook salmon were larger and more prevalent in inside waters than were ocean-type chinook salmon of the same ocean-age group. In the southeastern Alaska troll fishery, stream-type chinook salmon are also larger than ocean-type chinook salmon of the same ocean-age group (Van Alen and Wood, 1983; Van Alen et al., 1987), and ocean-type chinook salmon are generally more prevalent than stream-type chinook salmon in outside waters (Van Alen and Olsen, 1986; Van Alen et al., 1987).

Prerecruit chinook salmon were older and larger in the northern regions. Age data from the commercial troll fishery of southeastern Alaska similarly reveal that chinook salmon are older in northern regions (Van Alen and Olsen, 1986; Van Alen et al., 1987). In British Columbia, Healey (1986) found that age 0.2 and age 0.3 troll-caught chinook salmon dominated the catch, that larger age 0.3 fish were more common in northern and central regions, and that smaller age 0.2 fish were more common farther south off Vancouver Island. Age 0.2 chinook salmon also dominate the catch in the Strait of Georgia (Argue et al., 1977; Carter et al., 1986) and off the Washington coast (Wright et al., 1972). However, increased harvest of age 0.2 fish southward is also a reflection of lower minimum-size limits in these fisheries.

The 15–43 cm FL range of our troll-caught age -.0 chinook salmon during September in Alaska is consistent with other studies. Hartt and Dell (1986) reported a 16–36 cm FL range for age -.0 chinook salmon caught with small-mesh purse seines fished in the northeastern Gulf of Alaska from July to October. In another seine study, Fisher and Pearcy (1995) reported a 9–32 cm FL range for age -.0 chinook in shelf waters off the Oregon and Washington coasts from May to September. Of the smaller chinook salmon captured, Fisher and Pearcy (1995) found that chinook salmon <15 cm FL were most abundant in July and August and that chinook salmon <13 cm FL (primarily age 0.0 fish) were closely associated with the warm, low-salinity waters of the Columbia River plume. Moreover, Miller et al. (1983) hypothesized that offshore movement of chinook salmon is size dependent because few chinook salmon <13 cm FL are found in waters >30 m. Our gear test with smaller hooks and lures did indicate a lower length range for age -.0 fish sampled, but fish <15 cm FL were not encountered. Therefore, the absence of fish <15 cm FL in our study may have been a function of the deeper water (>37 m) that we sampled or of our later sampling time (September) when small age -.0 fish were unavailable. In contrast to the seine sampling, the greater upper length range for this age group caught on troll gear may be attributed to seine avoidance by larger chinook salmon. Chinook salmon occur deeper as they increase in length (Orsi and Wertheimer, 1995). Consequently, troll sampling may provide a more representative sample of larger age -.0 chinook salmon within this age group if larger fish were deeper than the seine nets.

Fishery size limits and gear selectivity can influence length distributions. The 66-cm-FL Alaska size limit for chinook salmon had little effect on the length distribution of the age -.0 or -.1 chinook salmon sampled in our study, because the range of length for these age groups seldom exceeded the size limit. However, the range of length for age -.2 chinook salmon usually exceeded the size limit. In the southeastern Alaska troll fishery, Van Alen and Wood (1983) have shown that the percent contribution of age -.2 chinook salmon increases during summer. Therefore, many larger age -.2 chinook salmon may have been removed by the troll fishery before we sampled in September. Healey (1986) reported that the average length of age 0.2 chinook salmon in the British Columbia troll fishery remained relatively constant over the fishing season and attributed this constancy to new recruits growing to legal size. Selectivity by trolling gear also influences length distribution; Orsi (1987) reported significantly more age-.2 chinook salmon caught in September–October on standard commercial gear than on small trolling gear. Other studies also document that large chinook salmon are generally caught with large trolling gear, such as plugs (e.g. Milne, 1955; Boydstun, 1972; Orsi et al., 1993). Thus, fishery size limits and removals, as well as gear selectivity, affected the length structure of age -.2 chinook salmon in our study.

Mean fork length of stream-type chinook salmon was consistently greater than that of ocean-type fish of the same ocean-age group, but this difference was less pronounced as ocean age increased. The greater mean fork length of age -.0 stream-type fish is a function of greater freshwater age and an earlier time of ocean entry. However, mean fork length of age -.2 ocean- and stream-type fish were nearly equivalent in September. Although Healey (1991) reported that rates of growth were similar between ocean- and stream-type fish during their ocean life, we found significantly higher growth rates for ocean-type fish. The higher growth rates for ocean-type fish in our study may explain why mean fork length of ocean- and stream-type fish converged as ocean age increased.

Average net migration rates decreased with increasing age for all stock groups of ocean- and stream-type chinook salmon. This decreased migration rate for older fish may be a consequence of residency in the sampling area or of interception of fish during a circuitous return migration. Highest migration rates were for age 1.0 fish from Washington and Oregon (6.9 km/d). Fisher and Pearcy (1995) reported that age 1.0 chinook salmon (75 km up the Columbia River) migrated at an average net rate of 4.1 km/d to ocean capture locations off Washington and Oregon. Our higher average net migration rates for age 1.0 chinook salmon from Washington and Oregon may have been a function of our capture locality, which would favor recoveries of fish from these stocks that had migrated northward most rapidly.

This study identifies the marine waters of southeastern Alaska as an important nursery area for an amalgam of prerecruit chinook salmon stocks originating from Oregon to Alaska. Stream-type stocks from southeastern Alaska and northern British Columbia typically use inside waters during their first year at sea; at the same time stream-type stocks of Washington and Oregon use both inside and outside waters. Ocean-type stocks from British Columbia, Washington, and Oregon first appear in marine waters of southeastern Alaska after their first winter at sea and use waters throughout the region during their second and third years at sea. Although our study on prerecruit chinook salmon has contributed to our understanding of the temporal and spatial occurrence of this species in southeastern Alaska, additional studies of prerecruits in this region are needed to further identify migration routes, distribution patterns, and residency time of specific stock groups.

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Abstract.—The spatial distribution of marine organisms is highly patchy. Because of this patchy distribution, data from marine abundance surveys are highly skewed and have a large variance. Compounding the problem of estimating the mean abundance from such data, is that occasionally a relatively huge catch will occur. These large catches are not "outliers" but do dominate the estimates of the mean and variance. A lognormal model of the nonzero survey values (a Δ-distribution) is used to model survey data. The estimators, based on the lognormal model, appear to be much more efficient for marine data than the usual sample estimators. In particular, the lognormal-based estimators provide reasonable estimates for data sets that contain a very large catch. The properties and efficiency of the Δ-distribution estimators are examined and the techniques are applied to various marine data sets.

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Estimating the mean and variance from highly skewed marine data

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Characteristically, the observed distribution of abundance data generated by marine surveys has a large variance, is highly skewed to the right, and contains a substantial proportion of zeros. Because of this large variability, the sample mean has a low level of precision even for relatively intensive surveys (Grosslein, 1971; Godø, 1994; Pennington and Godø, 1995). A common problem in the analyses and interpretation of skewed survey data, is that a single immense catch may account for 50% or more of the total catch during a survey (Sissenwine, 1978; Dew, 1990; McConnaughey and Conquest, 1992; Bowering and Brodie, 1994). These extreme values not only greatly affect the estimate of the mean but also of the variance (Otto, 1986). As McConnaughey and Conquest (1992) observed, although these large values cause much uncertainty for management, they reflect the spatial distribution of the species and are not outliers that should be discarded. In practice, the use of more efficient sampling schemes or estimators is the only realistic way to increase survey precision; the total number of samples that can be taken is limited by the high cost of sampling at sea (Gunderson, 1993).

One possible way to increase the precision of survey estimates is to model the observed distribution of catches and exploit the model's properties to develop more efficient estimators of population parameters (see, e.g. Pennington, 1983; MacLennan and MacKenzie, 1988; Lo et al., 1992; McConnaughey and Conquest, 1992; Conquest et al., 1996; Stefánsson, in press). For marine data, the distribution of the nonzero values is often well approximated by a lognormal distribution (e.g. Pennington, 1983; Smith, 1988; McConnaughey and Conquest, 1992; Conquest et al., 1996). Myers and Pepin (1990) found that of the 69 marine data sets they examined, only 5 differed significantly from the lognormal distribution. Thus the lognormal model has been used as a basis for developing survey abundance estimators (e.g. Pennington, 1983, 1986; Lo et al., 1992; McConnaughey and Conquest, 1992) and for estimating commercial catch (Conquest et al., 1996).

It is not surprising that marine abundance data often appear to follow a lognormal distribution. The factors that determine abundance over a region seem to have a multiplicative effect. When this is the case, survey data will be approximately lognormally distributed by the central limit theorem (see, e.g. Aitchison and Brown, 1957). More generally, the lognormal model has been useful for analyzing a wide range of ecological data. As Dennis and Patil (1988) put it: "Ecological abundance data are intrinsically positive, with a few enormously high data points typically arising in every study. The lognormal distribution is an ideal descriptor of such

data with a positive range, right skewness, heavy tail, and easily computed parameter estimates."

To estimate efficiently the mean of skewed marine survey data and to be able to assess its precision, I examined an estimator based on a lognormal model of the distribution. I present the estimator's theoretical efficiency, assess its performance by applying it to several real marine data sets, and give methods for constructing confidence intervals.

Statistical methods

Suppose the nonzero catches generated by a survey are lognormally distributed, i.e. the logged values are normally distributed. If the distribution contains a proportion of zeros, then it is called a Δ-distribution (Aitchison and Brown, 1957). If zeros do not occur, then it is the usual lognormal distribution.

Estimating the mean and variance of the Δ-distribution

As is the case for any distribution, the sample average, $\bar{x}$, and variance, s_x^2, are unbiased estimators of the mean and variance of the Δ-distribution. Because of the properties of the lognormal distribution, the minimum variance unbiased estimators (denoted by c and d) of the mean and variance of the Δ-distribution are given by (Aitchison and Brown, 1957)

$$c = \begin{cases} \frac{m}{n}\exp(\bar{y})g_m(s^2/2), & m > 1 \\ \frac{x_1}{n}, & m = 1 \\ 0, & m = 0 \end{cases} \quad (1)$$

and

$$d = \begin{cases} \frac{m}{n}\exp(2\bar{y})\left\{g_m(2s^2) - \left(\frac{m-1}{n-1}\right)g_m\left(\frac{m-2}{m-1}s^2\right)\right\}, & m > 1 \\ \frac{x_1^2}{n}, & m = 1 \\ 0, & m = 0 \end{cases} \quad (2)$$

where n is the number of observations, m is the number of nonzero values, $y = \ln(x)$, $\bar{y}$, and s^2 are the sample mean and variance of the logged nonzero values, x_1 denotes the single untransformed value when m equals one, and $g_m(t)$, which is a function of m and t (e.g. $t = s^2/2$ in Equation 1), is defined by

$$g_m(t) = 1 + \frac{m-1}{m}t + \sum_{j=2}^{\infty}\frac{(m-1)^{2j-1}}{m^j(m+1)(m+3)\ldots(m+2j-3)} \times \frac{t^j}{j!}. \quad (3)$$

Estimating the variance of $\bar{x}$ and c

Again for the Δ-distribution, the sample mean, $\bar{x}$, and c are both unbiased estimators of the mean. Likewise, the sample variance, s_x^2, and d are unbiased estimators of the population variance. If $\bar{x}$ is used to estimate the mean, then s_x^2/n, the sample variance divided by the sample size, is an estimate of the variance of $\bar{x}$. But s_x^2 can be a very inefficient estimator compared with d, and, therefore, it is frequently recommended that d/n be used to estimate the variance of $\bar{x}$ (Aitchison and Brown, 1957). The minimum variance unbiased estimator of the variance of c is given by (Pennington, 1983)

$$\mathrm{var}_{est}(c) = \begin{cases} \frac{m}{n}\exp(2\bar{y})\left\{\frac{m}{n}g_m^2(s^2/2) - \left(\frac{m-1}{n-1}\right)g_m\left(\frac{m-2}{m-1}s^2\right)\right\}, & m > 1 \\ \left(\frac{x_1}{n}\right)^2, & m = 1 \\ 0, & m = 0 \end{cases} \quad (4)$$

If $m = n$, i.e. there are no zeros, then Equations 1, 2, and 4 reduce to the usual estimators for the lognormal distribution.

Relative efficiency of $\bar{x}$ and c

For the two estimators of the mean, $\bar{x}$ and c, the one with the smallest variance is the most efficient estimator. The formulas in the last section give estimates of the variance based on the particular sample drawn from the distribution. The expected or true variance of $\bar{x}$ is (Aitchison and Brown, 1957)

$$\mathrm{var}(\bar{x}) = \frac{\exp(2\mu + \sigma^2)}{n}\left\{p[\exp(\sigma^2) - 1] + p(1-p)\right\}, \quad (5)$$

where μ is the mean and σ is the standard deviation of the log-transformed nonzero values, and p is the proportion of nonzeros. Smith (1988) derived the expected value of $var_{est}(c)$, which, in the same notation as above, is given by

$$\mathrm{var}(c) = \frac{\exp(2\mu+\sigma^2)}{n} \times \left\{\frac{1}{n}E_{m>0}\left[m^2\left\{\exp(\sigma^2/m)g_m(\sigma^4/2m)-1\right\}\right]+p(1-p)\right\}, \quad (6)$$

where

$$E_{m>0}[\cdot] = \sum_{m=1}^{n} m^2\binom{n}{m}p^m(1-p)^{n-m} \times \left\{\exp(\sigma^2/m)g_m(\sigma^4/2m)-1\right\}.$$

It can be shown using results from Bradu and Mundlak (1970) that the $var(c)$ is always less than or equal to $var(\bar{x})$, both decrease as n increases, but $var(c)$ decreases more quickly than does $var(\bar{x})$. For values of σ^2 typical for marine data, $var(c)$ is considerably smaller than $var(\bar{x})$ (Pennington, 1986; Smith, 1988). This can be seen in Figure 1 which contains plots of $var(c)$ divided by $var(\bar{x})$ versus sample size for a range of σ^2's appropriate for marine survey data.

Tracking trends in abundance

For a series of marine surveys, it is usually assumed that the mean catch per tow is proportional to population size. If this is the case, then the estimator, c, is an index of abundance. The mean of the lognormal distribution is given by $\exp(\mu + \sigma^2/2)$. McConnaughey and Conquest (1992) have suggested that for lognormally distributed survey data, $\exp(\bar{y})$, a slightly biased estimate of $\exp(\mu)$, may be a more stable index for following trends in abundance than estimates of the mean. That is, if σ^2 is constant over time (which is equivalent to the coefficient of variation of the untransformed variable being constant) then $\exp(\mu)$, the median of the lognormal distribution, will also be proportional to abundance. The variance of $\exp(\bar{y})$ can be considerably smaller than the variance of c.

The mean of the Δ-distribution is $p[\exp(\mu + \sigma^2/2)]$. If the mean is proportional to population size and σ^2 is constant for a survey series, then $p[\exp(\mu)]$ will also be an index of abundance. It can be shown with techniques similar to those in Pennington (1983) that the minimum variance unbiased estimator, k, of $p[\exp(\mu)]$ is

$$k = \begin{cases} \frac{m}{n}\exp(\bar{y})g_m\left(\frac{-s^2}{2(m-1)}\right), & m>1 \\ \frac{x_1}{n}, & m=1 \\ 0, & m=0 \end{cases} \quad (7)$$

and the minimum variance unbiased estimator of the variance of k is given by

$$\mathrm{var}_{est}(k) = \begin{cases} \frac{m}{n}\exp(2\bar{y})\left\{\frac{m}{n}g_m^2\left(\frac{-s^2}{2(m-1)}\right)-\left(\frac{m-1}{n-1}\right)g_m\left(\frac{-2s^2}{m-1}\right)\right\}, & m>1 \\ \left(\frac{x_1}{n}\right)^2, & m=1 \\ 0, & m=0 \end{cases} \quad (8)$$

As before, if $m = n$, then Equations 7 and 8 reduce to the lognormal case (Bradu and Mundlak, 1970).

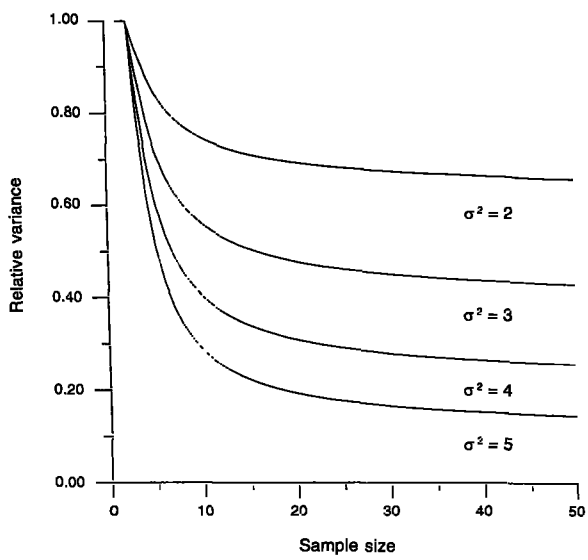

Figure 1

The relative efficiency of the estimators c and $\bar{x}$ for estimating the mean of the Δ-distribution. The plots show the $var(c)$ divided by the $var(\bar{x})$ as a function of sample size when the variance of the nonzero logged values, σ^2, equals 2, 3, 4, and 5, and when the proportion of nonzero values, p, is 0.8.

Confidence intervals

If n is large, then $c \pm 2[var_{est}(c)]^{1/2}$ and $k \pm 2[var_{est}(k)]^{1/2}$ are approximately 95% confidence intervals. For smaller n, a conservative approach for constructing confidence intervals is to calculate separate in-

tervals for p and for the mean (or median) of the lognormally distributed nonzero values. For example, if (p_L , p_U) is a 95% confidence interval for p and (L, U) is a 95% interval for the mean (or median) of the lognormal component (see, e.g. McConnaughey and Conquest, 1992), then (p_LL, p_UU) will have a confidence level of at least 90% (=0.95 × 0.95).

Examples

There are two types of data sets that are typical for marine abundance surveys. The first type has a single large catch that can be many times larger than the next biggest catch. This huge catch may account for more than 50% of the total catch taken during the survey. The other category, and the more common type, is that the distribution of catches is highly skewed, as is the case for the first type, but there are no isolated large catches that dominate the total catch. These are the basic types of data sets that would be expected if samples are taken from a highly skewed lognormal distribution.

Isolated large catches

Occasionally, a very large value can occur when samples are drawn from a lognormal distribution. The first example (Table 1) is an artificial data set generated from a lognormal distribution with $\mu = 0$ and $\sigma^2 = 4$. The mean of the distribution is 7.4 and its variance is 2,926. Because of one large point in the sample, the estimates, $\bar{x} = 38.8$ and $s_x^2 = 63{,}320$, are much larger than the true values. The estimated standard error of the sample mean based on the sample variance is 35.6 [= $(63{,}320/50)^{1/2}$].

The sample estimates of the logged values are $\bar{y} = 0.175$ and $s^2 = 3.921$. Hence the estimates of the mean and variance from the minimum variance unbiased estimators are [Equations 1 and 2, $m = n = 50$]

$$c = \exp(0.175)g_{50}(1.961) = 7.6$$

and

$$d = \exp(0.350)\left\{g_{50}(7.842) - g_{50}\left(\frac{48}{49} \times 3.921\right)\right\}$$
$$= 1.42 \times (922.83 - 34.07) = 1261,$$

which are much closer to the true values than are the ordinary sample estimates. The estimate of the standard error of the sample mean using d is 5.0 [=$(1261/50)^{1/2}$] as compared with an estimate of 35.6 based on the sample variance. The expected standard error of the sample mean (when $n = 50$) is 7.6 [=$(2926/50)^{1/2}$].

The estimated variance of c is given by (Equation 4)

Table 1

An artificial data set generated from a lognormal distribution, catch per unit of effort (CPUE) data for red king crab from a 1991 trawl survey in the Bering Sea, and CPUE data for petrale sole from a 1992 survey off the west coast of the United States.

Artificial data									
0.03	0.03	0.04	0.09	0.14	0.18	0.20	0.22	0.25	0.25
0.25	0.27	0.27	0.27	0.30	0.38	0.40	0.42	0.51	0.55
0.61	0.74	0.80	0.82	0.84	0.86	1.02	1.41	1.91	2.08
2.35	2.72	3.20	3.21	3.22	3.26	3.39	4.21	4.76	5.61
7.47	8.06	8.25	8.80	8.85	9.10	12.92	16.94	23.61	1782.19
Red king crab CPUE[1]									
65	66	69	71	72	73	76	78	78	79
81	83	84	85	86	108	141	144	152	154
154	157	160	161	165	183	204	234	263	265
292	313	317	339	413	435	455	469	569	609
625	746	758	813	909	1056	1145	1197	1339	1789
1842	2520	4194	4286	5424	32538				
Petrale sole CPUE[2]									
4.89	6.31	7.66	11.12	11.31	12.23	13.16	13.61	20.96	23.64
26.31	26.79	28.58	30.07	43.87	56.49	71.43	81.08	94.30	103.02
112.71	115.48	153.96	169.52	179.83	199.80	205.71	310.82	398.51	4635.18

[1] The data set also includes 24 zeros.
[2] Ten zeros are not shown.

$$\mathrm{var}_{est}(c) = \exp(0.350)\left\{g_{50}^2(1.961) - g_{50}(3.841)\right\}$$
$$= 1.42\left\{(6.39)^2 - 34.07\right\} = 9.7.$$

Thus the estimated standard error of c is 3.1 ($=(9.7)^{1/2}$) as compared with an expected value of 3.8 (from Equation 6, $p = 1$). For further examples of the performance of the estimators on lognormal data, see Aitchison and Brown (1957), Blackwood (1991), McConnaughey and Conquest (1992) and Conquest et al. (1996).

The next three examples are survey data that are similar in appearance to the artificial data set in that each contains a single large isolated catch. The first data set is from a trawl survey in the southeastern Bering Sea in 1991. In Table 1 is shown the survey catch per unit of effort (CPUE) of male red king crab, *Paralithodes camtschatica,* of legal size. The largest CPUE is six times greater than the second largest value and accounts for nearly 50% of the total survey catch. In Table 2 the estimates of the mean and the standard errors are calculated as above. The pattern of the estimates is similar to that for the artificial data. In particular, the estimate of the mean, c = 545.0, is much smaller than the sample mean (864.8) and appears to be more precise. The reason that c is so much lower than $\bar{x}$ is that, based on the Δ-lognormal model of the data, a CPUE as large or larger than the biggest value (32,538) would have occurred for approximately 1 in 2,200 tows during the 1991 crab survey, and c weighs the value accordingly. In contrast, the sample mean gives each CPUE value equal weight.

In Table 1, CPUE data are given for petrale sole, *Eopsetta jordani*, from a 1992 trawl survey off the west coast of the United States. The largest catch is 65% of the total catch and is 12 times larger than the next largest catch. Estimates of the mean and standard errors are given in Table 2.

The last example of this type of data set is from a trawl survey off the east coast of the United States. The data (Sissenwine, 1978) are the catch per tow in 1973 of Atlantic mackerel, *Scomber scombrus*. The largest catch (5,182 kg) is more than 25 times greater than the next largest (194 kg) and is 92% of the total catch. This is the one example presented for which lognormality of the nonzero values was rejected (P=0 .02). Though the estimate c = 2.0 kg/tow is considerably smaller than the sample mean ($\bar{x}$=26.2 kg/tow), it is much more consistent with previous and subsequent survey indices (e.g. 1.6 kg/tow in 1972 and 2.5 kg/tow in 1974) than is the sample mean (see Fig. 5 in Sissenwine, 1978).

No dominating large catch

The more usual type of survey data set is one that is highly skewed but does not contain a relatively large isolated value. A typical example of this sort of data is seen in Figure 2 which shows the catch per tow of juvenile Arcto-Norwegian cod, *Gadus morhua*, collected during a 1989 midwater trawl survey in the western Barents Sea (Helle, 1994). The estimate of the mean from c is 55.2 and from $\bar{x}$ is 49.7. Similarly, the estimate d is greater than the sample variance (Table 2).

Another example is from a 1989 zooplankton survey in the Barents Sea (Helle, 1994). Figure 3 is a plot of the biomass per tow of copepods sampled with a Juday plankton net. The frequency distribution is similar to that in Figure 2, and, again, the estimates c and d are larger than the ordinary sample estimates (Table 2).

The sample average and variance will be underestimates for most samples (i.e. be smaller than the true values). This is due to the sampling distribution of $\bar{x}$ and s_x^2, which, for a highly skewed distribution, will still be skewed to the right for small to

Table 2

Summary statistics for estimating the mean and standard errors for six data sets, where n is the sample size, m is the number of nonzeros, $\bar{x}$ is the sample mean, se_s is the sample standard error (SE), se_d is the SE based on a lognormal model, $\bar{y}$ and s^2 are the mean and variance of the nonzero logged values, c is the estimate of the mean based on a lognormal model, and $[var_{est}(c)]^{1/2}$ is its estimated standard error. The expected or true values for the artificial data are in parentheses.

Data set	n	m	$\bar{x}$	se_s	se_d	$\bar{y}$	s^2	c	$[var_{est}(c)]^{1/2}$
Artificial	50	50	38.8	35.6	5.0	0.175	3.921	7.6	3.1
			(7.4)	(7.6)	(7.6)	(0)	(4)	(7.4)	(3.8)
Red king crab	80	56	864.8	415.0	156.0	5.755	1.866	545.0	134.8
Petrale sole	40	30	179.2	115.2	46.9	3.96	2.238	112.1	39.8
Atlantic mackerel	216	67	26.2	24.0	1.4	–0.165	4.269	2.0	0.8
Juvenile cod	161	99	49.7	11.7	26.7	2.759	3.572	55.2	16.4
Zooplankton	160	160	478.1	68.9	93.2	5.338	1.876	525.7	77.2

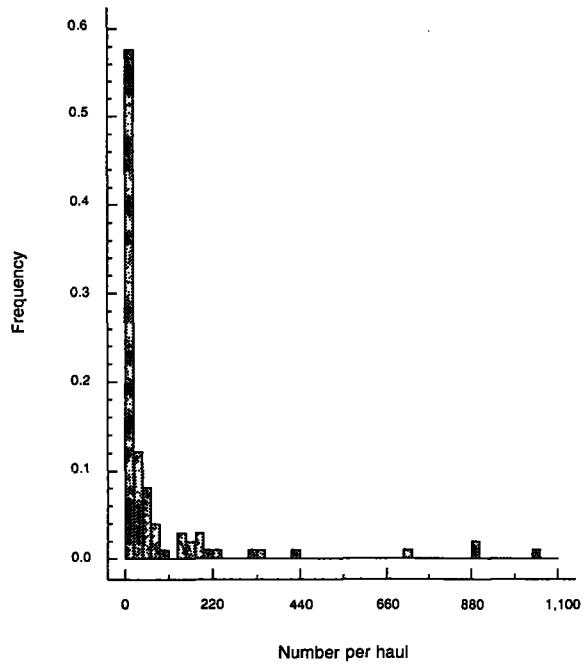

Figure 2

Frequency plot of the number per tow of juvenile Arcto-Norwegian cod from a 1989 midwater trawl survey in the Barents Sea (Helle, 1994). There were also 62 zeros (n=161) which are not included in the plot.

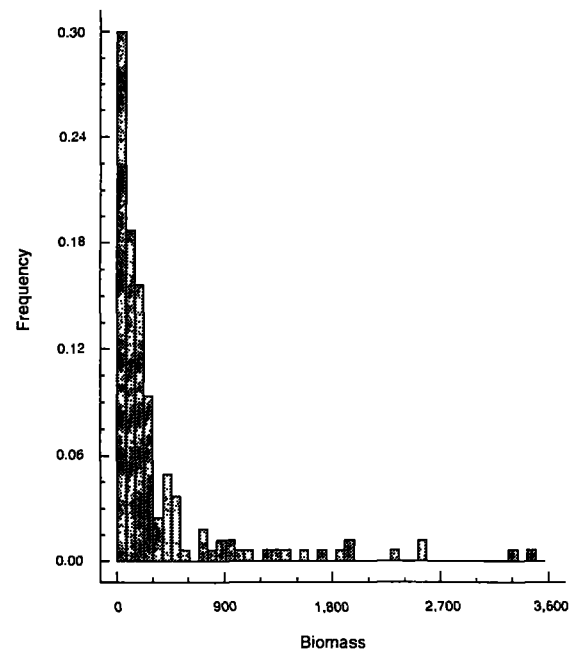

Figure 3

Biomass (μg/m^3) per tow of copepods *Calanus finmarchicus* and *Oithona similis*. Data are from a 1989 plankton survey in the Barents Sea (Helle, 1994). There were no zero values (n=160).

moderate sample sizes. The median can be much smaller than the mean for a skewed distribution, and, therefore, the sample estimators are not only less efficient but will underestimate the true values of the parameters most of the time (Pennington, 1983; McConnaughey and Conquest, 1992; Conquest et al., 1996). The sampling distribution of s_x^2 is much more skewed than is the sampling distribution of $\bar{x}$, which is the reason that s_x^2 often greatly underestimates its expected value more often than does $\bar{x}$ (Pennington, 1986). The sample estimators are unbiased, even though most of the time the estimates are low and are very high for the occasional sample that contains a huge catch (McConnaughey and Conquest, 1992).

Discussion

The estimators of abundance, based on the lognormal model, perform as expected on real survey data if the underlying model for the nonzero values is a lognormal distribution. The estimates are more precise, and the occasional huge catch does not affect the estimates nearly as much as it does the sample average (see also McConnaughey and Conquest, 1992). The Δ-estimators treat these large catches as part of the distribution, as a reflection of how fish are actually distributed spatially, eliminating the need to handle them as "outliers," that is, to discard the points arbitrarily in an analysis of the data. Since all models only approximate reality, an advantage in using lognormal-based estimators for marine data is that they appear to be fairly robust to deviations from the model (Blackwood, 1991; Pennington, 1991; Conquest et al., 1996).

The Δ-estimators can be much more efficient than the sample estimators but lose this advantage for small samples (see Smith, 1988; Fig. 1). Thus for stratified surveys in which the region is divided into many relatively small strata and only a few stations are selected in each stratum, little would be gained by using the Δ-estimators (Smith, 1988). Only a slight gain in precision is usually achieved by increasing the number of strata beyond 6 (Cochran, 1977). Consequently it appears that a better survey design would be one that has larger strata with at least 20–30 stations in each stratum (Fig. 1). Not only would this design improve the efficiency of the Δ-estimators but it would then be possible to exploit optimal sample allocation schemes that may be more efficient (Gavaris and Smith, 1987; Polacheck and Vølstad,

1993). For current surveys with sampling intensity proportional to stratum area, it would likely be better to combine the small strata into ones with larger sample sizes for calculating abundance estimates. Another way to increase sample sizes for future surveys and to improve survey efficiency in general would be to reduce tow duration and use the time saved to sample at more stations (Pennington and Vølstad, 1991, 1994).

It has been suggested that since the lognormal model may be incorrect or not robust, the sample average and variance are the preferred estimators (Jolly and Hampton, 1990; Myers and Pepin, 1990; Smith, 1990). Using finite population techniques, Smith (1990) examined the performance of the estimators based on the Δ-distribution and concluded that for small populations the estimators are biased and not robust to deviations from the model. But the sort of model-based bias that Smith considered is not a concern for marine surveys. Because for most, if not all, marine surveys, the population size, i.e. the total number of tows that could be made, is effectively infinite, whereas Smith's simulations were samples from populations of size 30. There is no reason that the Δ-estimators should be unbiased if applied to samples from small populations. For Smith's simulations, the usual properties of the lognormal-based estimators are apparent if the small samples (n=3) are assumed to be from a larger population. That is, if the samples of size 3 are assumed to come from a survey for which the possible number of tows (the population size) is large, then the estimators are unbiased (see Table 1 in Smith, 1990). The model-based bias that Smith observed is a function of population size, not a property as such of the Δ-estimators or the size of the sample.

What would cause concern is the possiblity that the underlying distribution may have appeared to be approximately lognormal but was not and that the departure from lognormality caused the lognormal-based estimates and inferences to be misleading. Myers and Pepin (1990) have claimed, motivated by some simulations, that lognormal-based estimators are very sensitive to undetectable deviations from lognormality. But to test a model fairly, the alternative models should be realistic. The nonrobustness that they observed was simply due to the contamination of lognormal distributions with very small values, the opposite of what causes the imprecision of abundance estimates from marine surveys, i.e. the large catches (Pennington, 1991). It was not only that the contaminating values were small, but there was a relatively high probability that small values would occur. Since $\ln x$ goes to minus infinity as x approaches zero, these small values resulted in large negative values on the log scale, which caused the extreme instability of the lognormal-based estimators in Myers and Pepin's simulations. Aitchison (1986, p. 270) made the same point when discussing a sensitivity analysis of another log-based procedure. Analyzing artificial data is no different from analyzing real data; all aspects of the simulated data should be examined carefully (see, e.g. McConnaughey and Conquest, 1992) to ensure that the resulting conclusions are relevant.

In practice, even if such small values were statistically "undetectable" (Myers and Pepin, 1991), one would know (e.g. by looking at the data) whether values could be arbitrarily close to zero and, if so, deal with them appropriately as in Pennington (1991). The small values that may occur after transforming abundance data for a particular length class with an age–length key (Myers and Pepin, 1991) will not cause any problems if the original catch at length data are distributed lognormally. This is because $\ln(ax) = \ln a + \ln x$, and, therefore, the log-based estimate of the mean of ax is a multiplied by that for x.

The reason most often given for using the sample estimates and not employing any modeling techniques is that the sample average and variance are always unbiased estimators (Myers and Pepin, 1990; Smith, 1990). Lognormal-based estimators may be slightly biased for some applications but they are not overly influenced by the occasional huge catches and therefore can have a considerably smaller mean square error than the sample estimates for highly skewed distributions (Conquest et al., 1996).

There are problems if the sample estimates are used for marine data (Lo et al., 1992). The estimators are very sensitive to large catches and therefore may be rather inefficient. Another difficulty is that for the sample sizes common for marine surveys, the distribution of the sample average may be far from normal for these highly skewed distributions (Sissenwine, 1978; McConnaughey and Conquest, 1992; Conquest et al., 1996). Thus the central limit theorem cannot be invoked to assess the uncertainty associated with the estimates or to make inferences. Likewise, the distribution of the Δ-estimator may not approximate a normal distribution for small samples, but for skewed distributions it appears to converge to normality more quickly than does the sample mean (Conquest et al., 1996). For small to moderate sample sizes, methods based on the lognormal model can be used to make confidence statements.

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Origin and genetic structure of chinook salmon, *Oncorhynchus tshawytscha*, transplanted from California to New Zealand: allozyme and mtDNA evidence

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Abstract.—Chinook salmon, *Oncorhynchus tshawytscha*, transplanted from the Sacramento River, California, to the Waitaki River catchment of New Zealand at the turn of the century rapidly colonized many South Island rivers. Allozyme genotype and mtDNA haplotype frequencies were obtained from tissue samples from chinook salmon in Waitaki, Rakaia, Waimakariri, and Clutha rivers in New Zealand and compared with data from populations in the Sacramento River to provide further information on the origin of the NZ populations and to ascertain the genetic changes that have taken place since the transplant. Neither allozyme nor mtDNA unequivocally identified an ancestral "seasonal" run (fall, winter, or spring) for the NZ chinook salmon. Sacramento River samples collectively diverged from the NZ samples at allozyme loci, and mtDNA indicated greater similarity between NZ samples and fall-run rather than winter and spring runs from the Sacramento River. Significant variation was detected by mtDNA analysis between only two of the four populations within NZ, one of which has been landlocked by an impassable dam since 1956. The allozyme data identified significant variation within NZ, although less than has been documented among Sacramento River populations. The NZ populations also showed less genetic diversity (mean number of alleles per locus, proportion of loci that were polymorphic, and mean heterozygosity) than the Sacramento River populations. These lower values are consistent with a population bottleneck in the first generations after transplantation into the Waitaki River catchment and with founder effects during the formation of populations in the other NZ rivers. The combination of genetic differences and phenotypic variation among the NZ populations indicates that Pacific salmon populations can develop rapidly after colonizing suitable habitat.

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Salmonids display great interpopulation variation in life history traits, structure, behavior, and other characteristics, reflecting differences in rearing conditions and genetic adaptation to local environments (Ricker, 1972; Saunders, 1981; Taylor, 1991). Fisheries management attempts to be population-specific, reflecting the importance attached to these adaptations (e.g. McDonald, 1981). The past few years have seen a series of reports documenting losses of discrete Pacific salmon populations in the U.S. Pacific Northwest (Nehlsen et al., 1991; Alkire[1]) and in particular states (Washington: Palmisano et al.[2];

[1] Alkire, C. 1993. The living landscape. Vol. 1: Wild salmon as natural capital. Vol. 2: Pacific salmon and Federal lands. The Wilderness Society, Seattle, WA, 174 p.

Washington Dep. Fisheries[3]; Oregon: Lichatowich, 1989; Nickelson et al.[4]; Kaczynski and Palmisano[5]; California: Brown et al., 1994). The listing of certain populations of chinook, *Oncorhynchus tshawytscha*, and sockeye, *O. nerka*, salmon under the U.S. Endangered Species Act has further focused attention on the concepts of population differentiation and local adaptation (Waples, 1995).

Despite the importance of the "stock concept" in salmon management and the abundant examples of variation among populations, there is little direct information on genetic differentiation through the processes of selection and drift. Transplants, however, provide an opportunity to study these processes. Salmonid transplants, undertaken since at least the middle of the last century, have met with mixed success. Freshwater populations have been very widely established outside the native range of such species as brook trout, *Salvelinus fontinalis* (MacCrimmon and Campbell, 1969) and rainbow trout, *O. mykiss* (MacCrimmon, 1971), but anadromous populations have proven difficult to establish inside or outside the species' endemic range (Withler, 1982; Fedorenko and Shepherd, 1986; Harache, 1992). For example, anadromous sockeye salmon, rainbow trout (steelhead), and Atlantic salmon (*Salmo salar*) have established only freshwater populations in New Zealand (McDowall, 1990), and the pink salmon (*O. gorbuscha*) transplant to Newfoundland was unsuccessful (Lear, 1980). The most long-standing, successful establishment of an anadromous salmonid outside its native range has been the transplant of chinook salmon to New Zealand (NZ) (Fedorenko and Shepherd, 1986; Harache, 1992).

Between 1900 and 1906, chinook salmon embryos, probably originating from Battle Creek, a tributary of the Sacramento River (Fig. 1), were shipped to a hatchery on the Hakataramea River, a tributary of the Waitaki River (Fig. 2) on the South Island of NZ (McDowall, 1994). Within about 10 years, chinook salmon had established self-sustaining runs in other major rivers on the east coast of the South Island up to 230 km away (McDowall, 1990). No subsequent introductions were made, thus NZ chinook salmon developed from a discrete parent stock, relatively free from hatchery influence. The Battle Creek population has been maintained at the Coleman Hatchery (Cope and Slater, 1957); thus we had the opportunity to compare the genotypes of this and other Sacramento River populations with the NZ chinook salmon. In addition, chinook salmon from NZ rivers differ from each other in important, heritable life

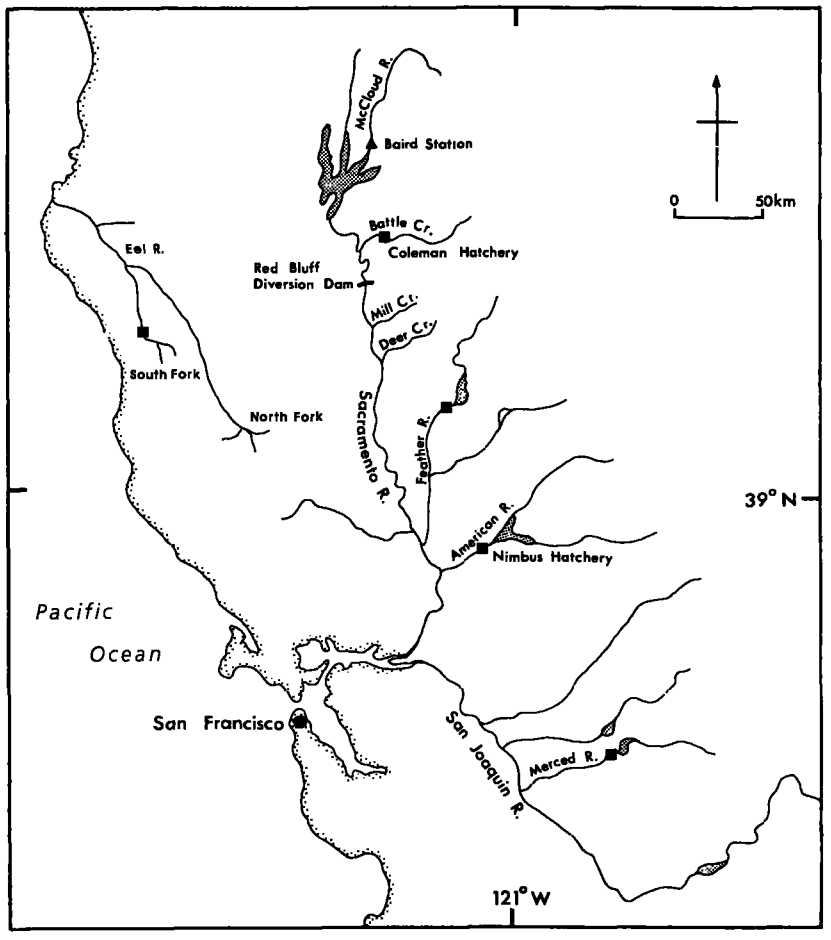

Figure 1

Map of the Sacramento River drainage showing the locations of populations of chinook salmon, *Oncorhynchus tshawytscha*, used in the genetic comparison with New Zealand populations.

[2] Palmisano, J. F., R. H. Ellis, and V. W. Kaczynski. 1993. The impact of environmental and management factors on Washington's wild anadromous salmon and trout. Washington Forest Protection Association and Washington Department of Natural Resources.

[3] Washington Department of Fisheries, Washington Department of Wildlife and Western Washington Treaty Indian Tribes. 1993. 1992 Washington State Salmon and Steelhead Stock Inventory, Olympia, WA, 211 p.

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[5] Kaczynski, V. W., and J. F. Palmisano. 1993. Oregon's wild salmon and steelhead trout: a review of the impact of management and environmental factors. Oregon Forest Industries Council, 328 p.

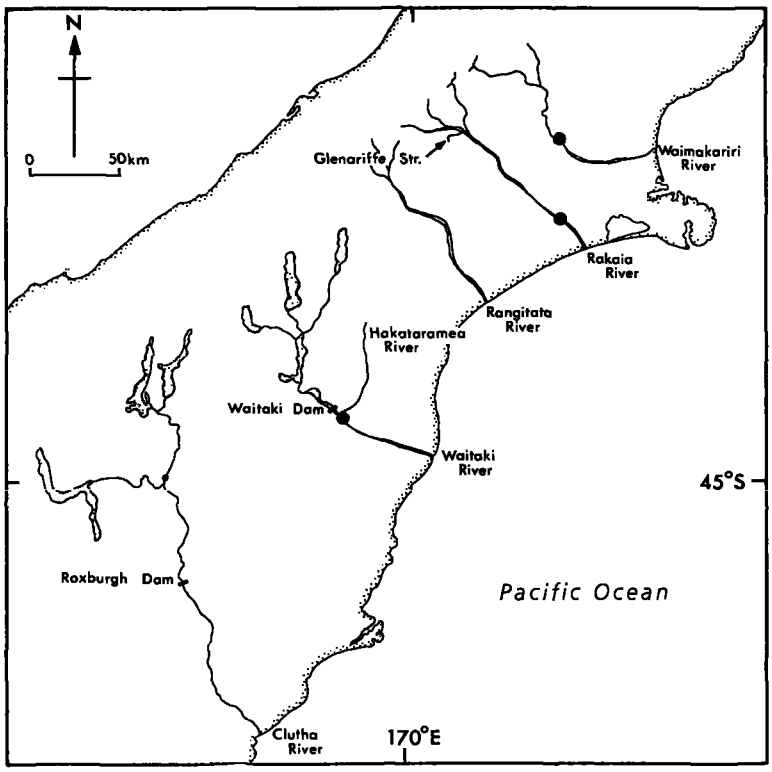

Figure 2

Map of the South Island of New Zealand showing the locations of populations of chinook salmon used in the genetic analysis.

history traits (Quinn and Bloomberg, 1992; Quinn and Unwin, 1993), raising the possibility that genetically distinct populations have evolved within about 20–25 generations and presenting the opportunity for an in-depth study of salmon population differentiation.

Genetic differentiation among populations may arise through selection regimes operating on heritable traits and through genetic drift at the time of colonization (founder effects) and after colonization. Examination of traits not subject to strong selection can provide insights into the importance of genetic drift. Allelic variation at protein-coding loci detected by protein electrophoresis, and more recently, direct examinations of mitochondrial (mt) and nuclear DNA have provided valuable sources of largely neutral molecular genetic markers that permit estimates of degrees of divergence among populations (e.g. Utter, 1991; Carvalho and Pitcher, 1994). Such techniques have helped identify source populations (Hendry et al., in press) and have shown differences between transplanted populations and their source population (Gharrett and Thomason, 1987; Ward et al., 1994) or differences among populations founded by colonization in the new habitat (Krueger and May, 1987). However, population divergence after transplantation is not always detected (Snowdon and Adam, 1992).

There is a substantial database for protein-coding loci on North American chinook salmon (e.g. Utter et al., 1989, 1992; Bartley and Gall, 1990; Bartley et al., 1992), including the Battle Creek population, and a growing database of mtDNA variation (Nielsen et al., 1994, a and b). These two types of data can be more powerful than either alone for studying relatively recent colonization events (Wade et al., 1994). The purposes of the present investigation were to use variation at protein-coding loci and mtDNA to investigate 1) the nature of the founding population (e.g. fall, winter, or spring), 2) whether NZ fish differ in gene frequencies from the descendants of the source population, 3) whether NZ populations differ from each other, and 4) whether NZ fish differ in the levels of genetic variation from descendants of the source population.

Materials and methods

History and origins of NZ chinook salmon

The first shipment of fertilized chinook eggs to NZ was collected from spring-run adults captured in the McCloud River, a tributary of the upper Sacramento River (Fig. 1), 2–27 Sept. 1875 (United States Commission of Fish and Fisheries, 1874–1901). Subsequent shipments of 100,000–500,000 chinook embryos from Baird Station on the McCloud River to the South Island continued to the end of the century, but no self-sustaining populations were established and records of even isolated individual salmon are subject to doubt (McDowall, 1994). There were apparently five shipments from California in the 1900's, arriving in NZ in January–February 1901 (500,000 embryos), 1904 (300,000), 1905 (300,000), 1906 (500,000), and 1907 (500,000; McDowall, 1994). McDowall (1994) concluded that the shipment which arrived in 1904 produced the first returns to the Hakataramea Hatchery in 1907 and that this and the subsequent shipments founded the NZ runs. These embryos were shipped from Battle Creek, but it is unclear whether they originated from Mill Creek or Battle Creek.

Collection of samples

Juvenile salmon (100 per population) were collected from the Waimakariri, Rakaia, and Waitaki rivers

(Fig. 2), three of the four major salmon-producing rivers in NZ (McDowall, 1990). Collection sites in the Waimakariri, Rakaia, and Waitaki rivers were 55, 18, and 57 km above the river mouths, respectively. All collections were made in mid-late summer (12 January to 2 February 1993), early enough in the season to ensure that both ocean-type and stream-type juveniles (Healey, 1991) would have been present (Hopkins and Unwin, 1987; Unwin and Lucas, 1993). Mean fork lengths (FL) ranged from 61 mm (Waitaki) to 76 mm (Waimakariri). Only 63 parr were caught in the Rakaia River mainstem, so another 38 (83 mm mean FL) were collected from the downstream trap on Glenariffe Stream, a major spawning tributary 94 km upstream from the mouth (Unwin, 1986). We also sampled 62 landlocked adults (409 mm mean FL) from Lake Dunstan, a hydroelectric impoundment in the upper Clutha River formed in 1992.

Allozyme analysis

Samples collected from NZ were frozen on dry ice and transported to the National Marine Fisheries Service Auke Bay Laboratory where they were stored at –80°C. Tissue extraction and protein electrophoresis procedures followed those described in Aebersold et al. (1987). Following initial screening for activity and variation at 71 loci, 24 polymorphic loci (Table 1) were selected for comparison with parallel allelic data reported for five Sacramento River populations by Bartley et al. (1992): fall chinook salmon from the Coleman Hatchery (Battle Creek), the Nimbus Hatchery (American River), and the Feather River Hatchery (all on tributaries of the lower Sacramento River); fall chinook salmon from the Merced River Hatchery on a tributary of the San Joaquin River; and wild winter-run chinook salmon from the upper Sacramento River. To provide additional perspective on the levels of genetic variation observed, we also analyzed data on fall chinook salmon from the South Fork of the Eel River, which enters the Pacific Ocean north of the Sacramento River (Bartley et al., 1992; Fig. 1). Compatible data within a subset of 10 out of the 24 polymorphic loci for three Sacramento River samples (Coleman Hatchery fall-run and both fall-run and spring-run from the Feather River Hatch-

Table 1

List of names and Enzyme Commission (E.C.) numbers of variable enzymes, and of designations, tissue distributions (E=eye, H=heart, L=liver, M=skeletal muscle, listed in sequence of optimal resolution) and relative mobilities of variant allelic forms of polymorphic loci.

Enzyme name	E.C. no.	Locus	Relative mobilities of variants	Tissue distribution
Aspartate aminotransferase	2.6.1.1	*mAAT-1**	-104	M, H
		*mAAT-2**	-125, -90	M, H
Adenosine deaminase	3.5.4.4	*ADA-1**	83, 108	M, E, H
Aconitate hydratase	4.2.1.3	*sAH**	86, 112	L
		*mAH-4**	119, 112	L
Glucose-6-phosphate isomerase	5.3.1.9	*GPI-B2**	60, 135	M
		*GPIr**	[1]	M
Glutathione reductase	1.6.4.2	*GR**	110	M, E, H, L
Hydroxyacylglutathione hydrolase	3.1.2.6	*HAGH**	65	M, H, L
L-iditol dehydrogenase	1.1.1.14	*IDDH-2**	61	L
Isocitrate dehydrogenase	1.1.1.27	*mIDHP-2**	150	M, E
		*sIDHP-1**	142, 83	M, H, E, L
		*sIDHP-2**	127, 50, 83, 66	H, E, L
Malate dehydrogenase	1.1.1.37	*sMDH-B2**	121, 70, 126	M, H, L
Malic enzyme	1.1.1.40	*sMEP-1**	78	M, H
Mannose-6-phosphate isomerase	5.3.1.8	*MPI**	109	M, H, E
Phosphogluconate dehydrogenase	1.1.1.44	*PGDH**	90	M, E, H
Phosphoglucomutase	5.4.2.2	*PGM-2**	166	M, H, L
Phosphoglycerate kinase	2.7.2.3	*PGK-2**	90, 74	M, E, L
Dipeptidase	3.4.- -	*PEP-A**	90	M, E, H, L
Proline dipeptidase	3.4.- -	*PEP-D2**	107	M, H
Tripeptide aminopeptidase	3.4.- -	*PEP-B2**	108	M, H
Triose-phosphate isomerase	5.3.1.1	*TPI-2.1**	104, 106	M, E, H
		*TPI-2.2**	102	M, E, H

[1] Allele was detected by the absence of a heteromeric band between *GPI-A** and *GPI-B1** subunits (see Utter et al., 1989).

ery) reported in Utter et al. (1989) were also included 1) to provide data for spring-run fish from the Feather River Hatchery that were not examined by Bartley et al. (1992) and 2) for comparison among different year classes of fall-run fish. Genetic nomenclature followed Shaklee et al. (1990).

Genetic data for NZ and California populations were analyzed with the BIOSYS-1 program[6] to calculate pairwise measures of genetic distances (Cavalli-Sforza and Edwards, 1967; Nei, 1972), gene diversity (F_{ST}, Wright, 1969), chi-square comparisons of heterogeneity, and to construct phenograms through the unweighted pair-group method (Sneath and Sokal, 1973). A neighbor-joining tree (Saitou and Nei, 1987) was constructed from a matrix of arc distances (from Cavalli-Sforza and Edwards [1967]) through the NTSYS-pc program (Rohlf, 1994). Conformance of genotypic proportions of NZ collections to those expected under Hardy-Weinberg (binomial) equilibrium was tested by Levene's (1949) formula for small sample size; the variant alleles were pooled in tests involving loci with more than two alleles.

mtDNA analysis

Total genomic DNA was extracted from a small section of caudal fin tissue from 172 juvenile NZ salmon with Chelex-100 (Walsh et al., 1991) according to the protocol in Nielsen et al. (1994a). A 2-µL aliquot of the chelex-treated supernatant containing salmon DNA was used as a template for amplification with the polymerase chain reaction (PCR) and conserved primers. Our PCR protocol used primers (S-phe and P2; sequences in Nielsen et al., 1994a) that amplify a highly variable segment of the mtDNA control region in salmonids. Amplification, purification, and sequencing of salmon mtDNA were done according to the protocol in Nielsen et al. (1994a). Sequencing reactions were separated in linear 9% polyacrylamide-7 M urea gels and were autoradiographed for 24 to 72 h at room temperature. Mitochondrial DNA sequences were scored with base-pair (bp) differences found within the amplified control region sequence (Nielsen et al., 1994a).

Data on NZ chinook salmon mtDNA sequence frequencies were compared with data from Sacramento River chinook salmon with known spawning seasons (Nielsen et al., 1994b) as follows: winter-run: 72 fish taken from 1991 to 1993 broodstock program at the Coleman Hatchery; fall-run: 359 fish taken from 1992 to 1994 at hatcheries on the American, Merced, and Feather rivers; and spring-run: 32 wild fish collected in Deer and Mill creeks (1991–93) and 27 adults from the Butte Creek spring-run population (1994).

To test for differences in mtDNA frequency among the NZ chinook salmon populations and between the NZ and Sacramento River runs we used an unbiased estimate of Fisher's exact test for population differentiation with a Markov chain analysis (GENEPOP[7]). The Markov model in GENEPOP was run with 4 seeds for the pseudo-random number generator, and the dememorisation number was set to 1,000, the number of batches to 50, and with the number of iterations/batch to 1,000.

Results

Protein-coding loci: genetic variation within populations

Tests for conformance to Hardy-Weinberg genotypic proportions in the NZ populations indicated no deviation from proportions expected in a random mating population. Two tests out of 42 deviated significantly from expected proportions at the 5% level of significance; deficiencies of heterozygotes were observed for *sAH** in the Waimakariri and for *PEPA** in the Waitaki populations. This proportion of deviations (0.048) would be expected by chance at this level of significance. Similar findings were reported by Bartley et al. (1992) for wild California populations, although somewhat higher rates of deviation occurred among hatchery samples. No deviations with Sacramento River samples were reported in Utter et al. (1989). Levels of genetic variation were generally higher in the Sacramento River collections than in the NZ or South Fork Eel River samples (Table 2). The highest mean number of alleles per locus, percentage of loci polymorphic, and mean heterozygosity were seen in the Sacramento River collections, and no overlap in percentage of polymorphic loci occurred between these and any of the other collections.

Protein-coding loci: genetic variation among populations

Allele frequencies at 24 polymorphic protein-coding loci (Table 3) varied considerably among populations. The gene diversity among populations (F_{ST}) averaged

[6] Swofford, D. L., and R. B. Selander. 1989. BIOSYS-1: a computer for the analysis of allelic variation in population genetics and biochemical systematics, release 1.7. Illinois Natural History Survey, 43 p.

[7] Raymond, M., and F. Rousset. 1994. GENEPOP, version 1.0, January 1994. Available through M. Raymond, Laboratoire de Génétique et Environnement, URA CNRS 327, Place E. Bataillon, 34095 Montpellier cedex 05, France. E-mail: Raymond@univ-montp2.fr.

Table 2

Genetic variability at 24 polymorphic protein-coding loci of chinook salmon from rivers in the Sacramento River drainage and South Eel River, California (CA), and from New Zealand (NZ). A locus was considered to be polymorphic if the frequency of the most common allele did not exceed 95%. Mean heterozygosity was the Hardy-Weinberg expected value (Nei, 1978). Standard errors are in parentheses. CA data are from Bartley et al. (1992).

Population	Mean sample size per locus	Mean no. of alleles per locus	% of loci polymorphic	Mean heterozygosity
Battle Creek, CA	100.0	2.1 (0.1)	58.3	0.156 (0.032)
Merced River, CA	100.0	1.8 (0.1)	46.2	0.141 (0.029)
Feather River, CA	100.0	2.0 (0.1)	50.0	0.151 (0.032)
American River, CA	100.0	2.0 (0.1)	58.3	0.164 (0.032)
Upper Sacramento River, CA	94.0	1.9 (0.1)	45.8	0.142 (0.033)
South Eel River, CA	95.8	1.6 (0.1)	29.2	0.113 (0.035)
Rakaia River, NZ	80.9	1.7 (0.1)	29.2	0.111 (0.033)
Waimakariri River, NZ	77.3	1.9 (0.1)	41.7	0.137 (0.032)
Waitaki River, NZ	67.1	1.8 (0.1)	33.3	0.117 (0.033)

over all loci was 0.051, and ranged among individual loci from 0.002 for *mAAT-2** and *PEP-D2** to 0.217 for *GPI-B2** (Table 4). Matrices of pairwise comparisons of two measures of genetic distance (Cavalli-Sforza and Edwards, 1967; Nei, 1972) among populations (Table 5) provided the basis for identifying possible distinct population groupings reflected in this diversity. The UPGM projection of pairwise measures of Nei's distance (Fig. 3A) separated the South Fork Eel River fish from the remaining collections. Two subgroups, comprising the Sacramento and NZ populations, were also apparent. In the Sacramento River subgroup, the Merced Hatchery (San Joaquin River) fall-run fish diverged from the Battle Creek (Coleman Hatchery), Feather River, and American River (Nimbus Hatchery) fall-run fish and from the wild Sacramento River winter-run fish. The three NZ populations grouped more closely within their subgroup than did the Sacramento River populations within theirs. The matrix of Cavalli-Sforza and Edwards distances (Table 5) revealed a comparable UPGM clustering (not pre-

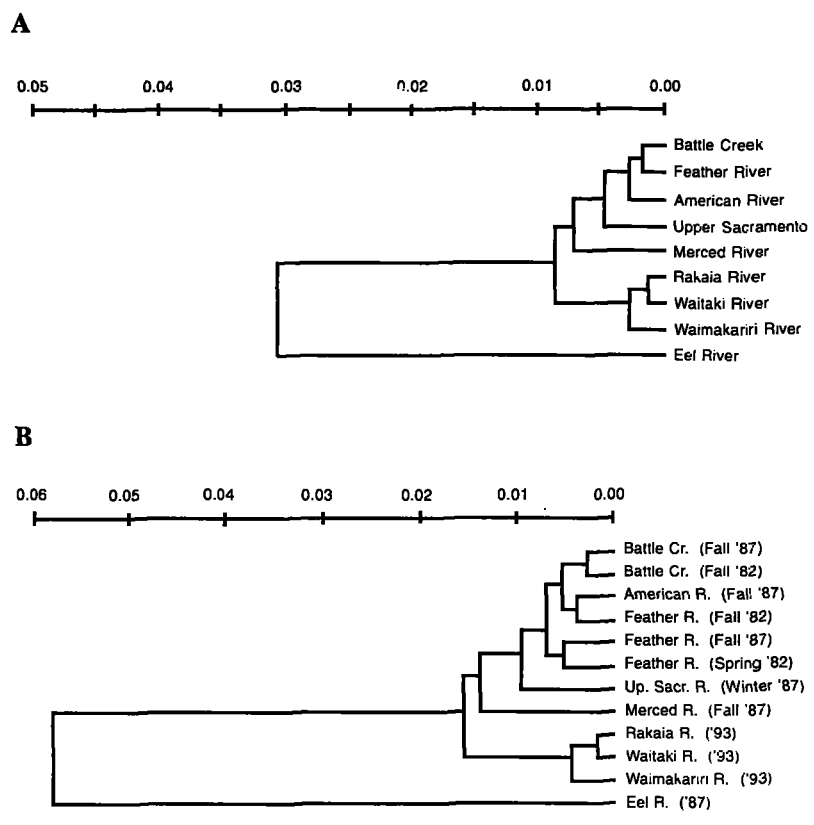

Figure 3

UPGM phenograms of chinook salmon populations from California and New Zealand based on pairwise Nei's (1972) relative genetic distance measures. (**A**) Data from 24 polymorphic loci for collections 1–9. (**B**) Data from 10 polymorphic loci for collections 1–12 (see Table 4 for details).

Table 3

Allele frequencies of 24 polymorphic protein-coding loci for chinook salmon collections (year follows in parentheses) from California: 1 = Battle Creek, fall-run (1987); 2 = Merced River, fall-run (1987); 3 = Feather River, fall-run (1987); 4 = American River, fall-run (1987); 5 = Upper Sacramento River, winter-run (1987); 6 = South Eel River, fall-run (1987) and New Zealand; 7 = Rakaia River (1993); 8 = Waimakariri River (1993); and 9 = Waitaki River (1993). Data for collections 1–6 are from Bartley et al. (1992). Additional California data for 10 loci (from Utter et al., 1989) are provided: 10 = Feather River, spring-run (1982); 11 = Battle Creek fall-run (1982); and 12 = Feather River, fall-run (1982).

	Collection											
Locus	1	2	3	4	5	6	7	8	9	10	11	12
mAAT-1*												
(*n*)	100	100	100	100	94	98	80	83	80			
**100*	0.960	1.000	0.975	1.000	0.995	1.000	1.000	1.000	1.000			
**-104*	0.040	0.000	0.025	0.000	0.005	0.000	0.000	0.000	0.000			
*mAAT-2**												
(*n*)	100	100	100	100	94	46	80	83	80			
**100*	0.995	1.000	0.995	1.000	1.000	0.989	1.000	0.982	1.000			
**-125*	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000			
**-90*	0.000	0.000	0.005	0.000	0.000	0.011	0.000	0.018	0.000			
ADA-1*												
(*n*)	100	100	100	100	94	99	81	83	23	50	300	200
**100*	1.000	0.870	0.955	0.960	1.000	1.000	1.000	0.982	0.978	1.000	0.999	1.000
**83*	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.012	0.000	0.000	0.001	0.000
**108*	0.000	0.130	0.045	0.040	0.000	0.000	0.000	0.006	0.022	0.000	0.000	0.000
sAH*												
(*n*)	100	100	100	100	94	99	81	83	80	50	300	200
**100*	0.775	0.765	0.885	0.835	0.862	0.995	0.778	0.831	0.850	0.720	0.815	0.797
**86*	0.200	0.165	0.105	0.130	0.128	0.005	0.210	0.157	0.131	0.240	0.173	0.195
**112*	0.025	0.070	0.010	0.035	0.011	0.000	0.012	0.012	0.019	0.040	0.012	0.007
mAH-4*												
(*n*)	100	100	100	100	94	99	81	74	55			
**100*	0.925	0.905	0.860	0.925	0.957	0.874	0.938	0.858	0.891			
**119*	0.020	0.065	0.035	0.020	0.011	0.126	0.062	0.142	0.100			
**112*	0.055	0.030	0.105	0.055	0.032	0.000	0.000	0.000	0.009			
GPI-B2*												
(*n*)	100	100	100	100	94	99	81	83	80	50	300	200
**100*	0.940	0.965	0.925	0.930	0.777	0.535	1.000	1.000	0.994	1.000	0.945	0.900
**60*	0.040	0.035	0.065	0.070	0.064	0.465	0.000	0.000	0.006	0.000	0.055	0.100
**135*	0.020	0.000	0.010	0.000	0.160	0.000	0.000	0.000	0.000	0.000	0.000	0.000
GPIr*												
(*n*)	100	100	100	100	94	99	81	83	79	50	300	200
**100*	0.715	0.755	0.615	0.655	0.644	1.000	0.469	0.392	0.538	0.576	0.705	0.689
**r*[1]	0.285	0.245	0.385	0.345	0.356	0.000	0.531	0.608	0.462	0.424	0.295	0.311
GR*												
(*n*)	100	100	100	100	94	99	81	83	79	50	300	200
**100*	1.000	1.000	1.000	1.000	1.000	1.000	0.981	0.958	1.000	1.000	1.000	1.000
**110*	0.000	0.000	0.000	0.000	0.000	0.000	0.019	0.042	0.000	0.000	0.000	0.000
HAGH*												
(*n*)	100	100	100	100	94	99	81	78	8			
**100*	1.000	1.000	1.000	0.990	1.000	1.000	0.975	0.865	1.000			
**65*	0.000	0.000	0.000	0.000	0.000	0.000	0.025	0.135	0.000			

continued on next page

Table 3 (continued)

Locus	Collection 1	2	3	4	5	6	7	8	9	10	11	12
IDDH-2*												
(*n*)	100	100	100	100	94	97	81	25	59			
**100*	0.990	0.990	0.975	0.990	0.984	0.985	1.000	1.000	1.000			
**61*	0.000	0.000	0.000	0.000	0.000	0.015	0.000	0.000	0.000			
**20*	0.000	0.010	0.025	0.010	0.016	0.000	0.000	0.000	0.000			
mIDHP-2*												
(*n*)	100	100	100	100	94	98	81	69	56			
**100*	0.905	0.885	0.950	0.830	0.941	0.990	1.000	1.000	0.973			
**150*	0.095	0.115	0.050	0.170	0.059	0.010	0.000	0.000	0.027			
*sMDH-B2**												
(*n*)	100	100	100	100	94	99	81	83	80	50	300	200
**100*	0.920	0.935	0.955	0.905	0.979	1.000	0.957	0.928	0.956	0.945	0.968	0.977
**121*	0.070	0.040	0.045	0.065	0.021	0.000	0.043	0.072	0.044	0.055	0.032	0.023
**70*	0.000	0.025	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
**126*	0.010	0.000	0.000	0.030	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
*sMEP-1**												
(*n*)	100	100	100	100	94	79	81	74	20			
**100*	0.805	0.860	0.810	0.775	0.851	0.557	0.895	0.858	0.775			
**78*	0.195	0.140	0.190	0.225	0.149	0.443	0.105	0.142	0.225			
*MPI**												
(*n*)	100	100	100	100	94	99	81	79	78	50	300	200
**100*	0.585	0.700	0.580	0.545	0.617	0.818	0.556	0.570	0.551	0.510	0.586	0.487
**109*	0.415	0.300	0.420	0.455	0.383	0.182	0.444	0.430	0.449	0.497	0.414	0.513
*PGDH**												
(*n*)	100	100	100	100	94	99	81	83	78			
**100*	0.975	0.900	0.960	0.920	0.979	1.000	0.975	0.976	1.000			
**90*	0.025	0.100	0.040	0.080	0.021	0.000	0.025	0.024	0.000			
*PGM-2**												
(*n*)	100	100	100	100	94	99	81	83	71			
**100*	0.990	1.000	0.995	1.000	0.995	1.000	0.994	0.988	0.972			
**166*	0.010	0.000	0.005	0.000	0.005	0.000	0.006	0.012	0.028			
*PGK-2**												
(*n*)	100	100	100	100	94	99	81	83	71	50	300	200
**100*	0.495	0.670	0.490	0.605	0.590	0.480	0.704	0.705	0.718	0.540	0.592	0.651
**90*	0.505	0.330	0.510	0.395	0.410	0.520	0.296	0.289	0.282	0.460	0.408	0.349
**74*	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.006	0.000	0.000	0.000	0.000
*PEP-A**												
(*n*)	100	100	100	100	94	99	81	83	80	50	300	200
**100*	0.810	0.950	0.850	0.875	0.894	0.965	0.951	0.952	0.938	0.890	0.869	0.905
**90*	0.190	0.050	0.150	0.125	0.106	0.035	0.049	0.048	0.063	0.110	0.131	0.095
PEP-D2												
(*n*)	100	100	100	100	94	98	81	82	70			
**100*	0.995	1.000	1.000	0.990	1.000	1.000	1.000	1.000	1.000			
**107*	0.005	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000			

continued on next page

Table 3 (continued)

Locus	Collection 1	2	3	4	5	6	7	8	9	10	11	12
*TPI-2.1**												
(*n*)	100	100	100	100	94	99	81	83	76			
*100	0.945	0.830	0.915	0.870	0.936	0.899	0.988	1.000	0.974			
*104	0.055	0.170	0.085	0.130	0.064	0.000	0.012	0.000	0.026			
*106	0.000	0.000	0.000	0.000	0.000	0.101	0.000	0.000	0.000			
*TPI-2.2**												
(*n*)	100	100	100	100	94	99	81	83	80			
**100*	0.930	0.965	0.950	0.960	1.000	0.975	0.988	0.982	1.000			
**102*	0.070	0.035	0.050	0.040	0.000	0.025	0.012	0.018	0.000			
*PEP-B2**												
(*n*)	100	100	100	100	94	99	81	45	69	50	300	200
**100*	0.890	0.955	0.950	0.940	0.862	0.965	0.957	0.900	0.949	0.950	0.842	0.889
**108*	0.110	0.045	0.050	0.060	0.138	0.035	0.043	0.100	0.051	0.050	0.158	0.111
*sIDHP-1**												
(*n*)	100	100	100	100	94	99	81	83	79			
**100*	0.995	1.000	1.000	1.000	0.952	1.000	1.000	1.000	1.000			
**142*	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000			
**83*	0.000	0.000	0.000	0.000	0.048	0.000	0.000	0.000	0.000			
*sIDHP-2**												
(*n*)	100	100	100	100	94	99	81	83	79			
**100*	0.905	0.995	0.895	0.875	0.910	0.859	0.914	0.873	0.956			
**127*	0.090	0.005	0.105	0.125	0.085	0.141	0.086	0.120	0.032			
**50*	0.000	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000			
**83*	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000			
**66*	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.006	0.013			

[1] Allele was detected by the absence of a heteromeric band between *GPI-A** and *GPI-B1** subunits (see Utter et al., 1989).

sented), and a neighbor-joining tree (Fig. 4) also displayed similar clustering, that separated the NZ and Sacramento River populations.

Relationships from the subset of 10 polymorphic loci (Fig. 3B) paralleled those indicated with 24 loci (Fig. 3A). Each of the additional three samples from Utter et al. (1989) were grouped within the clustering of Sacramento River collections reported by Bartley et al. (1992). Notably, the spring-run collection from the Feather River Hatchery was indistinct from fall-run collections from the Feather River and from other Sacramento River hatcheries. Furthermore, the stability of allele frequencies at these loci was evident for fall-run fish collected as juveniles in 1982 (Utter et al., 1989) and 1987 (Bartley et al., 1992).

Decreasing heterogeneity among the 24 loci was apparent when chi-square tests within subgroups were contrasted with those involving all collections (Table 4). Within the total grouping, all but two loci were heterogeneous ($P<0.01$). A lower level of significance occurred for 9 loci within the Sacramento River and for all but one locus among the NZ collections. Standardized measures of these differences indicated more than a doubling of heterogeneity for the Sacramento subgroup relative to the NZ subgroup, and a near doubling of the total heterogeneity relative to the Sacramento collections.

Much of the total heterogeneity reflected the distinction of the South Fork Eel River collection from the remaining group, notably owing to allele frequency differences approaching or exceeding 0.4 at *GPI-B2** and *GPIr**, and to only slightly lower distinctions at *sMEP-1**, and *MPI** (see Table 3). Allelic differences between the Sacramento and NZ subgroups were more subtle. Nonoverlapping frequencies at many loci (*GPI-B2**, *GPIr**, *IDDH-2**, *IDH-2**, *PGM-2**, *PGK-2**, *TPI-2.1**) contributed to their differentiation. In addition, some variants in the NZ subgroup were either absent in all the Sacramento subgroups (*GR**) or occurred at a very low frequency

and not in the Battle Creek population (*HAGH**).

Mitochondrial DNA: genetic variation among populations

There were no new base substitutions found in the 171-bp section of the mtDNA control region of the NZ chinook sequence that we sequenced, compared with mtDNA types reported for Sacramento River chinook (Table 1 in Nielsen et al., 1994b). However, because the base change recorded at bp 183 contained a cryptic deletion that was difficult to score consistently in the NZ fish, we pooled mtDNA types 1 and 4 (as previously reported), which were originally differentiated by a single deletion at bp 183. The same cryptic nucleotide deletion was found in haplotype 3 in the NZ chinook; therefore, the base cytosine (C) and the deletion found at this site were pooled for all populations, yielding five mtDNA types used in this analysis (Table 6).

The NZ salmon populations were dominated by mtDNA haplotype 1, representing 82% in the pooled sample compared with 69% in the Sacramento River population (Table 7). Haplotype 2 was rare in the NZ fish (only one sample was found, from the Waimakariri River) and detected only in fall-run fish from the Sacramento River. Haplotype 3 was detected at low frequencies in NZ and in the Sacramento River fall-run fish. This haplotype was found at higher frequencies in the 1994 spring-run samples taken at Butte Creek and not at all in the Deer and Mill Creeks spring-run collection (1991–93) or the winter-run California chinook. Fish carrying haplotype 5 in the Clutha and Waitaki NZ chinook shared a close frequency distribution to that observed in the Sacramento River fall-run fish. The frequency distribution of haplotype 5 in the Sacramento River fall-run population was primarily due to an increase in its relative abundance in one year class (1994). Haplotype 6 was found only in the winter-run Sacramento fish and not in any NZ population.

The Fisher's exact tests, which compared the total NZ chinook population with each of the three Sacramento River runs of chinook were compared, indicated that the NZ chinook differed significantly from the winter- and spring-run fish ($P<0.001$) but not from the fall-run samples ($P=0.08$). Haplotype frequencies varied among the four NZ populations, but the Clutha River population, with only two mtDNA variants (1 and 5), was the only population to differ ($P<0.01$) from any other population (Rakaia; Table 7).

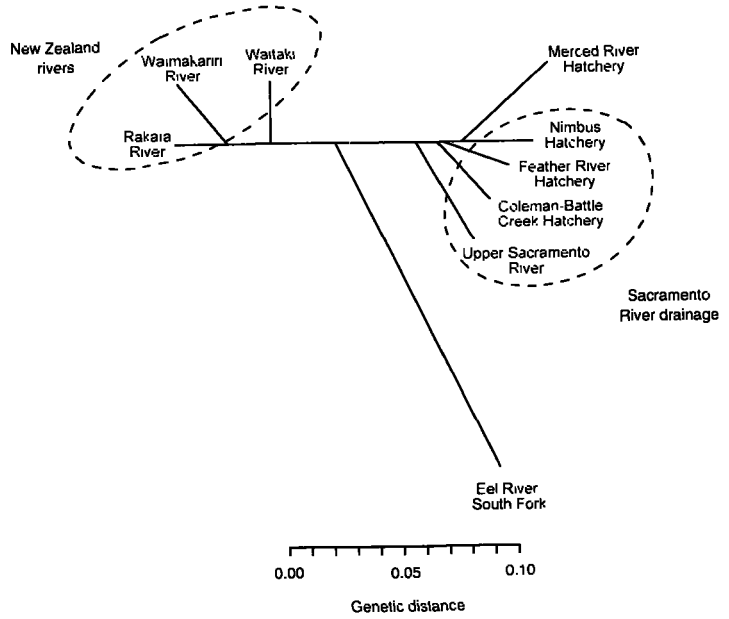

Figure 4

Neighbor-joining tree (Saitou and Nei, 1987) displaying relationships among chinook salmon populations from California and New Zealand based on a matrix of genetic distance measures (Cavalli-Sforza and Edwards, 1967; Table 5). Dashed circles enclose the three New Zealand and four Sacramento River populations.

Discussion

Contrasts among population groups

The allozyme and mtDNA data sets provided complementary and independent comparisons for considering the origin and differentiation of the NZ chinook salmon populations. At the broadest level, the Sacramento and NZ populations share a common lineage (Figs. 3 and 4). The collection from the Eel River, though geographically adjacent to the Sacramento drainage, is typical of a distinct coastal lineage, distinguished by high frequencies of *GPI-2** variation and monomorphism for *GPIr** (Utter et al., 1989; Bartley and Gall, 1990; Bartley et al., 1992). At a finer level, some details of the separate Sacramento and NZ subgroups were apparent from both data sets. The most obvious distinction was the greater degree of divergence among the Sacramento populations on the basis of comparative genetic distances (Table 4; Fig. 3), allelic heterogeneity and partitioning of gene

Table 4

Contingency chi-square (χ^2) analyses and degrees of freedom (df) among all collections (from South Fork Eel River, Sacramento River (CA), and from New Zealand) with data from 24 protein-coding loci, and the Sacramento River and New Zealand subgroups. "—" indicates fixation for common allele in compared group. Significance levels are indicated as follows: ns (P>0.05); * (0.05 > P> 0.01); ** (0.01>P>0.001); *** (P<0.001). Standardized measure is χ^2/df.

	Collections included in analysis								
	Total			Sacramento River			New Zealand		
Locus	χ^2	df	P	χ^2	df	P	χ^2	df	P
*mAAT-1**	40.052	8	***	18.035	4	**	—	—	—
*mAAT-2**	23.833	16	ns	7.886	8	ns	5.819	4	ns
*ADA-1**	117.915	16	***	53.655	4	***	5.731	4	ns
sAH	81.151	16	***	26.092	8	**	4.007	4	ns
*mAH-4**	108.921	16	***	25.984	8	**	8.349	4	ns
*GPI-B2**	606.586	16	***	106.551	8	***	2.054	2	ns
*GPIr**	202.800	8	***	11.804	4	*	6.991	2	*
*GR**	48.936	8	***	—	—	—	7.194	2	*
*HAGH**	168.593	16	***	7.896	4	ns	15.227	2	***
*IDDH-2**	48.413	24	**	13.442	8	ns	—	—	—
*mIDHP-1**	82.834	8	***	20.898	4	***	8.095	2	*
*sMDH-A2**	91.154	24	***	43.336	12	***	1.803	2	ns
*sMEP-1**	80.033	8	***	6.577	4	ns	4.105	2	ns
*MPI**	53.112	8	***	11.540	4	*	0.118	2	ns
*PGDH**	50.497	8	***	19.048	4	***	3.871	2	ns
*PGM-2**	15.185	8	ns	3.503	4	ns	2.6372	2	ns
*PGK-2**	67.987	16	***	19.290	4	***	1.915	4	ns
*PEP-A**	54.293	8	***	19.817	4	***	0.404	2	ns
*PEP-D2**	10.770	8	ns	5.249	4	ns	—	—	—
*TPI-2.1**	237.524	8	***	20.386	4	***	4.452	2	ns
*TPI-2.2**	72.565	16	***	13.327	4	**	2.729	2	ns
*PEP-B2**	29.622	8	***	17.997	4	**	3.624	2	ns
*sIDHP-1**	78.781	16	***	42.576	8	***	—	—	—
*sIDHP-2**	60.541	32	**	22.329	16	**	10.752	4	*
Totals	2,387.107	320	***	548.327	136	***	99.878	50	***
Standarized measure		7.36			4.42			2.08	
F_{ST}		0.051			0.013			0.005	

Table 5

Matrix of genetic distance coefficients based on 24 protein-coding loci. Below the diagonal (****) are estimates of Nei's (1972) genetic distance; above the diagonal are Cavalli-Sforza and Edwards (1967) chord distances.

	Collection								
Collection and site	1	2	3	4	5	6	7	8	9
1 Battle Cr.	****	0.097	0.060	0.067	0.077	0.162	0.100	0.122	0.092
2 Merced R.	0.006	****	0.082	0.072	0.107	0.172	0.111	0.133	0.093
3 Feather R.	0.002	0.006	****	0.059	0.076	0.159	0.098	0.116	0.082
4 Nimbus R.	0.002	0.004	0.002	****	0.091	0.167	0.107	0.127	0.090
5 Upper Sacra. R.	0.003	0.006	0.003	0.004	****	0.162	0.102	0.124	0.092
6 South Eel R.	0.023	0.025	0.023	0.024	0.022	****	0.180	0.190	0.166
7 Rakaia R.	0.007	0.008	0.006	0.006	0.006	0.038	****	0.053	0.063
8 Waimakariri R.	0.011	0.013	0.008	0.009	0.008	0.042	0.002	****	0.085
9 Waitaki R.	0.006	0.007	0.004	0.004	0.005	0.031	0.002	0.003	****

diversity (Table 2). Greater mtDNA haplotype diversity also occurred within the Sacramento subgroup where haplotype 6, detected in winter-run fish, was absent from the NZ fish. These observations comport with the introduction of Sacramento River chinook from a single source to NZ a century ago.

In the NZ collections, the common clustering (Figs. 3 and 4) and generally lower heterozygosities and percentages of polymorphic loci (Table 2) support the occurrence of a limited effective population size (i.e. a "bottleneck") during the founding and perhaps during the early generations of these populations. Enhanced genetic drift resulting from a bottleneck followed by a larger and more stable population size would explain the common clustering of these collections and the lower levels of genetic variation, compared with those observed in the Sacramento River collections. There are no records of population sizes in the first few generations, but natural mortality and the general tendency of salmon to home would have reduced the number of adults colonizing the rivers. Current populations (catch plus escapement) are on the order of 10,000 adults in the four major rivers, including the three sampled in this study.

Several factors might have contributed to the initial bottleneck. The founding population probably represented more females than males, as hatchery staff commonly spawn females with a few "choice" males. The founding individuals experienced a very different environment and presumably a different selection regime from the Sacramento River. The NZ chinook salmon rivers lack the estuary used by fall chinook salmon in the Sacramento River system (Kjelson et al., 1982), and smolts unable to make the abrupt transition to seawater may have died. The surviving smolts of the first generation experienced ocean currents, temperature, and other factors influencing migratory patterns and orientation that differed from those experienced off the coast of California. There may have been strong selection for coastal distribution or other behavior patterns facilitating homeward orientation. Upon return, the mature adults found short, steep, gravel-rich, unstable, recently deglaciated rivers, whose channels lacked woody debris. In addition to these habitat differences that may have exerted selection on the founding generations, the nature of the salmonid mating system (semelparous life cycle and intrasexual competition for nesting sites or mates) also generates considerable variation in reproductive success, especially among males (e.g. Fleming and Gross,

Table 6

Four variable base-pair sites and nucleotide changes found in five chinook salmon mtDNA types from four wild populations in New Zealand and from fish collected in the Sacramento River, California, 1991–93.

MtDNA type	*n*	Variable sites 47	125	134	183
1 and 4	479	G	T	C	C/*
2	15	A	T	C	C
3	59	G	T	A	C/*
5	107	G	T	C	A
6	2	G	81i[1]	C	C

[1] The symbol "81i" represents an 81-bp exact repeat. An asterisk (*) represents a nucleotide deletion. The complete sequence amplified in chinook salmon by the primers S-phe and P2 is given in Nielsen et al. (1994a).

Table 7

The numbers of fish (% in parentheses) found in five variable mtDNA haplotypes in populations of chinook salmon from New Zealand and the Sacramento River.

Population	*n*	mtDNA haplotype 1 and 4	2	3	5	6
Winter-run (CA)	72	70 (97)	0	0	0	2 (3)
Fall-run (CA)	359	233 (65)	14 (4)	35 (10)	77 (21)	0
Spring-run (CA)	59	35 (59)	0	16 (27)	8 (14)	0
CA total	490	338 (69.0)	14 (2.9)	51 (10.4)	85 (17.3)	2 (0.4)
Clutha (NZ)	62	51 (82)	0	0	11 (18)	0
Waitaki (NZ)	34	26 (76)	0	1 (3)	7 (21)	0
Rakaia (NZ)	37	30 (81)	0	6 (16)	1 (3)	0
Waimakariri (NZ)	39	34 (87)	1 (3)	1 (3)	3 (8)	0
NZ total	172	141 (82.0)	1 (0.6)	8 (4.7)	22 (12.8)	0

1994; Quinn and Foote, 1994) and may have reduced the effective population size further.

Ancestral population of New Zealand chinook salmon

Although the genetic and historical data clearly point to a seeding of NZ chinook from a Sacramento River population, identification of the specific ancestral population remains difficult. In addition to possible genetic changes in NZ chinook salmon over the years, the California populations have also undergone complex changes in abundance, habitat, and management since the turn of the century. Moreover, the seasonal runs are not monophyletic races but have apparently evolved independently in suitable habitats; hence major ancestral groups are generally based more on geography than on the timing of a run (Utter et al., 1993).

Aside from confirming a Sacramento River origin, the allozyme data provided no clues about the ancestral population. Both the absence of distinct alleles or of distinguishing frequencies of common alleles among contemporary temporal segments within the Sacramento River and the high genetic drift associated with the presumed bottlenecking in NZ precluded resolution from these nuclear variants. The mtDNA D-loop data, which theoretically provide higher resolving capabilities owing to higher mutation rates and greater population divergence of the haploid genome (Brown et al., 1982; Hoelzel et al., 1991), gave some clues but no definitive answers about the ancestral population (Table 7). The rate of molecular base changes at any one locus can vary according to the number and size of colonies, migration rates, sex ratios, type of parental transmission, as well as the expected rate of genetic drift (Birky et al., 1989; Martin and Palumbi, 1993). The haplotype profile of the Sacramento River fall-run fish resembled that of the combined NZ fish, sharing four haplotypes (1 and 4, 2, 3, 5). In contrast, the winter-run fish were the most distinct, lacking haplotypes 2, 3, and 5, and were represented by a unique haplotype 6 in two individuals. The spring-run sample contained haplotype 3 at a significantly higher frequency than that found for any NZ populations but shared a similar frequency profile for haplotype 5 with the combined NZ sample.

The genetic signatures of the spawning runs of chinook salmon found in the Sacramento River have probably changed since the transfers to NZ at the turn of the century owing to population bottlenecks (particularly the winter-run), hatchery manipulation, impacts from fisheries, changes in habitat, and changes in the thermal regime leading to overlap in temporal spawning populations. Prior to development of the Sacramento River system, Battle Creek had fall and spring runs of chinook salmon, and the current populations in the hatchery may have introgressed to some extent or been altered by interchange with chinook from other populations, despite efforts to maintain the runs separately. Cope and Slater (1957) noted that changes in the river's temperature regime delayed the arrival of spring-run fish at Battle Creek and that "This behavior, together with the fact that these two runs were forced to spawn on the same riffles, with the blocking of the river at Keswick Dam, is presumed to have brought about some mixing of the two stocks . . . when their spawning periods overlap in September. . . . At the hatchery . . . the dividing point between the spawning seasons of the two runs has been more or less arbitrarily set at September 25." Contemporary chinook salmon runs are defined by the timing of adult migration up the Sacramento River (Healey, 1991; Fisher[8]): fall-run (September–October), winter-run (November–February), and spring-run (March–May). These runs also differ in their spawning periods: fall-run (October–December), winter-run (May–June), and spring-run (August–September). Currently, there is also a putative "late fall-run," spawning in winter; unsampled in this study, these fish differed marginally from the fall-run in haplotype frequencies (Nielsen et al., 1994b). According to temporal criteria, the type of chinook embryos sent to NZ at the turn of the century were probably fall-run fish because Thomson (1922) reported that the shipments from California arrived ". . . early in January." Both the spawning season of the winter-run populations (late spring to early summer) and their mtDNA haplotype distribution indicate that they did not found the NZ chinook runs.

Some of the allozyme data raise additional questions about the ancestral population. Allelic variants at two loci occurred in two of the three NZ collections that were either rare (*HAGH*65*) or did not occur in any Sacramento River fish (*GR*110*). The occurrence of both of these variants in two populations (Rakaia and Waimakariri) and at frequencies as high as 0.135 (*HAGH*65*) minimizes the possibility of mutation after colonization. More likely, the variants were present in the founder population. If so, these alleles have drifted to a very low frequency or out of the sampled California populations or they were present in unusually high proportions in the founder population in NZ or in the two rivers in particular.

[8] Fisher, F. 1995. Calif. Dep. Fish and Game, Red Bluff, CA. Personal commun.

Interpopulation differences in NZ chinook

The reduced divergence among the three NZ populations indicated by the allozyme data, relative to the Sacramento River populations, may reflect the recent origins of the NZ groups. The similar magnitude of divergence evident among the NZ populations and between years within two Sacramento River fall-run hatchery populations (Fig. 3B) suggested no differentiation beyond year-class variation of a single population. The frequency of mtDNA types among the NZ stocks also did not indicate isolation between most populations. However, Clutha River fish (which expressed only two of the five haplotypes found in NZ samples) tended to be the most different, especially from Rakaia River fish. The Clutha River population, for which we had no allozyme data, was planted from the Hakataramea River in 1917 (McDowall, 1994) but has been landlocked since 1956 by Roxburgh Dam and may have undergone a population bottleneck after completion of the dam. The Clutha River population is thus less susceptible to genetic exchange than the three anadromous populations sampled, likely to be less polymorphic, and hence is not typical of NZ chinook.

The gene-frequency differences among the anadromous populations are consistent with panmixia caused by straying or successful transfers of salmon among the rivers. Unwin and Quinn (1993) documented straying rates of about 12% by hatchery-released chinook salmon from the Rakaia River to other NZ rivers. In addition, during the 1980's several million juvenile salmon were transferred from the Rakaia, Rangitata, and Waimakariri Rivers to virtually all major east coast rivers except the Rakaia River. Nevertheless, the populations now differ in many life history traits, including fecundity (Quinn and Bloomberg, 1992), freshwater and marine age, length at age, weight at length, date of return to freshwater, and spawning date (Quinn and Unwin, 1993), and egg size and body shape.[9] These phenotypic differences are consistent with some level of genetic isolation among the populations but do not demonstrate it (Waples, 1995).

Our results provide a perspective on the management and conservation of salmon populations. Founder effects or strong selection against certain genotypes can reduce the genetic diversity of populations established by colonization, relative to the source population. However, the NZ experience indicates that this may not prevent the transplant from being successful. The life history differences among NZ populations indicate that salmon populations may evolve quite quickly, although the genetic basis of the life history differences seen in NZ has yet to be demonstrated. The implications of such rapid evolution are open to interpretation. One might argue that it demonstrates the importance of the stock concept in salmon management because reduced gene flow and population adaptation are such fundamental aspects of salmon biology. One might be encouraged to attempt to restore salmon populations to areas from which they have been extirpated, given a suitable source population. However, skeptics of the application of the species concept (including the U.S. Endangered Species Act) to salmon populations might argue that the rapid diversification of salmon populations indicates that they are more plastic than has been assumed and that only a diverse gene pool needs be preserved, not every spatially and genetically discrete population. The concept of "evolutionarily significant unit" (Waples, 1995) provides a compromise by focusing on critical genetic and ecological variables involved in grouping and managing populations. In any case, it is important to remember that the success of the NZ chinook transplant was the exception and that the vast majority of other transplants have failed. Presumably, local adaptation was not sufficiently rapid or flexible to prevent extinction.

[9] Unwin, M. J., M. Kinnison, N. Boustead, and T. P. Quinn. In prep. Variation in body size and morphology of adult chinook salmon (*Oncorhynchus tshawytscha*) from two New Zealand populations and their ancestral Sacramento River, California, population, ninety years later. Natl. Inst. of Water and Atmosphere, P.O. Box 8602, Christchurch, New Zealand.

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Abstract.—Smooth dogfish, *Mustelus canis*, were collected with weirs, seines, gill nets, trawls, and by hook and line from 1988 to 1990 in the Little Egg Harbor–Great Bay estuary of southern New Jersey to determine their foraging habits, growth, and seasonal, tidal, and diel patterns of abundance. Young of the year (YOY) were collected from May to October, with apparently newborn individuals dominating catches from May to July. Subadult and adult individuals were rare. Young of the year reached 550–700 mm total length (TL) by October, growing an estimated 1.9 mm TL/day and 6.0 g/day. Tidal and diel patterns suggest that smooth dogfish use shallow shoal and marsh creek habitats primarily during night hours. High catches during flood tides also suggest increased activity at that time. A comparison of abundance patterns among gears suggests that marsh creeks may be particularly important to newborn individuals during June–July. From an analysis of sex ratio patterns, young of the year do not appear to aggregate by sex or exhibit different emigration patterns between sexes. Smooth dogfish YOY feed primarily on small shrimps, *Crangon septemspinosa* and *Palaemonetes vulgaris*, polychaete worms, and the crabs *Callinectes sapidus*, *Libinia* sp., and *Ovalipes ocellatus*. The abundance of YOY within the estuary strongly suggests that estuaries are critically important nursery habitats for smooth dogfish within the Mid-Atlantic Bight.

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Seasonal abundance, growth, and foraging habits of juvenile smooth dogfish, *Mustelus canis*, in a New Jersey estuary*

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The smooth dogfish, *Mustelus canis*, is one of the most abundant inshore sharks in the western Atlantic (Smith, 1907; Bigelow and Schroeder, 1948, 1953; Hoese, 1962; Compagno, 1984). Despite its abundance, little ecological information, other than anecdotal accounts of growth, and seasonal and life history patterns, is available (Castro, 1983; Compagno, 1984). The most comprehensive accounts of smooth dogfish are found in two summaries by Bigelow and Schroeder (1948, 1953); however, little data on distribution, length frequency, or reproduction are presented in these general descriptive accounts. Food habits have been examined by Field (1907) and Breder (1921). Several studies have examined physical aspects of reproduction (Fowler, 1918; TeWinkel, 1950, 1963, 1964; Graham, 1967; Gilbert and Heath, 1972; Hisaw and Abramowitz[1]), other physiology and behavior (Parker, 1909, 1913; Ifft and Zinn, 1948; Clark, 1963; Gilbert, 1963) and growth (Moss, 1972; Francis, 1981). Although a small fishery for smooth dogfish has grown in recent years, with landings in excess of 780,000 lb and valued at over $100,000 during 1992,[2] the greatest value in smooth dogfish has probably been its extensive use as a subject for research in medical physiology, morphology, and molecular biology (e.g. Greig, 1977; Kalmijn, 1977; Hodgson and Mathewson, 1978; Casterlin and Reynolds, 1979, a and b; Bartlett, 1982; Barry et al., 1988).

In this study we examine aspects of smooth dogfish habitat during that part of the first year of life when estuaries are used as nurseries. More specifically, we collect data with a variety of gears within an estuary of southern New Jersey to determine seasonal abundance and habitat use patterns, growth, and food habits of smooth dogfish.

* Contribution 96-12 from the Institute of Marine and Coastal Sciences, Rutgers University, New Brunswick, New Jersey 08903.

[1] Hisaw, F. L., and A. A. Abramowitz. 1937. The physiology of reproduction in the dogfish, *Mustelus canis*. Annual Rep., Woods Hole Oceanogr. Inst. 1937: 21–22.

[2] Fishery Analysis Div., Fisheries Information Section, National Marine Fisheries Service, Gloucester, MA.

Materials and methods

Study area

The study was conducted in polyhaline (22–33‰) sections of the Little Egg Harbor–Great Bay estuary in southern New Jersey during 1988–90 (Fig. 1). Primary sampling was conducted within tidal marsh creek and adjacent bay shoal habitats with several gear types (Table 1). The four primary study creeks (Schooner, New, Foxboro, and Story Island creeks) were approximately 1.0 km long blind cul-de-sacs that received fresh water only through local runoff (Fig. 1). Story Island Creek was intertidal except for a shallow (<0.5 m) subtidal cove formed at the mouth at low tide. The other three creeks were subtidal with maximum depths of 0.5–2.0 m at low tide. All creeks had a mud substrate and were located 1.3–2.9 km from Little Egg Inlet (for a more complete description of the study creeks see Rountree [1992]). The marsh creeks are typically separated from the adjacent bay by a shallow sill formed at the creek mouth. Beyond the sill, Story Island and Foxboro creeks emptied onto extensive bay shoals (<2 m at high tide) bordering the relatively deep (4–9 m at high tide) Marshelder Channel (Fig. 1). In contrast, New and Schooner creeks each emptied directly into deep channels (Fig. 1).

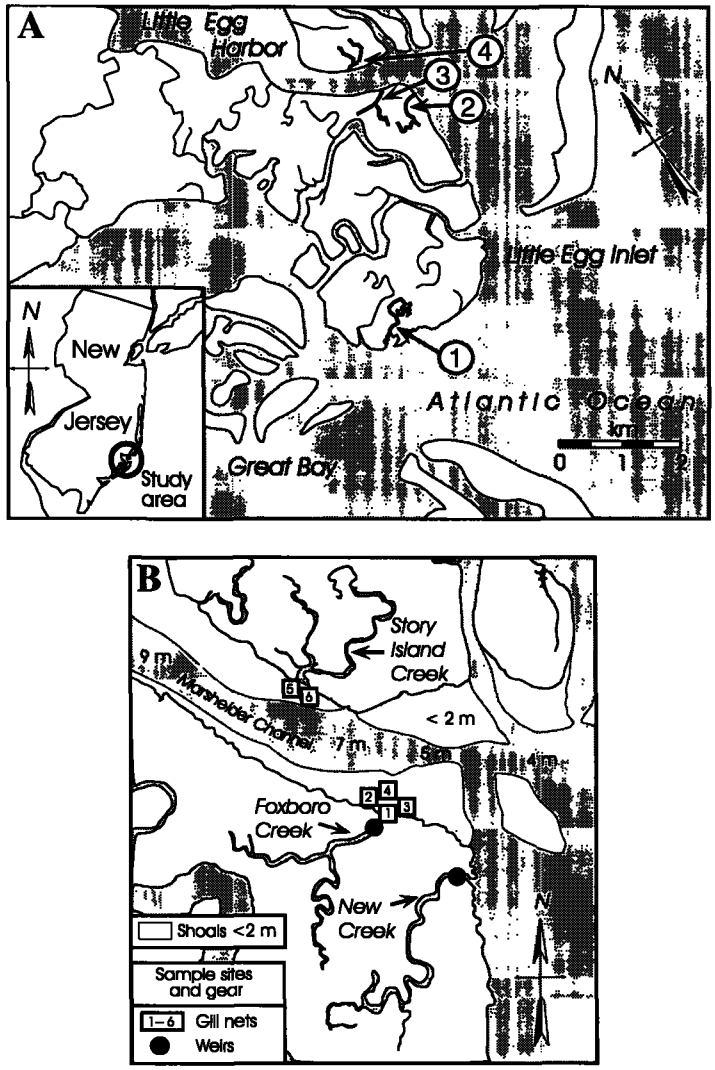

Figure 1

(**A**) Little Egg Harbor–Great Bay estuary indicating the location of four marsh creek (1=Schooner, 2=New, 3=Foxboro, and 4=Story Island) sampling sites for smooth dogfish, *Mustelus canis*. (**B**) Detail of the primary sampling area including Foxboro, Story Island, and New creeks. Gill-net sites include the mouth of Foxboro (net 1) and Story Island (nets 5 and 6) creeks, and the shallow bay shoals adjacent to Foxboro Creek (nets 2–4).

Sampling techniques

The creeks were sampled with weirs, seines, and gill nets (Table 1). Shallow bay shoal habitats adjacent to Foxboro and Story Island creeks were sampled with gill nets and hook and line (Fig. 1). Additional data were derived from extensive trawl collections made in many habitats throughout the estuary, including other marsh creeks and Marshelder Channel in the vicinity of Foxboro Creek (Szedlmayer et al., 1992; Szedlmayer and Able, in press).

Weir and seine sampling For each sampling event, a temporary weir was erected at high tide approximately 30 m above the creek sill. The creek was blocked off entirely by two wing nets (15.2 m × 3.0 m; 6.4-mm mesh) that ran at an angle from each creek bank to a weir (1.2 m wide × 3.0 m long × 3.0 m high; 6.4-mm mesh) located in the center of the creek channel. Deployment of the weir and wings began about 30 min before slack high tide and was completed within 1 h. Fish moving out of the creek with the ebb tide were led along the wings into the weir, where they were trapped by two sets of internal doors. Live fish were removed from the weir at low tide through a codend after raising the weir above the water line. The weir was removed from the creek after each sampling event.

In an effort to capture fish that did not move into the weir during the ebb tide, seine samples were taken at low tide (immediately prior to hauling the weir) within the approximately 100-m^2 triangular area enclosed by the wings. See Rountree and Able (1992) for a more complete description of the weir and seine sampling methods.

Intensive weir and seine sampling was conducted approximately fortnightly from April to November 1988 in Schooner and Foxboro creeks and from April to October 1989 in Schooner, Foxboro, and New creeks (Table 1). During 1988, consecutive day and night tides were sampled within each creek, whereas only night tides were sampled during 1989. Day and night tides were those in which at least the last two hours of flood occurred after sunrise or sunset, respectively. During 1988 and 1989 all creeks were sampled within a three-d period during each sampling week.

Gill-net sampling Standardized gill-net sampling at fortnightly intervals was conducted during May and July–November 1990 with six gill nets (23 m long × 1.8 m high; 38-mm^2 mesh; Table 1). One net was set on the sill at the mouth of Foxboro Creek, and three were set in the shallow bay shoals adjacent to the creek. Two additional nets were set in the mouth of Story Island Creek (Fig. 1). The first gill net was stretched across the mouth of Foxboro Creek so as to block fish passage completely. However, at Story Island Creek two nets were stretched across the creek mouth but did not completely block the creek entrance. Gill nets were deployed at night between 1600–2200 h at either high or low tide and were checked 2–6 times until 0900–1100 h the next day. Catches of smooth dogfish were standardized by catch per unit of effort (CPUE) which was determined "as the number of fish captured in a net check divided by the time elapsed since the previous check (expressed as number/net hours)." Sampling effort was similar on ebb and flood tides (298 and 252 net h, respectively; Table 1). These data were supplemented with data from irregular gill-net collections made on four dates during 1988 and on two dates during 1989 within either Foxboro or Schooner creeks (Table 1).

Other sampling Irregular collections with hook and line were made in the immediate vicinity of Foxboro Creek, although some collections were made in other areas of the bay (Table 1), and standardized otter-trawl tows (4.9-m opening, 19-mm-mesh wings, 6.3-mm-mesh liner) were made during the day at 13 locations throughout the Little Egg Harbor–Great Bay

Table 1

Sampling effort and size ranges of smooth dogfish, *Mustelus canis*, collected in the Little Egg Harbor–Great Bay estuary of southern New Jersey during 1988–90.

				Young-of-the-year total length (mm)				Other total length (mm)			
Gear	Year	Sampling period	Sampling effort	Mean (SE)	Min	Max	*n*	Mean (SE)	Min	Max	*n*
Weir	1988	Apr–Nov, fortnightly (day and night)	42 sets	421 (5)	285	539	68	— (—)	—	—	—
	1989	Apr–Oct, fortnightly (night)	27 sets	388 (9)	299	545	37	627 (—)	627	627	1
Seine	1988	Jul–Nov, fortnightly (day and night)	32 hauls	422 (7)	369	453	12	— (—)	—	—	—
	1989	Apr–Oct, fortnightly (night)	25 hauls	387 (29)	320	481	6	— (—)	—	—	—
Gill net	1988	Jun–Sep (irregular)		400 (11)	318	462	14	945 (131)	728	1,180	3
	1989	Aug–Sep (night)	138 h[1]	499 (12)	366	604	22	— (—)	—	—	—
	1990	May, Jul–Nov, fortnightly (night)	550 h	520 (3)	389	699	448	825 (68)	592	1,025	8
Hook-and-line	1988	Jun–July (day and night)	2 dates	473 (11)	418	515	9	1,123 (39)	1,070	1,200	3
	1989	Jun–Sep, irregular (day and night)	5 dates	380 (6)	321	517	48	— (—)	—	—	—
	1990	May–Jun, irregular (day and night)	7 dates	397 (7)	325	460	33	996 (158)	715	1,260	3
Otter trawl	1988	June–Dec, monthly (day)	342 tows	429 (9)	380	472	11	1,156 (11)	1,126	1,220	7
	1989	Jan, Mar–Jun, Sep–Oct, monthly Jul–Aug, fortnightly (day)	563 tows	419 (19)	371	522	7	— (—)	—	—	—
	1990	Apr–Dec, monthly (day)	560 tows	355 (11)	326	379	5	— (—)	—	—	—

[1] Total number of hours fished summed over all nets.

estuary (Table 1). Four replicate 2-min tows were made at each location. One of the trawl stations was located in Marshelder Channel in the vicinity of Foxboro and Story Island creeks. Trawl samples were collected monthly, except for fortnightly sampling during July, August and September 1989 and 1990 (Szedlmayer et al., 1992; Szedlmayer and Able, in press).

Sex ratio patterns

The sex ratio (percent female and male) was determined for each net check in which at least three fish were collected. The sex ratio of smooth dogfish observed at each net check was used as a proxy for the sex ratio of smooth dogfish schools. If this assumption is valid, then significant deviations from equal proportions would suggest that schools segregate by sex. We also tested for temporal changes in sex ratio, which would suggest differential timing of seasonal movements by sex. Deviations from expected ratios were tested by chi-square analysis (SAS Institute, Inc., 1988).

Growth rate

Temporal trends, and differences between sexes in absolute growth rates were estimated by linear regression of fish size on date of capture. Length outliers from each sampling period, which were assumed to represent age-1 or older individuals from an examination of length-frequency distributions (Table 1; Fig. 2), were removed prior to the regression. An-

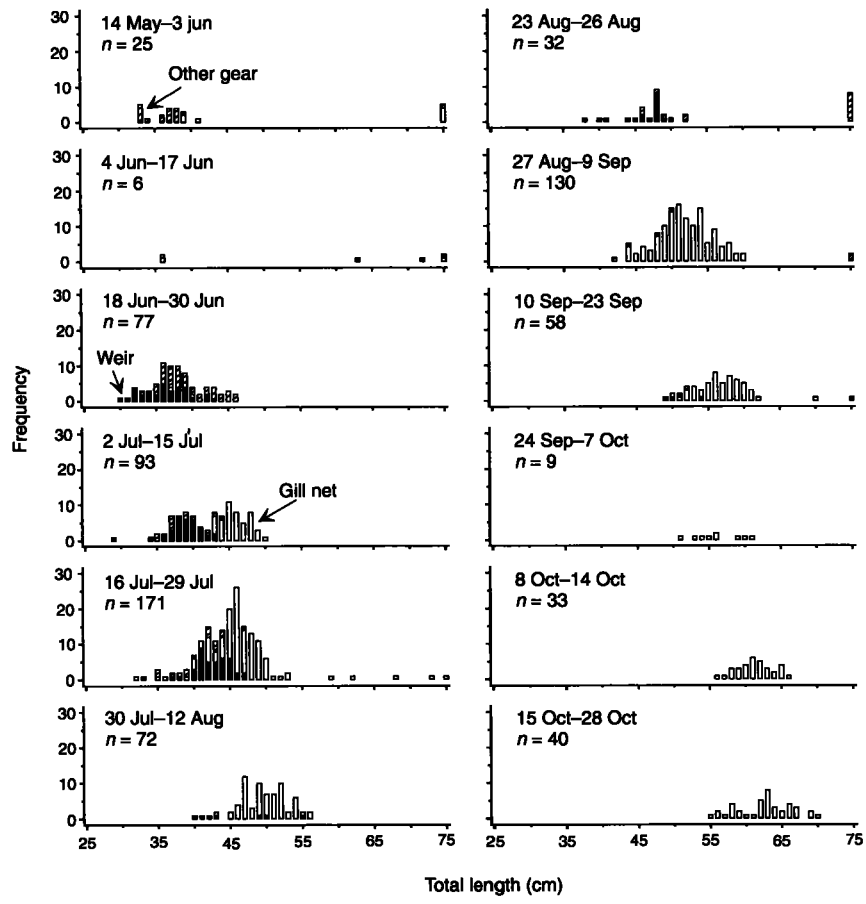

Figure 2

Total length (TL) frequency distribution of smooth dogfish over fortnightly sampling periods, based on data pooled over all years (1988–90) and sampling gears (weir, seine, hook and line, otter trawl, and gill net). Solid bars indicate weir or seine samples, open bars indicate gill-net samples, and striped bars indicate combined hook-and-line and otter-trawl samples. All individuals >75 cm TL are lumped into the 75-cm size class.

nual and sex-stage effects on growth rates were tested with an Analysis of Covariance (ANCOVA) with the following model:

$$\text{Length} = \text{Year Sex Year*Sex Date Year*Date Sex*Date Year*Sex*Date},$$

with the SAS GLM procedure (Freund et al., 1986; SAS Institute Inc., 1988), where year and sex are class variables and date is a covariate. The test of the main effects (year and sex) represents a test for differences in y-intercepts, whereas the test of the interaction with the covariate represents a test for heterogeneity of slopes (Freund et al., 1986). Growth in terms of body weight was similarly tested.

Habitat use patterns

A statistical comparison of smooth dogfish abundances among marsh creeks was made by using an ANOVA, based on night-time weir sampling in Foxboro, Schooner, and New creeks conducted during 1989. We previously reported a comparison between day and night abundances of smooth dogfish in Foxboro and Schooner creek sampling during 1988 as part of a study of diel variation in marsh creek faunal composition (Rountree and Able, 1993). Descriptive statistics, based on night-time gill-net sampling in 1990, were used to compare catches between marsh creek and adjacent bay shoal habitats as well as between ebb- and flood-tide stages. Because time of day, tide stage, and seasonal effects could not be partitioned in the 1990 gill-net sampling, no attempts were made to statistically test hypotheses of habitat or tide stage differences in catches. For example, gill-net sampling was biased between habitats because nets stretched across creek mouths were presumably more efficient than those placed in the open bay. Additionally, because tide and diel cycles are not correlated, sampling on flood and ebb tides were sometimes conducted weeks apart (i.e. it was impossible to sample on both flood and ebb tides at the same location and time).

Foraging habits

Smooth dogfish collected in 1988–90 during gill-net, hook-and-line, and trawl sampling were measured live, packed in ice, and transported to the laboratory for freezing. Because of the large number of smooth dogfish captured during 1990 gill-net sampling, a subsample of at least three fish was retained from each net check for food habit analysis. The remaining fish were tagged and released. The released fish were tagged to prevent bias in the catch estimated from recaptures. Fish were tagged just posterior to the first dorsal fin with individually coded yellow T-bar anchor tags (total tag length, 40 mm; Hallprint Pty. Ltd., Holden Hill, South Australia). Because no tagged individuals were recovered during our gill-net sampling, CPUE adjustments were not necessary.

In the laboratory, thawed smooth dogfish were remeasured and weighed prior to stomach removal. The total stomach contents were then weighed and the prey items were identified to the nearest taxon, enumerated, and weighed (wet WT). An index of gut fullness (%full) that incorporates body weight rather than gut capacity (Hyslop, 1980) was calculated as

$$\%full = [(prey\ WT)/(total\ body\ WT - total\ gut\ WT)] \times 100,$$

where *prey WT* = the weight of a given prey species (or sum of all prey species);
total body WT = the total weight of the smooth dogfish; and
total gut WT = the weight of the entire gut contents (excluding the stomach itself).

Tidal and temporal (hour of the night) effects on stomach, large intestine, small intestine, and total digestive tract fullness were examined from 1990 gill-net samples. After having been thawed in the laboratory, the entire digestive tract was excised and sectioned into stomach, large intestine (spiral valve), and small intestine (colon and rectum). The total contents of each section, as well as the total for all sections combined, were then weighed. After pooling data from all collections for each tide stage, hourly mean fullness values were calculated for each gut section separately, as well as for the total. The effect of tide stage (ebb vs. flood) on gut fullness indices was tested separately for each section of the digestive tract and for the total digestive tract, with analysis of variance (ANOVA; Sokal and Rohlf, 1981). Use of the fullness index, described above, allowed us to reduce bias due to variation in dogfish size in the ANOVA. The data were arcsine–square-root transformed prior to analysis.

Results

Life history stages and seasonal abundance patterns

Most smooth dogfish collected in the study area were YOY according to size at date of capture (Fig. 2) and according to an assumed length of 80–90 cm at ma-

turity (Castro, 1983; Compagno, 1984). A total of 720 YOY and 25 subadult (60–80 cm) to adult (80–130 cm TL) smooth dogfish were collected (Table 1). A single well-defined size cohort of YOY dominated catches on the basis of data pooled over all years and gears (Table 1; Fig. 2). The smallest individuals (<40 cm) collected during May, June, and early July had fresh umbilical scars. Although adults were not abundant, they were collected from May to September. Their relative rarity, however, may have been due to gear avoidance, because we frequently observed adults during night flood tides in the shallow bay in the vicinity of Foxboro and Story Island creeks from May to July. Additionally, on several occasions we observed adults that repeatedly came into contact with gill nets without becoming entangled. A few intermediate-size individuals (60–70 cm TL) were collected in June, July, and September. These individuals appeared to be small subadults from their length at date of capture (more strikingly, they were far more robust than the YOY and lacked umbilical scars) and were excluded from the growth analysis for the YOY.

The occurrence of YOY in the study area was highly seasonal. They appeared first in May and apparently left the study area by November (Figs. 3 and 4). The timing of fall migration out of the estuary was well defined by their absence in weir, gill-net, and trawl samples during November. The first appearance of YOY during the spring, however, was less well defined because of the lack of gill-net sampling during this period, despite their absence in April weir and seine sampling as well as January–April trawl sampling. Young of the year were abundant in weir and seine collections only during June and July (Fig. 3).

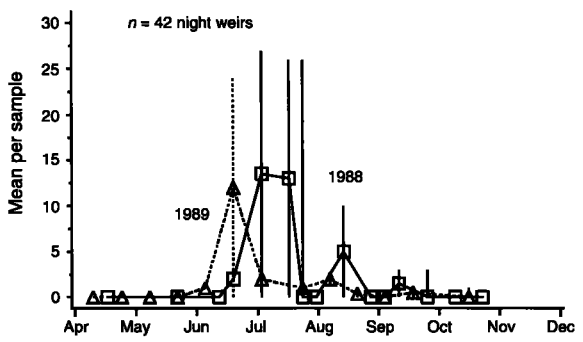

Figure 3

Seasonal abundance of smooth dogfish, based on night weir samples pooled from three subtidal marsh creeks (Foxboro, New and Schooner) during 1988 and 1989 (vertical lines represent one standard error about the mean). Smooth dogfish were absent from day weir samples.

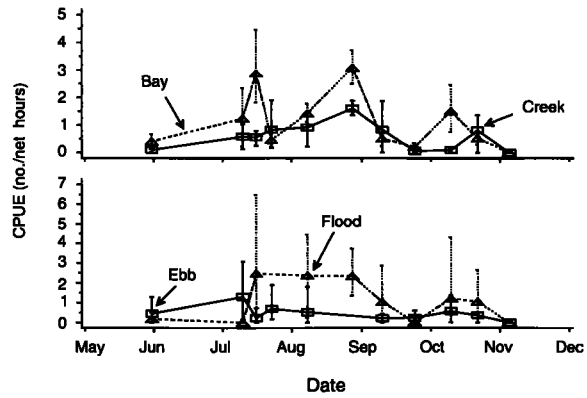

Figure 4

Seasonal abundance (CPUE expressed as the mean number per hour per net) of smooth dogfish collected with gill nets set in marsh creeks and in the adjacent shallow bay during 1990. Data are grouped by habitat (top) and tide stage (bottom) for comparison. Vertical lines are ranges.

In contrast, they were collected regularly in gill-net samples from both the bay shoal and marsh creek sill locations from June through October (Fig. 4). Peak CPUE in gill-net sampling occurred from July to August. Young of the year collected by weir tended to be smaller than those collected by other gears during June–August (Fig. 2). No tagged (n=138) YOY were recaptured during our sampling; however, two individuals were recaptured off North Carolina the following winter: one inshore near Cape Fear, North Carolina, in December 1990 and a second off the beach at Cape Hatteras, North Carolina, in March 1991.

Sex ratio

Sex ratios of the YOY did not differ significantly from 1:1, averaging 51.8 % (standard error [SE]=2.8) females per net check (n=55 net checks with three or more fish). No significant temporal effect on sex ratio was observed.

Growth

Young of the year exhibited a very rapid growth rate of 1.9 mm TL/day, or 6.0 g/day (Table 2), and reached 550–700 mm TL by the end of October (Fig. 2). There was a significant annual affect on growth rates for both length and weight (i.e. the slopes were not homogeneous among years; ANCOVA, $P \leq 0.0001$; Table 2; Fig. 5). No effect of sex on growth was observed (Table 2; Fig. 5). Because the slopes were heterogeneous among years, differences in intercepts among years could not be tested; however, a significant dif-

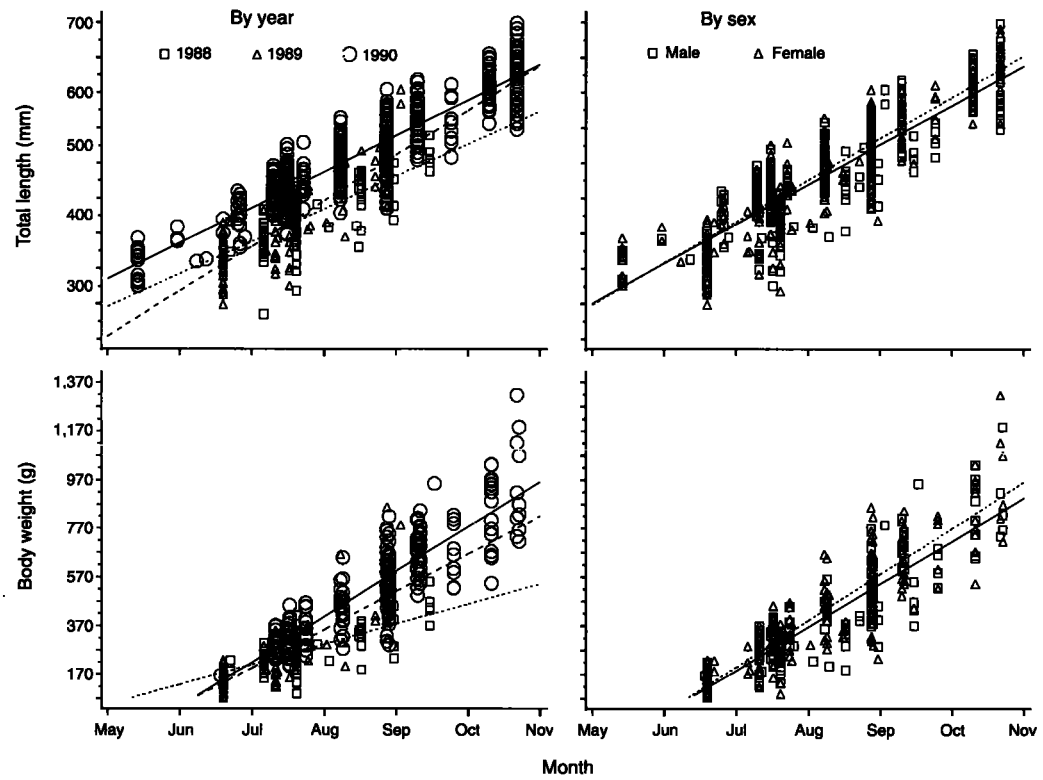

Figure 5

Comparison of total length (TL) and body weight (WT) growth rates of smooth dogfish by sampling year and sex. Linear regression parameter estimates and statistics are given in Table 2.

Table 2

Growth rates of young-of-the-year smooth dogfish collected from the Little Egg Harbor–Great Bay estuary of southern New Jersey between 1988 and 1990, estimated by linear regression of total length and body weights on dates of capture. All parameter statistics are significant at $P \leq 0.0001$.

	Length (mm TL/d)			Weight (g/d)		
	Slope (SE)	r^2	n	Slope (SE)	r^2	n
Year[1]						
1988	1.51 (0.14)	0.50	114	2.70 (0.28)	0.47	103
1989	2.09 (0.11)	0.74	120	5.08 (0.31)	0.73	101
1990	1.66 (0.04)	0.82	486	6.04 (0.24)	0.76	208
Sex[2]						
Male	1.84 (0.05)	0.78	345	5.78 (0.22)	0.80	181
Female	1.93 (0.05)	0.79	329	6.20 (0.23)	0.78	196
Pooled	1.91 (0.04)	0.78	720	6.01 (0.15)	0.79	412

[1] Growth rates are highly significantly different among years (ANCOVA, $P \leq 0.0001$) for length and weight.
[2] Samples sizes are lower because sex was not determined for some individuals during 1988. Growth rates are not significantly different between sexes.

ference in the y-intercepts between sexes was observed for weight (ANCOVA, $P \leq 0.001$; Fig. 5), suggesting that females may have been born slightly heavier (approx. 42 g) than males. A highly significant length-weight relationship was obtained (Fig. 6). No differences in the length-weight relationship were found between sexes.

Habitat use patterns

Habitat type (tidal creek versus adjacent bay shoals), time of night, and tide stage (ebb versus flood) had a strong effect on CPUE of smooth dogfish in gill-net collections (Figs. 4 and 7). Most smooth dogfish were captured on flood tides (Fig. 4), with flood tide CPUE averaging 1.1 fish/net h (SE=0.2), and ebb tide CPUE averaging 0.5 fish/net h (SE=0.1). Catches were greatest at 2100 h (3 fish/net h) and declined sharply by 0300 h (<0.6 fish/net h), and dropped to near zero by 0600 h (Fig. 7). Catches tended to be greater in the bay shoal habitat than at the creek sills (Fig. 4), with CPUE averaging 1.2 fish/net h (SE=0.2) and 0.6 fish/net h (SE=0.1), respectively. Abundance of YOY in weir samples varied significantly ($P \leq 0.5$) among Foxboro, Schooner, and New creeks, averaging 3.7, 0.3, and 0.8 individuals/weir, respectively.

Foraging habits

Dominant prey of YOY smooth dogfish included the shrimps *Crangon septemspinosa* and *Palaemonetes vulgaris*, polychaetes, and the crabs *Callinectes sapidus*, *Libinia* spp., and *Ovalipes ocellatus* (Table 3). The diet of YOY included several other small decapod crabs, razor clam *(Ensis directus)*, and small fishes (*Menidia menidia* and *Fundulus heteroclitus*). Often, YOY dogfish stomachs contained the walking legs or chelae of crabs, rather than entire individuals. Soft shell individuals of the various crab species were also frequently consumed. Whole crabs, other than those recently molted, were rarely observed.

There were no strong tidal or hourly trends in gut fullness (Fig. 8). No empty stomachs were found. Stomach fullness averaged 5.04 % body wt (SE=0.21, n=136), and 4.21 % body wt (SE=0.21, n=107) for individuals captured during flood and ebb tides, respectively. Stomach fullness increased slightly from early evening (averaging about 4 % body wt at 1900 h) to early morning (averaging about 5 % body wt at 0600 h). Three fish examined during mid-afternoon also had high levels of food in their stomachs (4–6 % body wt at 1200–1300 h). Intestine fullness remained remarkably constant regardless of time of night (hourly means ranging from 0.4–0.5% body wt, and 1.5–1.9 % body wt for the small and large intestine, respectively). We did not observe any strong decline in stomach fullness or any increase in intestinal fullness that would suggest noncontinuous feeding.

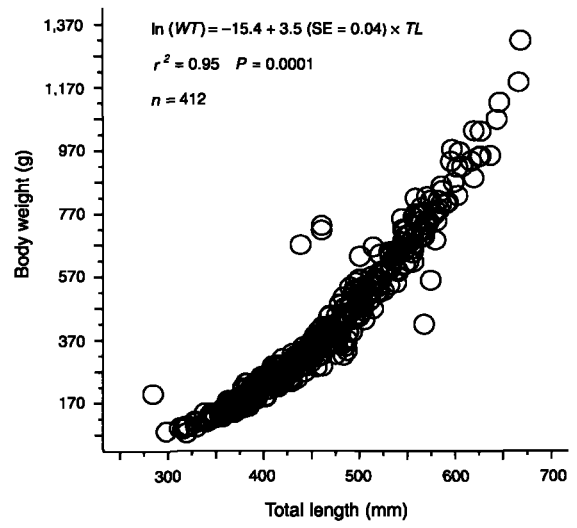

Figure 6

Total length (TL)-body weight (WT) relationship for smooth dogfish based on data pooled over all years and gears (n=412, r^2=0.96, $P \leq 0.0001$).

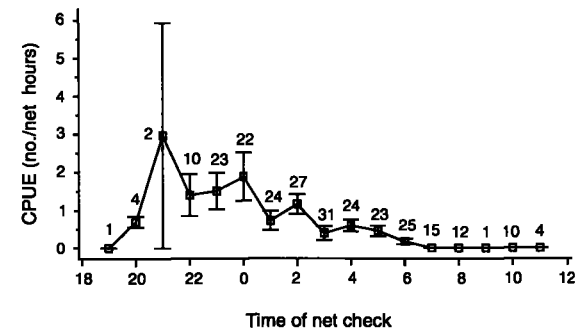

Figure 7

Hourly mean abundance (CPUE per hour per net) of smooth dogfish collected during the night with gill nets set in marsh creeks and adjacent bay habitats during 1990. Data are grouped by ebb- and flood-tide stage. Vertical lines are ranges.

Discussion

Life history stages and seasonal abundance patterns

Smooth dogfish are seasonal residents in New Jersey estuaries; adults are present April–September,

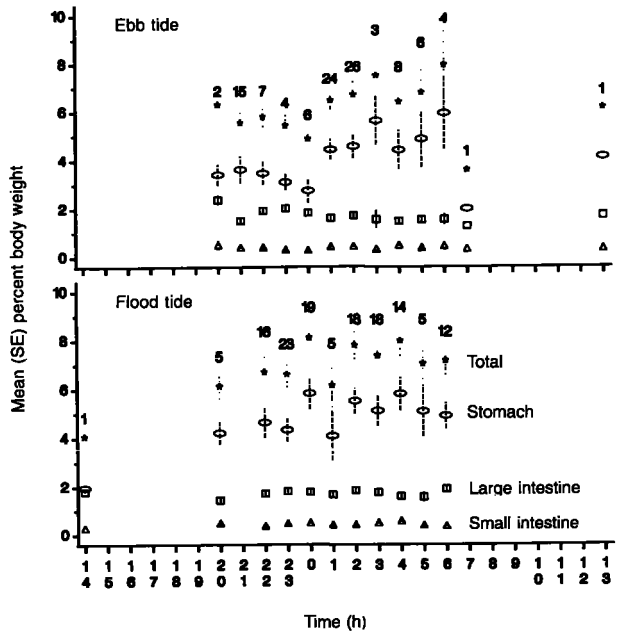

Figure 8

Hourly change in total digestive tract, stomach, large intestine, and small intestine fullness expressed as mean percent of body weight for smooth dogfish caught during ebb (top) or flood tide (bottom). Vertical bars are ranges in percent of body weight for individual fish. Numbers above symbols indicate the number of stomachs sampled during that hour.

and YOY are present May–October (Figs. 2–4). Most adults, however, appear to leave the estuary by mid-July (Rountree, personal observ.). The rarity of adult individuals in our samples results partly because they avoid gear and partly because they do not appear to use the shallow creeks and thus were not captured in weir sampling. However, adults were frequently observed in the bay and are often caught by local fishermen during late spring–early summer (Rountree, personal observ.). The near absence of subadults, however, in our collections may reflect a true rarity in the estuary.

The coincidental arrival of both mature adults and newborn YOY to Mid-Atlantic Bight estuaries suggests that adults use estuaries as a parturition ground. However, we did not observe any evidence of parturition within the estuary during our study, other than the capture of YOY presumably only days old (Rountree, personal observ.). It is not known whether parturition actually occurs in the estuaries or in inshore marine waters (surf zone to inner shelf) or in both. Uncertainty of the importance of estuaries as parturition habitats is underscored by the fact that the use of estuaries and coastal waters is characteristic only for the northern Atlantic population. The same species may only inhabit deeper shelf waters in other areas (Bigelow and Schroeder, 1948; Baughman and Springer, 1950; Hildebrand, 1953).

The size of smooth dogfish at birth has been widely reported as 34–39 cm (Bigelow and Schroeder, 1948; Hildebrand, 1953; Heemstra, 1973; Castro, 1983; Compagno, 1984), despite the fact that Bigelow and Schroeder (1953) later reported size at parturition to be 29–37 cm TL (11.5–14.5 inches). Because we collected post parturition individuals as small as 28 cm TL (Fig. 2), we suggest that a range of 28–39 cm TL at parturition is more accurate. However, we know of no published data on size at parturition, other than anecdotal accounts (Field, 1907; Smith, 1907; Fowler, 1918; Baughman and Springer, 1950; Hildebrand, 1953; Graham, 1967). Until length-frequency data of full-term embryos can be compared with length-frequency data for post parturition YOY, our estimate of 28–39 cm at birth should be used cautiously. Assuming this estimate is correct, we conclude from the size distribution of YOY that parturition of YOY in New Jersey waters occurs from mid-May through July (Figs. 2 and 5). Similar periods of parturition

Table 3

Food habits of 85 young-of-the-year smooth dogfish (mean, 417 mm; range 318–586 mm TL) collected in Little Egg Harbor–Great Bay estuary with gill net, trawl, and hook and line from April to November 1988–90. Percent frequency of prey among stomachs, mean number and weight of prey per stomach, and mean gut fullness index (100 × prey weight/body weight) are given for all prey occurring in at least 1% of the stomachs. The combined rank is a rank of the sum of the ranks for each measure. No stomachs were empty.

Prey species (or category)	Percent frequency	Mean (SE) number	Mean (SE) weight	Mean (SE) fullness	Combined rank
Crangon septemspinosa	65	1.41 (0.20)	0.32 (0.06)	0.21 (0.04)	1
Polychaete	47	0.48 (0.06)	0.17 (0.04)	0.09 (0.03)	5
Unidentified crabs	47	0.48 (0.06)	0.58 (0.13)	0.21 (0.04)	1
Palaemonetes vulgaris	32	1.34 (0.42)	0.54 (0.19)	0.25 (0.08)	3
Callinectes sapidus	12	0.22 (0.06)	0.86 (0.40)	0.27 (0.14)	4
Libinia sp.	9	0.12 (0.04)	0.53 (0.26)	0.14 (0.07)	6
Ovalipes ocellatus	9	0.12 (0.04)	0.22 (0.11)	0.06 (0.03)	7
Miscellaneous	8	0.09 (0.03)	0.04 (0.02)	0.01 (0.01)	11
Unidentified fish	8	0.09 (0.04)	0.07 (0.04)	0.02 (0.01)	8
Unidentified bivalve	7	0.08 (0.03)	0.02 (0.01)	0.01 (0.01)	14
Cancer sp.	5	0.09 (0.04)	0.06 (0.03)	0.02 (0.01)	10
Ensis directus	5	0.05 (0.02)	0.06 (0.03)	0.02 (0.01)	13
Upogebia affinis	2	0.06 (0.03)	0.13 (0.08)	0.04 (0.02)	9
Menidia menidia	2	0.02 (0.02)	0.12 (0.09)	0.04 (0.03)	12
Isopoda	1	0.04 (0.03)	<0.01	<0.01	16
Carcinus maenus	1	0.01 (0.01)	<0.01	<0.01	17
Neopanopeus sp.	1	0.01 (0.01)	<0.01	<0.01	17
Fundulus heteroclitus	1	0.01 (0.01)	0.10 (0.10)	0.04 (0.04)	15
Unidentified shrimps	1	0.01 (0.01)	<0.01	<0.01	17
Pagurus longicarpus	1	0.04 (0.04)	<0.01	<0.01	17
Total crabs	95	1.06 (0.11)	2.26 (0.48)	0.70 (0.16)	
Total shrimps	98	2.76 (0.46)	0.86 (0.20)	0.46 (0.09)	
Total other	89	0.96 (0.11)	0.73 (0.20)	0.29 (0.08)	
Total		4.79 (0.44)	3.85 (0.53)	1.46 (0.18)	

have been reported elsewhere (Bigelow and Schroeder, 1948, 1953; Graham, 1967; Castro, 1983; Compagno, 1984; Hisaw and Abramowitz[1]).

Growth rate

Our estimates of growth rates, based on length-frequency analysis, suggest that smooth dogfish YOY grow very fast during the nursery period (nearly 2 mm TL/day) and attain a size of 55–70 cm TL (mean=63 cm) by the time they leave the estuary in the fall. That such high growth rates are possible is confirmed by a single tag return (out of 17 fish tagged during 1989 weir sampling) in which a YOY male grew 44 mm in 24 days, averaging 1.8 mm TL/day. Similar growth-rate estimates have previously been reported. Hisaw and Abramowitz[1] suggested that smooth dogfish females grow about 20–30 cm per year, which corresponds to lengths of 48–70 cm TL by their first year. Moss (1972) later used tooth width and tooth replacement data to estimate a growth rate of 1.4–1.7 mm TL/day for the first year, which overlaps with our growth-rate estimates (Table 2). Extrapolation from the von Bertalanffy growth curve provided by Moss (1972) suggests that fish reach about 60 cm by the end of their first six months of life (roughly October). This estimate agrees well with our estimate. Moss's (1972) growth estimate also reveals no difference in growth between sexes during the first year, which agrees with our observations.

The significant annual differences in our growth rate estimates probably resulted from annual differ-

ences in the timing of peak abundance of YOY in the weir samples (Fig. 3) and to sampling bias among the gears. The bimodal length-frequency pattern observed in July (Fig. 2) was caused by the later occurrence of YOY during 1989 compared with 1988 (Fig. 3) and results in an increased slope of the regression of length on date for 1989 compared with 1988 and 1990. Bigelow and Schroeder (1953) and Graham (1967) also noted annual variation in peak abundance of YOY. The cause of this annual variation is not known at this time.

The statistically significant differences in the y-intercepts for weight between sexes is puzzling. If real, it suggests that females are larger at birth than males and, given that adult females tend to be larger than adult males (Bigelow and Schroeder, 1948; 1953; Castro, 1983; Compagno, 1984), that this size difference is maintained throughout life despite equal growth rates. However, data on actual size at birth are necessary to confirm this hypothesis.

Habitat use patterns

Smooth dogfish exhibit a strong nocturnal pattern in habitat use. We have previously reported from weir sampling that smooth dogfish appear to use subtidal marsh creeks exclusively during the night (Rountree and Able, 1993). In fact, no dogfish have been collected during the day in the creeks that we studied despite intensive sampling (Table 1). The hourly YOY CPUE pattern in the more recent gill-net sampling supports this observation (Fig. 7). Additionally, smooth dogfish are known to exhibit a nocturnal activity rhythm (Casterlin and Reynolds, 1979a). Also, individuals that were trapped in the creeks by the weir and its wings appeared to become increasingly stressed as low tide approached. Stressed individuals were often observed to thrash around with their heads out of the water. These patterns strongly suggest that YOY smooth dogfish undergo nocturnal tidal migrations in and out of the bay shoal and marsh creek habitats during the night.

Bay shoal habitats may be important YOY habitats within the estuary. Young of the year were very abundant within Foxboro and Story Island creeks, which bordered extensive shoal areas (Fig. 1), but were much less abundant at New Creek and Schooner Creek, which both empty directly into deep channels. Abundances in Foxboro Creek weir samples were significantly greater than in either Schooner or New creek. The low abundance in New Creek weir collections is particularly striking because YOY were abundant in Foxboro Creek despite it being located less than 300 m away. The importance of bay shoals adjacent to marsh creeks is supported by our observations (from informal gill-net sampling) that smooth dogfish were more abundant in Schooner Creek during 1987 prior to dredging of the adjacent shoal (Rountree, personal observ.).

It is noteworthy that smooth dogfish YOY were abundant in subtidal creek weir collections only during June–July (despite regular sampling from April to November) but were abundant in gill-net collections just outside the creeks through October (Figs. 3 and 4). Additionally, YOY captured by weirs in creeks tended to be smaller than those captured by other gears in bay habitats (Fig. 2). These patterns suggest that creek habitats are more important for newborn and smaller individuals than for older and larger individuals.

Foraging habits

The diet of YOY smooth dogfish comprised mainly benthic crustaceans and polychaetes (Table 3). Prey of YOY are typical of the dominant shallow estuarine faunal components in the area (Sogard and Able, 1991; Rountree and Able, 1992; Szedlmayer and Able, in press). The prevalence of *Crangon septemspinosa* and *Palaemonetes vulgaris* in the diet may explain the importance of the creek habitats to the smallest individuals during June and July because abundances of these two prey species exhibit a strong peak in marsh creeks at that time (Rountree and Able, 1992). Although smooth dogfish collected in shallow bay shoal and marsh creek habitats exhibited very full stomachs (Table 3; Fig. 8), the role of foraging behavior in the apparent tidal movements of smooth dogfish into these habitats is uncertain because of our lack of day samples. If the shoal and creek habitats were important foraging habitats, we would expect to see much higher gut fullness during ebb tide (when fishes are presumably leaving the shallows). Instead we observed slightly higher fullness values during flood tide.

The only published data on smooth dogfish feeding habits were produced more than seventy years ago (Fields, 1907; Breder, 1921). Breder (1921) also examined food habits of YOY from New Jersey (based on size information he gives) and reported a similar diet to that presented here. Bigelow and Schroeder (1953) later published a summary of dogfish food habits based on these studies but primarily considered the diet of adults. Interestingly, American lobster, *Homarus americanus*, figured prominently in the food habits of smooth dogfish taken from Cape Cod (Fields, 1907) but were not observed during our study presumably owing to the scarcity of settled juvenile lobsters in southern New Jersey estuaries (although pelagic-stage juveniles are common, [Able, unpubl. data]).

Conclusions

Young-of-the-year smooth dogfish use New Jersey estuaries as nurseries during late spring through fall, when pups grow rapidly to a size of 55–70 cm TL, prior to migration from the estuaries by the end of October. Smooth dogfish make tidal migrations into shallow bay shoal and tidal marsh creek habitats primarily at night, possibly to take advantage of high concentrations of small crustacean prey. As a result, shallow bay shoal and tidal marsh creek habitats appear to be critical nursery areas for smooth dogfish in New Jersey estuaries.

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Morphometry of juvenile and subadult *Loligo pealei* and *L. plei* from the northern Gulf of Mexico

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Abstract.—Two species of *Loligo* are abundant in northern Gulf waters: the long-finned squid, *Loligo pealei*, and the arrow squid, *Loligo plei*. Variability within species and similarities between the species often hamper accurate identification. The two species more closely resemble each other in areas of sympatry, and there is overlap in almost all of the diagnostic characters. Small specimens of *Loligo* are not easily identified, and there are few studies detailing their morphometry. Because of the taxonomic uncertainties associated with the identification of juveniles and subadults of *L. pealei* and *L. plei*, the species were differentiated by isoelectric focusing, and morphometric characters and indices of potential use in species separation were evaluated. Emphasis was placed on those taxonomic characters suitable for use in the field. Best discrimination between the two species was achieved with combinations of measurements of characters and calculated indices associated with cartilaginous structures (funnel cartilage length, gladius width [GW], nuchal cartilage length, and rachis width [RW]) and the shape of the gladius. An arbitrary cutoff in GW/RW ratio of 2.7 (ratio of the greatest width of the gladius to the width of the free rachis at the junction of the vane) correctly classified 100% of the *L. plei* and 91% of the *L. pealei*. The overall shape of the gladius (broader and more rounded in *L. pealei*), presence or absence of marginal ribs in the vane of the gladius, and the nature of the junction of the vane and free rachis (junction gradual and not distinct in *L. pealei*) were also useful in distinguishing the two species.

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Although squid are conspicuous components of the marine ecosystem and form a substantial portion of the invertebrate biomass in the northern Gulf of Mexico, many aspects of their life history and structural characteristics are poorly known. Three species of loliginid squid are abundant in northern Gulf waters (Rathjen et al., 1979): the brief squid, *Lolliguncula brevis* (Blainville 1823), the long-finned squid, *Loligo pealei* Lesueur 1821 (also known as the longfin inshore squid [Roper et al., 1984]), and the arrow squid, *Loligo plei* Blainville 1823. The lack of knowledge about the species of *Loligo* in the Gulf can, in part, be attributed to the difficulties in identifying juveniles. Recent interest in locating new or underutilized squid species, or both, and the recognition of the importance of documenting changes in marine biodiversity have increased emphasis on the need to improve taxonomic resolution in this important invertebrate group.

Although the adults of *L. pealei* and *L. plei* have been described by numerous authors (e.g. Haefner, 1964; LaRoe, 1967; Cohen, 1976; Roper et al., 1984), variability within species and similarities between the species often hamper precise identification. Species variability has been documented in the long-finned squid, *L. pealei*. Cohen (1976) noted that populations of long-finned squid varied widely both within and between geographic areas. In areas of sympatry with *L. plei*, the two species more closely resemble each other, and with the exception of gladius shape and the hectocotylus in adult males, there

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is overlap in all other diagnostic characters (Cohen, 1976). This problem is particularly acute in the northern Gulf of Mexico, where the two species are common. Hixon (1980) noted that all external characters and morphometric indices overlapped in immature specimens taken in waters off Texas. Difficulties in separating the species were best summarized by LaRoe (1967) who stated, "there are differences between the species, but there is a continuum between them in their range of variation for most characters; there appear to be no distinct boundaries to separate the two species."

The purpose of this study is to examine variability in morphological characteristics between juveniles and subadults of *L. pealei* and *L. plei* in the northern Gulf of Mexico and to determine diagnostic criteria for their identification. Emphasis is placed on taxonomic characters suitable for use in the field. Because of the taxonomic uncertainties associated with identification of immature and small specimens of the two *Loligo* species, an electrophoretic technique (isoelectric focusing) was used to establish species-specific protein patterns. Biochemical differentiation of species provided more accurate assessment of morphological variability between the two species. This contrasts with previous studies in which morphological variability was assessed by using specimens identified by morphological criteria.

Materials and methods

Field procedures

Squid samples were collected by personnel of the National Marine Fisheries Service, Mississippi Laboratories, Pascagoula, Mississippi, aboard the National Oceanic and Atmospheric Administration Ship RV *Oregon II*. Samples used here were obtained during the Southeast Area Monitoring and Assessment Program (SEAMAP) resource survey Cruise 93-03 (205), conducted from 6 June to 21 July 1993. Otter-trawl samples (n=230) were taken in an area from 88° to 97°30'W (Mobile, Alabama to Brownsville, Texas) in depths from 9 to 110 meters (Fig. 1). Station selection and field processing procedures followed established SEAMAP protocol.[1] All specimens of *Loligo*

[1] Nichols, S., and G. Pellegrin. 1989. Trends in catch per unit effort for 157 taxa caught in the Gulf of Mexico Fall Groundfish Survey, 1972–88. Summary Rep., Mississippi Laboratories, NMFS, NOAA, 158 p.

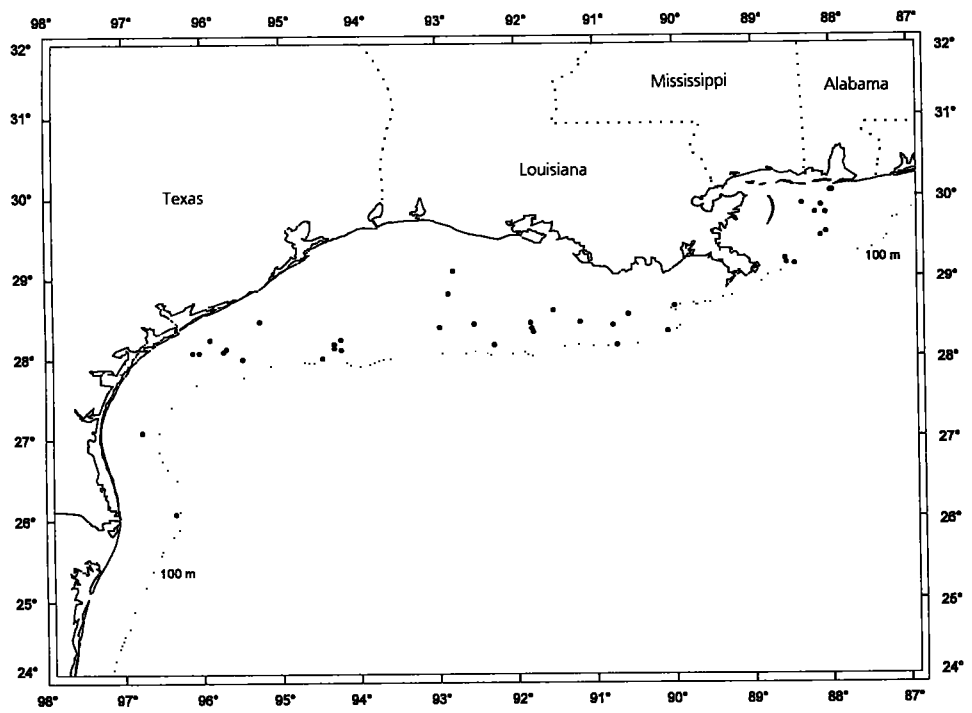

Figure 1

Location of trawl stations in the northern Gulf of Mexico where *Loligo pealei* and *Loligo plei* were collected.

were sorted from the trawl samples, counted, and weighed. They were frozen (–20°C) on board within two hours of capture to deter tissue degradation. Large, more readily identifiable squids were frozen separately for later use in biochemical determinations of species-specific protein patterns, whereas the smaller squids from each station were frozen together. All samples were sealed in polyethylene bags in which the air had been squeezed out to prevent freezer-burn during storage. The frozen squids were placed in chilled containers for transportation from the ship to the Gulf Coast Research Laboratory (GCRL), Ocean Springs, Mississippi, following completion of the cruise. Squids were stored at –20°C in the laboratory.

Laboratory procedures

Initial research efforts centered on establishing nonvariant protein patterns that could be used to separate the two *Loligo* species. Ten large specimens of each *Loligo* species (greater than 200-mm mantle length) were selected from the frozen samples and tentatively identified at GCRL with the morphological criteria provided by Bane and Wagner,[2] Voss (1956), LaRoe (1967), Cohen (1976), and Roper et al. (1984). These criteria included shape of the hectocotylus in males, overall body shape, the size and shape of the fins, and the dentition of the tentacular suckers. A sample of mantle tissue was removed from each squid, refrozen, and stored at –70°C. Frozen squids were shipped on dry ice to the National Museum of Natural History, Washington, D.C., for confirmation of field identifications. Following verification of identification of specimens based on morphological criteria, mantle tissue from each individual was analyzed electrophoretically and diagnostic protein bands were determined.

To evaluate morphometric parameters of potential value in field separation of *L. plei* and *L. pealei*, specimens of juvenile and subadult *Loligo* spp. (n=304) ranging in size from 29.0 to 238.0 mm mantle length (ML) were selected from the squid samples frozen in the field. Squids were selected from each of three geographic areas over the complete range of depths sampled (less than 18 m, 18–36 m, 37–55 m, 56–73 m, 74–110 m) within each area. Designation of geographic areas followed Nichols and Pellegrin[1]: Texas (Brownsville to Galveston), West Delta (Galveston, TX, to the Mississippi River), and East Delta (Mississippi River to Mobile, AL). Juvenile and subadult squids were selected from 41 stations without regard to probable species or sex. Specimens were thawed, individually numbered, and weighed to the nearest 0.1 g. Visual inspection for the presence of nidamental glands or the spermatophoric sac was used to separate females from males.

The diagnostic measurements and indices used by Voss (1956), Haefner (1964), Cohen (1976), and Hixon (1980) were reviewed for their potential usefulness in taxonomic resolution of the *Loligo* species. Eleven morphometric measurements and selected indices (ratios of measured characters) of potential value in separating species and sex within a species were determined (Table 1; Fig. 2).

Morphometric characters were measured with digital calipers to the nearest 0.1 mm. Because some individuals were damaged, the number of measured characters per individual varied. Squids >100.0 mm ML were not well represented in the sample aliquot. Large males of both *L. pealei* and *L. plei* were included in the aliquot, but there were few females of similar size. For that reason, size limitations were placed on the data used in regression analyses, with

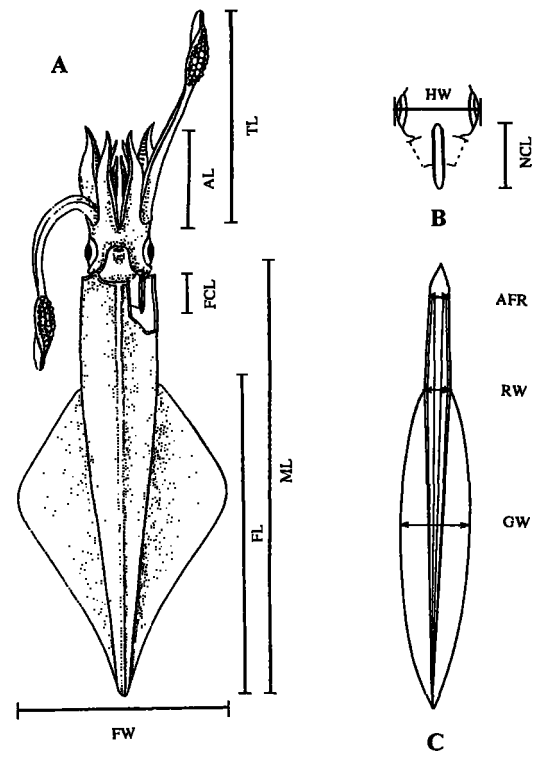

Figure 2

Morphometric characters measured for *Loligo pealei* and *Loligo plei* : (**A**) ventral view, modified from Roper et al. (1984); (**B**) head, dorsal view, from Cohen (1976); (**C**) gladius. Abbreviations are defined in Table 1.

[2] Bane, G. W., and A. Wagner. 1985. Key to important squids of the northern Gulf of Mexico. Coastal Fisheries Institute, Center for Wetland Resources, Louisiana State Univ., Baton Rouge, LA, LSU-CFI-85-21, 10 p.

the limits dependent upon the size-frequency distribution of the specimens. Size-class ranges for tests of sexual dimorphism were from 50.0 to 150.0 mm ML for *L. pealei* and from 40.0 to 110.0 mm ML for *L. plei*. When characters and indices were compared between the two species, squids from 20.0 to 150.0 mm ML were used in the analyses. Both individual characters and indices were regressed against mantle length to determine their potential value in differentiating species, or sex within a species, for squids of a given size.

After external measurements were recorded for each squid, the mantle was opened and the gladius removed. Drawings of the gladii were made by means of photocopies of the actual gladii as patterns. A piece of mantle tissue was taken from each squid, frozen immediately, and stored at –70°C. Specimens were refrozen and stored at –20°C.

Isoelectric focusing (IEF), a technique which separates proteins according to their isoelectric points along a continuous pH gradient (Righetti et al., 1990), was used to characterize mantle protein patterns. Mantle tissue was minced and then homogenized in BSS buffer (0.05 M Tris at pH 7.5, 0.25 M sucrose, 0.01 M KCl, 0.01 M $MgCl_2$, 0.001 M $CaCl_2$, 0.001 M phenylmethylsulfonyl fluoride) with an Ultra-Turex™ (Type TP 18/10 S1) homogenizer. The homogenate from each squid was centrifuged separately at 14,000 RPM (23,460 RCF) for 20 minutes at 4°C with a Beckman™ Model J-21C refrigerated centrifuge. The supernatants were recovered and frozen separately at –70°C. Total protein in each supernate was measured (Bio-Rad™ Bradford Protein Assay Kit) in order that the same amount of protein (35 µg) was loaded in each lane of the gel.

Isoelectric focusing separations were made in 0.5-mm polyacrylamide gels with an LKB Ultraphor™ apparatus. Proteins were separated with ampholytes of the 4.0–6.5 pH range by using 0.1 M glutamic acid as the analyte and 0.1 M beta-alanine as the catholyte. The gels were prefocused at 2,000 V for 30

Table 1

Morphometric characters and indices in *Loligo pealei* and *Loligo plei*.

Parameter	Definition[1]
Measured characters	
AFR (anterior free rachis)	Width of free rachis at terminus of marginal ribs
AL (arm length)	Length of right arm IV from proximalmost sucker to arm tip (left if right arm missing)
FCL (funnel cartilage length)	Greatest length of entire right funnel cartilage
FL (fin length)	Fin length from point on dorsal mantle midway between anterior fin insertion, to posterior body tip
FW (fin width)	Greatest width of both fins between lateralmost points
GW (gladius width)	Greatest width of gladius vane
HW (head width)	Greatest head width at level of eyes (head strongly ventrodorsally compressed between two fingers)
ML (mantle length)	Mantle length, from dorsal anterior margin to posterior end
NCL (nuchal cartilage length)	Greatest length of entire nuchal cartilage
RW (rachis width)	Width of gladius rachis at junction of vane
TL (tentacle length)	Length of right (left if right tentacle missing) tentacle from junction of arms III and IV to tip
W (weight)	Specimen wet weight to the nearest 0.1 g
Morphometric indices	
AL/ML	Arm length: mantle length index
FCL/ML	Funnel cartilage length: mantle length index
FL/ML	Fin length: mantle length index
FW/FL	Fin width: fin length index
FW/ML	Fin width: mantle length index
GW/ML	Gladius width: mantle length index
GW/RW	Gladius width: rachis width index
HW/ML	Head width: mantle length index
NCL/FCL	Nuchal cartilage length: funnel cartilage length index
NCL/ML	Nuchal cartilage length: mantle length index
RW/ML	Rachis width: mantle length index
TL/AL	Tentacle length: arm length index
TL/ML	Tentacle length: mantle length index
W/ML	Wet weight: mantle length index

[1] Modified from Cohen (1976).

minutes. The samples were then loaded and focused for 3 hours at 2,000 V. The gels were fixed, washed with destaining solution, and stained with Coomassie Blue R-250. They were washed again in destaining solution, dried, and photographed. Protein bands from the juvenile and subadult squids were compared with protein bands from the positively identified adult specimens for species identification.

Statistical analysis of data

Two approaches were used in morphometric analysis of data: comparisons were made between species and by sex within each species. All data were analyzed with Statgraphics Plus, Version 7.1 computer software. Student's *t*-test (α=0.05) was used to compare the means of indices to determine if any index could be used to distinguish between the two species or between sexes within a species. Both linear and multiplicative regression techniques were employed to examine the relation of each measured character and each index (dependent variable) to mantle length (independent variable). Correlation coefficients (r) and coefficients of determination (r^2) were calculated for each regression to measure strength of the relationship and goodness of fit of the calculated regression line, respectively.

Coefficients of determination were considered high when 85% of the total observed variability was accounted for by the mathematical model. Tests were conducted for differences in the slopes of the regression lines. The null hypothesis was that there was no significant difference (α>0.05) between the slopes. A discriminant analysis was employed to identify the relative contribution of measured characters or indices, or both, in discriminating between the two species. For each individual, the characters and indices were entered with their respective species classification codes. Analyses were performed as follows: 1) all characters, 2) all indices, and 3) selected characters or indices, or both (singly or in combination), based on discriminant function coefficients. From these analyses, characters or indices (or both), were ranked by comparing their percentage success in species differentiation.

Figure 3

Protein electrophoretic patterns of mantle tissue from *Loligo pealei* and *Loligo plei* (numbers=pH, letters=protein bands).

Table 2

Isoelectric points (pH) used to separate *Loligo pealei* and *Loligo plei*.

Band	pH	Species
a[1]	5.97	*L. plei*
b[1]	5.60	*L. plei*
c	5.41	*L. plei, L. pealei*
d	5.02	*L. plei, L. pealei*
e[2]	4.89	*L. pealei*
f	4.76	*L. plei, L. pealei*

[1] Unique to *L. plei*.
[2] Unique to *L. pealei*.

Results

Biochemical analyses

Isoelectric focusing patterns of mantle tissue proteins are shown in Figure 3. Proteins used to differentiate between the species were labeled *a* through *f* according to their decreasing order of isoelectric points (Table 2). Both species had unique protein bands and were easily separated: bands *a* and *b* were unique to *L. plei* and band *e* to *L. pealei*. Bands *c*, *d*, and *f* were shared by both species.

General description of juveniles and subadults

In fresh specimens, the chromatophores of the mantle generally are red in color in *L. plei* and brown in *L.*

pealei. Color, however, is not a reliable means of separating the species. Well-defined lines of chromatophores ("flame stripes") occur on the ventral surface of the mantle in large males of *L. plei*; however, specimens of *L. pealei* also may have a similar, though less defined, color pattern. The mantle is long, slender, and cylindrical in both *L. pealei* and *L. plei*, but the posterior end of the mantle is more acutely pointed in *L. plei*. Juvenile and subadult *L. pealei* are more robust than *L. plei* of similar mantle length: the head and eyes of the former species are moderately large and the arms and tentacles are thick, muscular, and long. The more robust character of *L. pealei* is particularly evident when compared with *L. plei* of the same mantle length. The fins are rhomboidal in shape in both species.

Fin length as a percentage of mantle length is variable in individuals of both species, but it is generally greater in *L. pealei* than in *L. plei* in specimens of similar mantle length (Table 3). Mean fin length in relation to mantle length of *L. pealei* was 50% in the size class 90.0 to 99.9 mm, and the mean ratio increased as mantle length increased. However, fin length to mantle length ratio of individual *L. pealei* could be 50% in specimens as small as 70.0 mm ML; the ratio of FL to ML was not consistently 50% or greater until the individual mantle length reached 110.0 mm. For *L. plei*, the ratio of fin length to mantle length was less than 50% for individual squid smaller than the 120.0 to 129.9 mm ML size class. Mean fin length to mantle length did not exceed 50% until size class 140.0 to 149.9 mm ML.

Morphometric analyses

Individual measurements were taken of 304 juvenile and subadult squids (*L. pealei*, n=151; *L. plei*, n=153). All specimens were immature according to the maturity classification scheme of Macy (1982). The relationships between fin length and mantle length, fin width and mantle length, and rachis width and mantle length were best represented by the linear model. The relationships between weight, head width, funnel cartilage length, nuchal cartilage length, gladius width, arm length, and tentacle length, with mantle length as the independent variable, were best represented by the multiplicative model. All indices were best represented by the linear model.

Sexual dimorphism

Loligo pealei Sex could be determined for only 36% of the specimens identified as *L. pealei* (n=62). Males

Table 3

Fin length in relation to mantle length in *Loligo pealei* and *Loligo plei*.

Mantle length (mm)	Fin length as % of mantle length							
	L. pealei				*L. plei*			
	n	Mean	±SD	Range	n	Mean	±SD	Range
20–29.9	0				1	20.7		
30–39.9	1	37.6			9	27.2	±3.3	18.1–29.5
40–49.9	27	37.6	±2.6	31.7–42.6	22	31.5	±3.1	26.3–37.6
50–59.9	47	40.6	±2.8	33.3–45.3	44	34.6	±2.3	26.9–38.7
60–69.9	16	43.2	±1.9	40.5–46.4	41	36.7	±2.1	33.1–40.3
70–79.9	9	46.2	±2.4	43.5–50.8	12	39.2	±2.0	35.8–42.9
80–89.9	7	47.0	±2.9	41.7–52.2	9	41.7	±1.3	39.9–43.9
90–99.9	13	50.0	±3.9	42.5–57.1	5	44.3	±2.9	40.0–47.5
100–109.9	5	50.4	±1.8	47.8–53.2	3	46.0	±2.1	43.5–48.7
110–119.9	4	52.0	±1.9	50.4–55.2	0			
120–129.9	8	53.4	±3.1	49.7–58.6	3	47.8	±1.3	46.6–49.6
130–139.9	4	55.8	±1.6	53.4–57.6	1	47.5		
140–149.9	3	54.9	±0.9	54.1–56.1	1	50.5		
150–159.9	1	54.3			1	51.7		
160–169.9	0				1	53.4		
170–179.9	2	56.2	±1.7	54.5–57.9	0			
180–189.9	0				0			
190–199.9	2	59.5	±0.5	59.0–60.0	0			
≥200	2	59.8	±1.5	58.3–61.3	0			

used in statistical analyses ranged in size from 50.0 to 147.0 mm and females from 64.0 to 140.0 mm ML. Results of statistical analyses of tests of sexual dimorphism for characters and indices are shown in Table 4.

Coefficients of determination (r^2) were high for both males and females for AL, FCL, FL, GW, NCL, RW, and W when regressed on mantle length. The slopes of the regression lines were similar between sexes for W and GW, but females were heavier than males (Fig. 4) and had a broader gladius (Fig. 5). There were also no significant differences between males and females in the slopes of the regression lines for AL, FCL, FL, NCL, and RW, and the 95% confidence intervals of the regression intercepts overlapped. Fin width was highly correlated with ML only in females. Overlap occurred in all measured characters.

Significant differences were found in the slopes of the regression lines only for W/ML. With the exception of W/ML in females, all indices had low coefficients of determination. Means of the indices of FW/ML, GW/ML, GW/RW, and RW/ML were significantly higher in females than in males; however, overlap was high.

Loligo plei Sex could be determined for 51% of the specimens identified as *L. plei* (n=73). Males used in statistical analyses ranged in size from 52.0 to 107.0 and females from 46.0 to 101.0 mm ML. Results of statistical analyses of tests of sexual dimorphism for characters and indices are shown in Table 5.

No significant differences were found between the sexes in the slopes of the regression lines for any of the characters. Weight (Fig. 6) and GW (Fig. 7) were highly correlated to ML in both males and females; however, there was no significant difference in the slopes of the regression lines, and the 95% confidence intervals of the regression intercepts overlapped. Females were heavier than males of similar length, and the gladius was broader in female specimens. Fin length and RW were also highly correlated with ML but, as with W and GW, there was no significant difference in the slopes of the regression lines and the 95% confidence intervals of the regression intercepts overlapped. Fin width, FCL, and NCL were highly correlated with mantle length only in males.

With the exception of FCL/ML in males, all indices had low coefficients of determination. There were significant differences in the means of FW/FL,

Table 4

Statistical tests of sexual dimorphism in *Loligo pealei* (sample sizes are given in parentheses). Abbreviations are defined in Table 1. NS = not significant.

	AL	FCL	FL	FW	GW		
Male (r^2)	0.85 (27)	0.92 (28)	0.97 (28)	0.81 (28)	0.95 (28)		
Female (r^2)	0.88 (18)	0.93 (19)	0.96 (19)	0.90 (19)	0.93 (19)		
Slope test	NS	NS	NS	NS	NS		
	HW	NCL	RW	TL	W		
Male (r^2)	0.62 (28)	0.95 (28)	0.90 (28)	0.50 (22)	0.96 (28)		
Female (r^2)	0.67 (19)	0.96 (19)	0.92 (19)	0.62 (15)	0.98 (19)		
Slope test	NS	NS	NS	NS	NS		
	AL/ML	FCL/ML	FL/ML	FW/FL	FW/ML	GW/ML	GW/RW
Male (r^2)	0.00 (27)	0.64 (28)	0.64 (28)	0.56 (28)	0.00 (28)	0.17 (28)	0.03 (28)
Female (r^2)	0.15 (18)	0.74 (19)	0.53 (19)	0.20 (19)	0.05 (19)	0.00 (19)	0.05 (19)
Slope test	NS	NS	NS	NS	NS	NS	NS
t-test of means	NS	NS	NS	NS	P=0.0097	P<0.0001	P=0.0076
Means (M, F)	0.58, 0.60	0.15, 0.16	0.50, 0.51	1.08, 1.14	0.53, 0.58	0.15, 0.17	2.99,3.17
	HW/ML	NCL/FCL	NCL/ML	RW/ML	TL/AL	TL/ML	W/ML
Male (r^2)	0.50 (28)	0.49 (28)	0.14 (28)	0.33 (28)	0.21 (22)	0.21 (22)	0.87 (28)
Female (r^2)	0.41 (19)	0.29 (19)	0.56 (19)	0.08 (19)	0.09 (15)	0.25 (15)	0.95 (19)
Slope test	NS	NS	NS	NS	NS	NS	P=0.0145
t-test of means	NS	NS	NS	P=0.0241	NS	NS	NS
Means (M, F)	0.21, 0.22	1.22, 1.20	0.18, 0.19	0.050, 0.052[1]	2.67, 2.68	1.55, 1.61	0.38, 0.41

[1] Difference between means is small but t-test is significant.

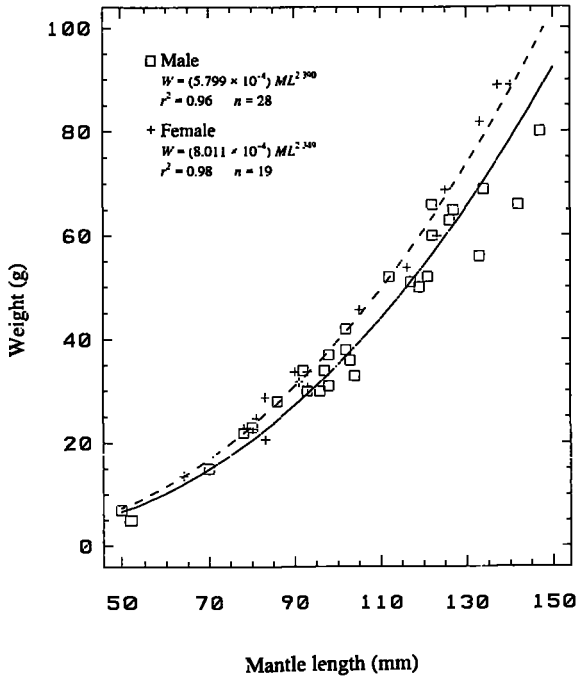

Figure 4

Regression of weight (W) on mantle length (ML) for male and female *Loligo pealei*.

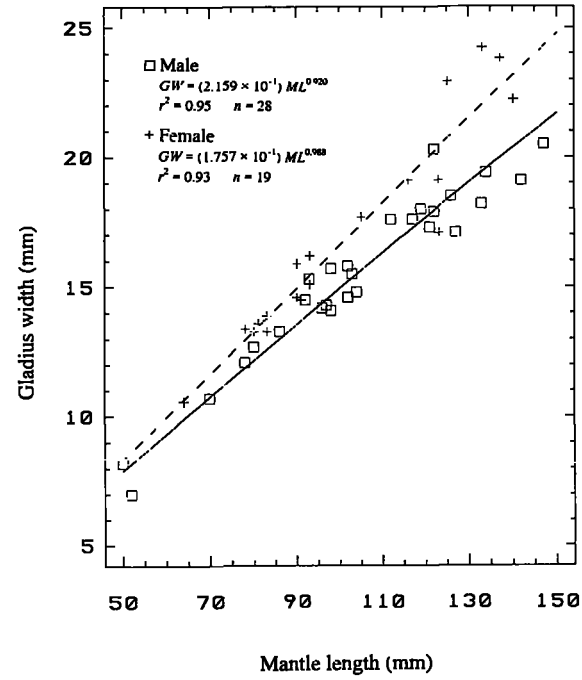

Figure 5

Regression of gladius width (GW) on mantle length (ML) for male and female *Loligo pealei*.

Table 5

Statistical tests of sexual dimorphism in *Loligo plei* (sample sizes are given in parentheses). Abbreviations are defined in Table 1. NS = not significant.

	AL	FCL	FL	FW	GW		
Male (r^2)	0.73 (14)	0.88 (14)	0.97 (14)	0.90 (14)	0.96 (14)		
Female (r^2)	0.60 (51)	0.53 (51)	0.97 (51)	0.83 (50)	0.86 (50)		
Slope test	NS	NS	NS	NS	NS		
	HW	NCL	RW	TL	W		
Male (r^2)	0.59 (14)	0.91 (14)	0.90 (14)	0.39 (9)	0.93 (14)		
Female (r^2)	0.28 (51)	0.66 (51)	0.86 (50)	0.58 (36)	0.92 (51)		
Slope test	NS	NS	NS	NS	NS		
	AL/ML	FCL/ML	FL/ML	FW/FL	FW/ML	GW/ML	GW/RW
Male (r^2)	0.59 (14)	0.91 (14)	0.80 (14)	0.49 (14)	0.01 (14)	0.39 (14)	0.06 (14)
Female (r^2)	0.03 (51)	0.61 (51)	0.74 (51)	0.50 (50)	0.01 (50)	0.10 (50)	0.09 (50)
Slope test	NS	NS	NS	NS	NS	NS	NS
t-test of means	NS	NS	NS	P=0.0322	NS	P<0.0001	P=0.0012
Means (M, F)	0.50, 0.49	0.14, 0.14	0.39, 0.38	1.13, 1.22	0.44, 0.46	0.13, 0.14	2.08, 2.24
	HW/ML	NCL/FCL	NCL/ML	RW/ML	TL/AL	TL/ML	W/ML
Male (r^2)	0.69 (14)	0.51 (14)	0.61 (14)	0.41 (14)	0.19 (9)	0.54 (9)	0.73 (14)
Female (r^2)	0.45 (51)	0.21 (51)	0.50 (51)	0.36 (50)	0.00 (36)	0.10 (36)	0.77 (51)
Slope test	NS	NS	NS	NS	NS	NS	NS
t-test of means	NS	NS	NS	NS	NS	NS	NS
Means (M, F)	0.20, 0.20	1.17, 1.17	0.16, 0.17	0.06, 0.06	3.08, 3.18	1.52, 1.58	0.16, 0.15

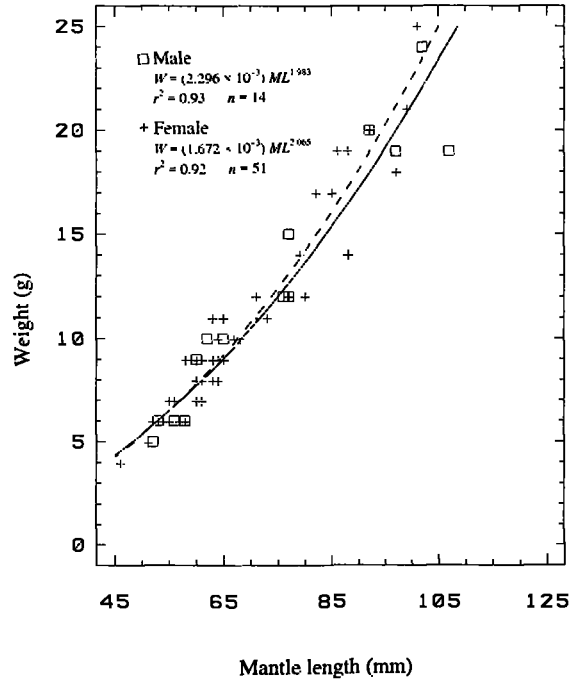

Figure 6

Regression of weight (W) on mantle length (ML) for male and female *Loligo plei*.

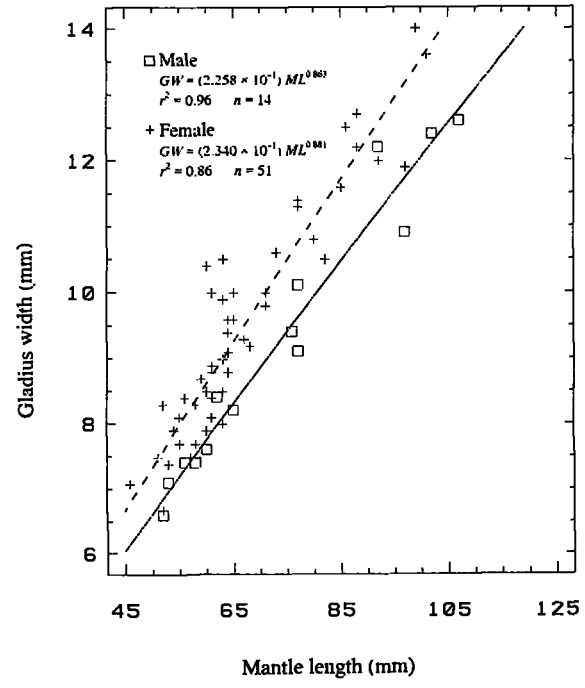

Figure 7

Regression of gladius width (GW) on mantle length (ML) for male and female *Loligo plei*.

GW/ML, and GW/RW, and means were higher for these indices in females. Overlap occurred in all indices.

Species comparisons

The specimens of *Loligo pealei* used in species comparisons ranged in size from 37.0 to 147.0 mm ML, whereas specimens of *L. plei* ranged in size from 29.0 to 148.0 mm ML. Results of statistical analyses of tests of species comparisons for characters and indices are shown in Table 6.

There were significant differences in the slopes of the regression lines for all characters except HW and RW. Variability in W was low in both species and overlap occurred in only the smaller size classes (Fig. 8). Coefficients of determination also were high for FL, FW, GW, NCL, and RW in both species; however, overlap occurred in all characters (Figs. 9–13, respectively). Arm length and FCL were highly correlated with mantle length only in *L. pealei*.

Significant differences occurred in the slopes of the regression lines for the following indices: AL/ML, FCL/ML, FL/ML, FW/FL, GW/ML, NCL/ML, RW/ML, TL/AL, and W/ML. With the exception of W/ML for *L. pealei*, the coefficients of determination were low. Although little of the variability was explained by the regression lines for GW/RW regressed on mantle length, a scatter plot of the GW/RW ratios showed minimal overlap; thus this index may have predictive value in separating juveniles and subadults of the two species (Fig. 14). Significant differences were found between mean indices for all but FW/FL and NCL/FCL. Mean indices were greater in *L. pealei* for all ratios with the exception of RW/ML and TL/AL.

Overlap was high for all indices with the exception of GW/RW. Both the scatter plot (Fig. 14) and frequency histogram (Fig. 15) showed relatively low overlap in the GW/RW indices. The GW/RW index was higher for *L. pealei* in most instances. Only 9% of the *L. pealei* specimens were in the range of overlap, and this overlap was more common in smaller squid, including a distinct mode of small *L. pealei* within the GW/RW range of *L. plei* (Fig. 15).

Discriminant function coefficients were highest for cartilaginous structures. Results of discriminant analyses showed that no character, index, or combination of the two, classified *L. pealei* with 100% accuracy (Fig. 16; Table 7). Rachis width in combination with NCL enabled separation at an accuracy level of 93%, and in combination with FCL or GW separated 95% of the specimens of *L. pealei*. Indices that allowed separation of *L. pealei* from *L. plei* at accuracy levels of 92% and above included the GW/RW

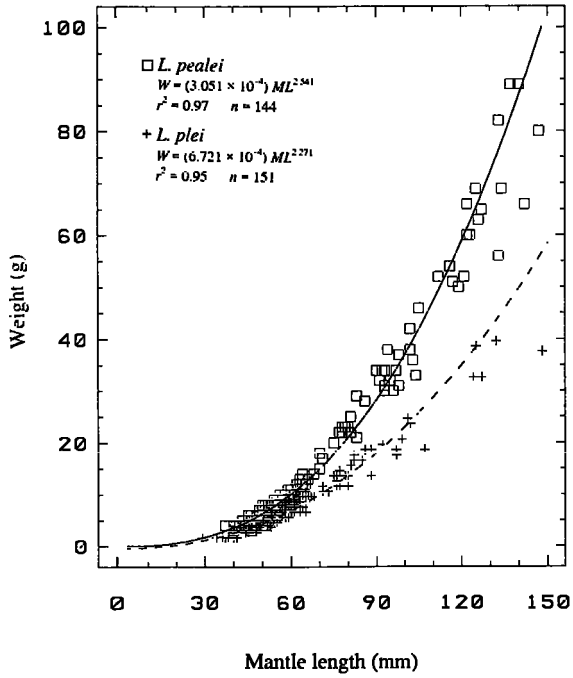

Figure 8

Regression of weight (W) on mantle length (ML) for *Loligo pealei* and *Loligo plei*.

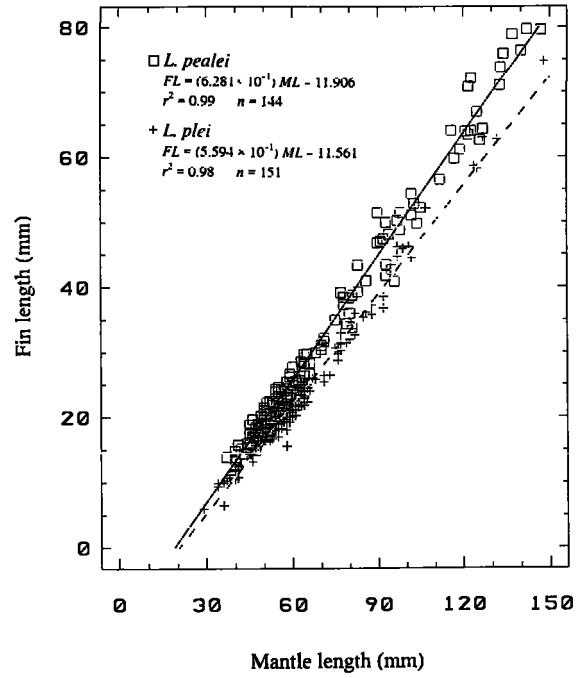

Figure 9

Regression of fin length (FL) on mantle length (ML) for *Loligo pealei* and *Loligo plei*.

Table 6

Species comparison of characters and indices for *Loligo pealei* and *Loligo plei* (sample sizes are given in parentheses). Abbreviations are defined in Table 1. NS = not significant.

	AL	FCL	FL	FW	GW		
L. pealei (r^2)	0.94 (141)	0.95 (144)	0.99 (144)	0.93 (143)	0.96 (143)		
L. plei (r^2)	0.75 (151)	0.84 (151)	0.98 (151)	0.91 (150)	0.90 (150)		
Slope test	P=0.0130	P<0.0001	P<0.0001	P<0.0001	P=0.0022		
	HW	NCL	RW	TL	W		
L. pealei (r^2)	0.71 (143)	0.97 (144)	0.94 (144)	0.84 (106)	0.97 (144)		
L. plei (r^2)	0.66 (151)	0.91 (151)	0.89 (150)	0.66 (109)	0.95 (151)		
Slope test	NS	P<0.0001	NS	P=0.0133	P<0.0001		
	AL/ML	FCL/ML	FL/ML	FW/FL	FW/ML	GW/ML	GW/RW
L. pealei (r^2)	0.00 (141)	0.65 (144)	0.78 (144)	0.44 (143)	0.01 (143)	0.02 (143)	0.02 (143)
L. plei (r^2)	0.10 (151)	0.61 (151)	0.76 (151)	0.48 (150)	0.00 (150)	0.17 (150)	0.00 (150)
Slope test	P=0.0011	P=0.0001	P=0.0102	P=0.0017	NS	P=0.0006	NS
t-test of means	P<0.0001	P<0.0001	P<0.0001	NS	P<0.0001	P<0.0001	P<0.0001
Means (*L. pealei*, *L. plei*)	0.59, 0.49	0.17,0.15	0.44, 0.36	1.27, 1.24	0.55, 0.44	0.16, 0.14	3.13, 2.18
	HW/ML	NCL/FCL	NCL/ML	RW/ML	TL/AL	TL/ML	W/ML
L. pealei (r^2)	0.19 (143)	0.44 (144)	0.33 (144)	0.00 (144)	0.34 (105)	0.36 (106)	0.95 (144)
L. plei (r^2)	0.47 (151)	0.26 (151)	0.45 (151)	0.17 (150)	0.00 (109)	0.06 (109)	0.86 (151)
Slope test	NS	NS	P<0.0001	P<0.0001	P=0.0005	NS	P<0.0001
t-test of means	P<0.0001	NS	P<0.0001	P<0.0001	P=0.0080	P<0.0001	P<0.0001
Means (*L. pealei*, *L. plei*)	0.25, 0.20	1.15, 1.17	0.19, 0.17	0.05, 0.06	2.98, 3.13	1.75, 1.51	0.23, 0.13

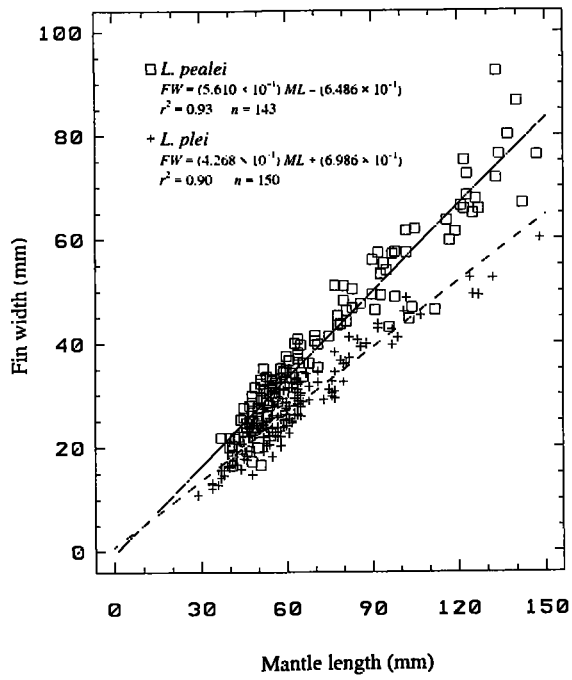

Figure 10

Regression of fin width (FW) on mantle length (ML) for *Loligo pealei* and *Loligo plei*.

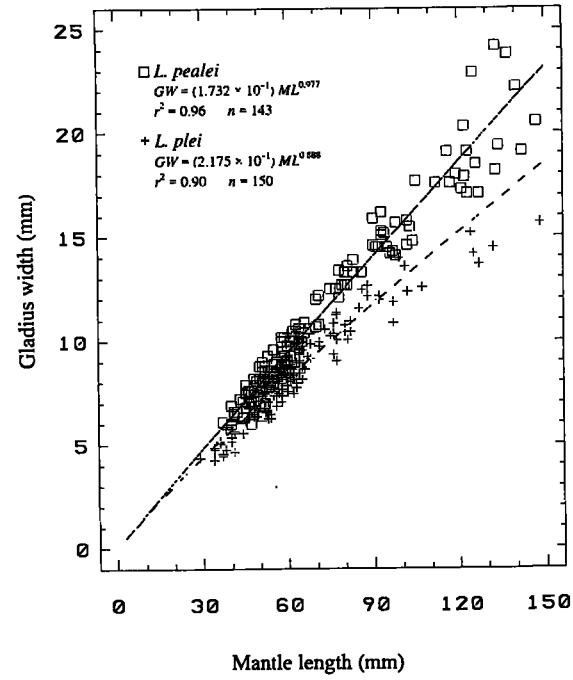

Figure 11

Regression of gladius width (GW) on mantle length (ML) for *Loligo pealei* and *Loligo plei*.

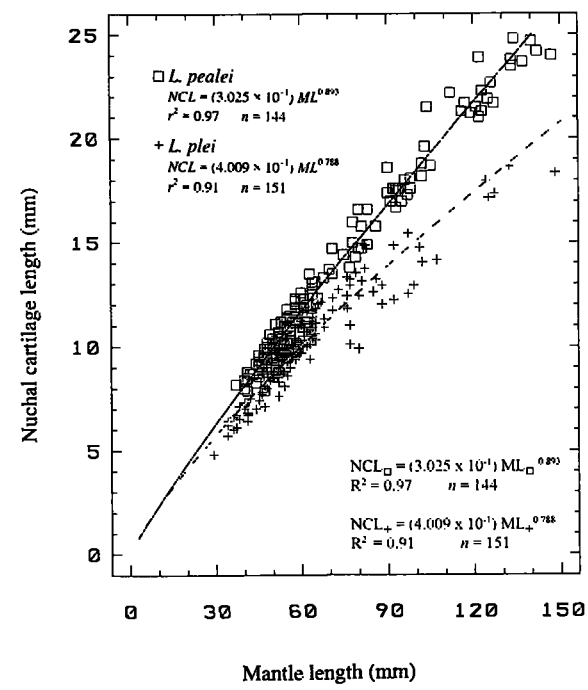

Figure 12

Regression of nuchal cartilage length (NCL) on mantle length (ML) for *Loligo pealei* and *Loligo plei*.

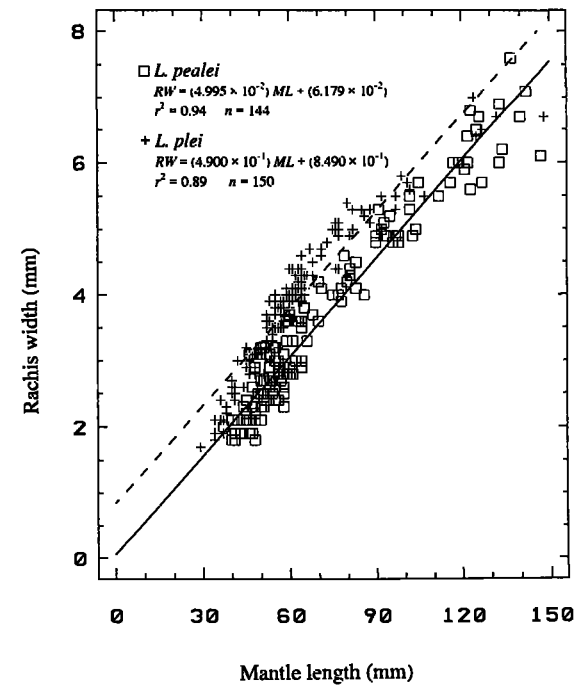

Figure 13

Regression of rachis width (RW) on mantle length (ML) for *Loligo pealei* and *Loligo plei*.

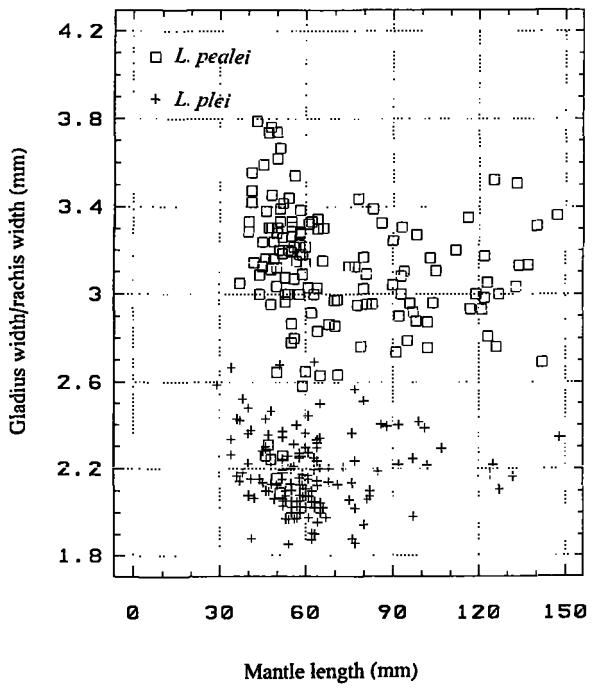

Figure 14
Cluster plot of gladius width/rachis width (GW/RW) on mantle length (ML) for *Loligo pealei* and *Loligo plei*.

ratio alone and this index in combination with either FCL/ML, GW/ML, NCL/ML or RW/ML. The RW/ML ratio in combination with FCL/ML, GW/ML, or NCL/ML provided for similar levels of accuracy. In contrast, *L. plei* could be correctly classified at 100% accuracy with the combination of FCL and RW (Table 8). Correct classification levels of 98% and 99% were obtained when RW was combined with GW or NCL, respectively. High levels of separation in *L. plei* also occurred with the indices GW/RW or RW/ML in combination with selected indices (Table 8). With the GW/RW index alone, 98% of the *L. plei* specimens were correctly classified.

Structure of the gladius

The gladius in *L. pealei* is broad and feather-shaped in all specimens (Fig. 17, A and B). The gladius is more rounded in females than in males. The greatest gladius width occurs at the mid-point of the vane. The ratio of the greatest width of the gladius to the greatest width of the rachis ranges from 2.26 to 3.36 in males and from 2.74 to 3.52 in females. The rachis has a single median rib with marginal ribs on each side that fuse in the posterior 1/3 of the rachis. The anterior and posterior tips of the rachis are pointed. The vane is broad and without ribs. The

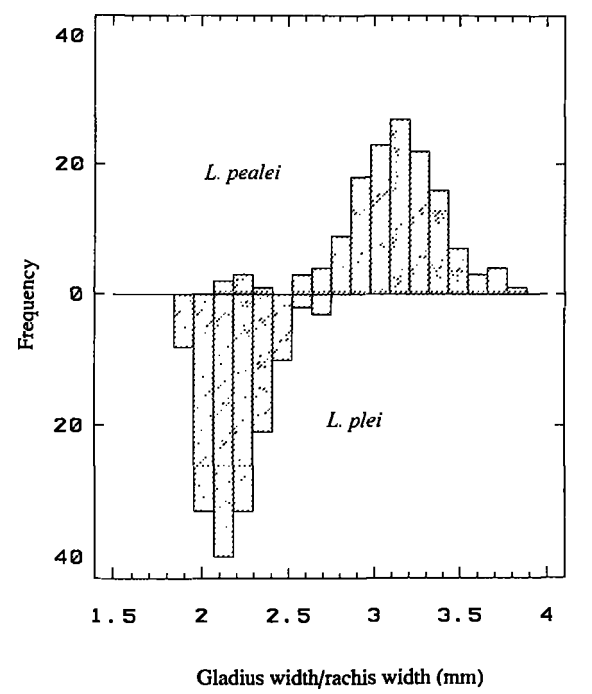

Figure 15
Frequency histogram for gladius width/rachis width (GW/RW) for *Loligo pealei* and *Loligo plei*.

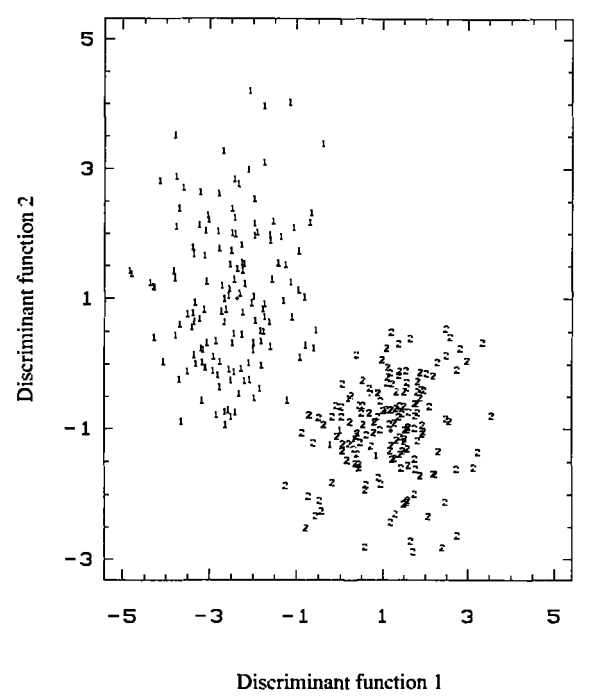

Figure 16
Discriminant analysis plot for *Loligo pealei* (function 1) and *Loligo plei* (function 2).

margins of the vane are curved, thin, and converge both anteriorly and posteriorly. The junction of the rachis and the vane is gradual and not distinct. The free rachis tapers anteriorly from the junction of the vane to the terminus of the marginal ribs. The ratio of AFR/RW ranges from 0.633 to 1.100 in males and from 0.684 to 0.946 in females.

The gladius in *L. plei* is slender and sword-shaped in all specimens (Fig. 17, C and D). The greatest gladius width in males occurs in the anterior 1/4 of the vane. In females, the greatest width occurs near the mid-point of the vane. The ratio of the greatest width of the gladius to the greatest width of the rachis ranges from 1.85 to 2.34 in males and from 1.98 to 2.69 in females. One median rib occurs on the rachis with marginal ribs on each side that fuse in the posterior 1/3 of the rachis. Anterior and posterior tips of the rachis are very pointed. The vane tapers both anteriorly and posteriorly. The junction of the rachis and the vane is abrupt and distinct. The vane in both sexes has marginal ribs that gradually curve inward, anterior to the midpoint of the vane. The lateral margins of the vane are usually straighter in males than in females. The posterior tip of the rachis is less flexible than the anterior tip owing to the convergence and fusion of the ribs of the vane and the rachis. The thickness of the ribs in both the rachis and the vane increases with increasing size of the specimen. The ribs usually are more pronounced in males than in females. The ribs in the vane of small specimens are distinguishable only as a color variation when held up to the light. The free rachis tapers from the junction of the vane to the terminus of the marginal ribs. The ratio of AFR/RW ranges from 0.701 to 1.043 in males and from 0.829 to 1.360 in females.

Table 7

Percent *Loligo pealei* separated from *Loligo plei* by using cartilaginous structures (sample sizes are given in parentheses). Abbreviations are defined in Table 1.

	FCL	GW	NCL	RW	
FCL	49 (151)	61 (150)	69 (151)	95 (151)	
GW		46 (150)	46 (150)	95 (150)	
NCL			45 (151)	93 (151)	
RW				61 (151)	
	FCL/ML	**GW/ML**	**GW/RW**	**NCL/ML**	**RW/ML**
FCL/ML	72 (151)	81 (150)	95 (150)	79 (151)	93 (151)
GW/ML		83 (150)	92 (150)	86 (150)	95 (150)
GW/RW			92 (150)	93 (150)	93 (150)
NCL/ML				77 (151)	92 (151)
RW/ML					88 (151)

Table 8

Percent *Loligo plei* separated from *Loligo pealei* by using cartilaginous structures (sample sizes are given in parentheses). Abbreviations are defined in Table 1.

	FCL	GW	NCL	RW	
FCL	83 (153)	80 (152)	80 (153)	100 (152)	
GW		79 (152)	82 (152)	98 (152)	
NCL			82 (153)	99 (152)	
RW				53 (152)	
	FCL/ML	**GW/ML**	**GW/RW**	**NCL/ML**	**RW/ML**
FCL/ML	73 (153)	82 (152)	98 (152)	75 (153)	95 (152)
GW/ML		77 (152)	98 (152)	81 (152)	98 (152)
GW/RW			98 (152)	99 (152)	99 (152)
NCL/ML				75 (153)	97 (152)
RW/ML					87 (152)

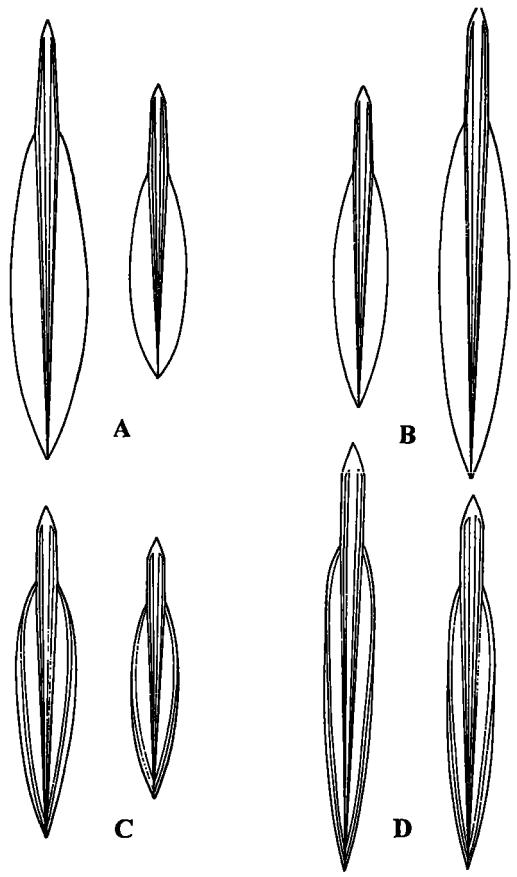

Figure 17
Illustrations of gladii traced from photocopies: *Loligo pealei* (**A**) female (**B**) male; *Loligo plei* (**C**) female (**D**) male.

Discussion

Isoelectric focusing of mantle proteins seems to provide a reliable means of distinguishing between the two species of *Loligo* in the Gulf of Mexico and to enable accurate identification of small, immature specimens. Garthwright et al. (1989) also biochemically separated *L. plei* and *L. pealei* but used the technique of horizontal starch gel electrophoresis. Morphometric analyses provided information on sexual dimorphism within the species and on species differences and similarities in specimens from the northern Gulf of Mexico, already identified to species by means of IEF.

Comparisons of morphometric characters and indices between males and females of each species were made in an effort to determine their value as a rapid means for fishery biologists to distinguish the sexes in the field. Although statistically significant differences were evident in many of the selected morphometric characters and indices, both between sexes within a species and between species, the differences were small and overlap usually was high. The majority of squids examined in this study were between 40.0 and 80.0 mm ML, and greatest overlap in characters and indices occurred in this size range.

Tests of sexual dimorphism in measured characters regressed against mantle length for *L. pealei* indicated no significant differences between males and females in the slopes of the lines for W and GW. Females were heavier than males and the GW was broader in females than in males in all size classes. Weight and GW also were highly correlated to ML in both males and females of *L. plei*; however, no significant difference existed in the slopes of the lines, and the 95% confidence intervals of the regression intercepts overlapped. Differences in weight between males and females were more pronounced in *L. pealei*. Haefner (1964) noted little difference in the weight–length relationship between males and females of *L. pealei* below 95 mm ML; however, at mantle lengths greater than 95 mm ML, females began to outweigh males. Hixon (1980) also found that the rate of increase in weight per unit increase in mantle length was faster in females than in males. Both Haefner (1964) and Hixon (1980) attributed this faster rate of increase in females to sexual maturation and the increase in weight of the female reproductive structures. For northernmost populations of *L. pealei* off New England, females less than 170.0 mm ML generally weighed less than males (Lange and Johnson, 1981). Maturation at smaller sizes in southern populations of long-finned squid could account for this difference in the weight–length relationship between females and males in comparisons of data for northern and southern populations. Both Cohen (1976) and Hixon (1980) noted that *L. pealei* seems to mature at smaller sizes in the warmer portion of its range. Width of the gladius also has been linked to sexual maturation in female *Loligo*. Cohen (1976) noted that in mature females the broadest portion of the gladius, the vane, covers the full ovary and may provide support and protection for the eggs. In the present study, the gladius was broader in females of both species.

Although there were differences in morphometric characters and indices between sexes within a species, these differences were subtle and usually were more apparent in larger specimens. The high overlap both in measured characters and in indices precluded their use as a reliable means of distinguishing the sexes in juvenile and subadult specimens. Gender-specific morphological characters (e.g. hectocotylus or sexual organs) appear to be the only precise means of differentiating males and females of the two species. In those specimens in which these characters are undeveloped, no way was discovered to distinguish between the sexes.

Juvenile and subadult *L. pealei* and *L. plei* overlapped in all measured characters. For those characters in which there was a significant difference in the slopes of the regression lines and for which the coefficients of determination were high (FL, FW, GW, NCL, and W), the overlap generally was higher in the smaller size classes. Differences in W, NCL, and GW were more pronounced in larger specimens. Increases in measured characters per unit increase of mantle length were higher in *L. pealei*.

Both Cohen (1976) and LaRoe (1967) reported differences in fin lengths between *L. pealei* and *L. plei* and suggested that this character could be used to differentiate between the two species. Cohen (1976) found that fin length in relation to mantle length was similar in both species in small specimens. However, she noted that fin length was equal to or greater than half the mantle length of *L. pealei* when mantle length exceeded 55.0 mm, whereas fin length was equal to or greater than half the mantle length in specimens of *L. plei* only after mantle length exceeded 95.0 mm. Fin length/mantle length proportions in the present study corroborate these data for juvenile and subadult specimens from the northern Gulf of Mexico. Fin lengths were less than 50% of the mantle length in both species in all specimens under 70.0 mm ML. In *L. pealei*, the mean fin length of specimens from 90.0 to 99.9 mm ML was equal to 50% of the mantle length, and this percentage increased with increasing size. Fin length in relation to mantle length was 50% in *L. plei* only at mantle lengths of 120.0 mm and larger. LaRoe (1967) also listed width of the gladius and length of the funnel cartilage as useful characters to separate the species; however, Cohen (1976) noted that the overlap in values for these characters negated their usefulness. The present data show overlap in GW in all but the larger size classes. Overlap in FCL was more prevalent in smaller size classes, but in specimens greater than 90.0 mm ML, it may be a useful character.

The shape of the gladius and the area of the junction of the vane and free rachis were distinct in both species over the size range of individuals examined. The gladius in *L. pealei* was broader and more rounded than was the gladius in *L. plei*. It was feather-shaped in all specimens and the vane was without ribs. The junction of the vane and the free rachis was gradual and not distinct. The gladius in *L. plei* was more slender, elongated, and resembled a sword or dagger in shape. Ribs in the vane were more obvious in larger specimens. The lateral margins of the vane were usually straighter and the ribs in the vane were more pronounced in males than in females. The junction of the vane and free rachis was abrupt and distinct.

The best discrimination between the two *Loligo* species was based on combinations of measurements of the characters and calculated indices associated with cartilaginous structures. Funnel or nuchal cartilage lengths combined with rachis width measurements or indices enabled greatest percent separation of the species. Characters and indices based on gladius shape also had high percentage levels of separation. Highest correct classification of *L. pealei* (95%) by discriminant analysis was achieved by combining RW with either FCL or GW or by combining the GW/ML and RW/ML indices. *Loligo plei* were classified with 100% accuracy by combining FCL and RW.

Numerous studies cite the GW/RW ratio as a reliable index for species differentiation. Roper et al. (1984) summarized taxonomic data for the two species and reported GW/RW ratios from 2.4 to 3.7 for *L. pealei* and from 1.5 to 2.4 for *L. plei*. Cohen (1976), Whitaker (1978), and Hixon (1980) also used the GW/RW index to distinguish the two species of *Loligo* and used the ratio of 2.4 to differentiate between the species: below 2.4 for *L. plei* and above 2.4 for *L. pealei*. The present study is the first to use IEF to identify juvenile and subadult *L. pealei* and *L. plei* and thus provides a more accurate base from which to assess morphological variation between the species. The GW/RW ratios in the present study ranged from 1.9 to 2.7 for *L. plei* and from 2.1 to 3.8 for *L. pealei*. Separation of the species was best accomplished with a GW/RW ratio of 2.7. Applying the ratio of 2.4 to the present data resulted in overlap in both species; 10% of the *L. plei* had an index greater than 2.4, and 4% of the *L. pealei* had an index below 2.4. By using 2.7 as the critical value, all the *L. plei* were separated and 91% of the *L. pealei* could be identified. Hixon (1980) also found specimens of *L. plei* with GW/RW ratios above 2.4. He identified 21 mature females and one male *L. plei* from Texas waters with GW/RW indices ranging from 2.4 to 2.9. He attributed the greater index in the females to the wider vane associated with sexually mature individuals. This does not explain the higher GW/RW indices recorded for some specimens of *L. plei* in this study, because all individuals were immature. Also puzzling are the specimens of *L. pealei* with GW/RW ratios below 2.7. Because all specimens in the present study were identified biochemically, errors in identification should be negligible. According to Cohen (1976), *L. pealei* is composed of morphologically variable populations and greater variation occurs in areas where *L. pealei* co-occurs with *L. plei*. In these areas of sympatry, there is a closer resemblance between species. Cohen (1976) found a single specimen of *L. pealei* with a GW/RW ratio below 2.4, and this specimen was from an area where both species occur. The possibility of

genetic introgression was considered by Cohen (1976), but currently there is no evidence of hybridization between any of the loliginid species.

The original intent of this study was to examine selected morphometric characters of potential value in differentiating the two common species of *Loligo* in the field. Juvenile and subadult squids comprise a substantial portion of the invertebrate biomass in the northern Gulf of Mexico, and difficulty in separating the species of *Loligo* has been a contributing factor in our lack of knowledge of this group. No single character or index enabled 100% separation of the species in the size classes of squid under study. Overlap was high in many of the measured characters and indices and precluded their use as reliable determinants of species. LaRoe (1967) and Cohen (1976) also found high overlap in measured characters and indices for the two species and suggested that more than one character or index had to be used to separate the species. In the present study, combinations of characters or indices associated with cartilaginous structures (FCL, GW, NCL, and RW) enabled greatest percent separation.

The single GW/RW ratio of 2.7 enabled correct identification of 91% of *L. pealei* and 100% of *L. plei*. This percent separation was similar to that achieved in the discriminant analysis for the GW/RW ratio. The most practical method for separation of the species in the field is use of the 2.7 GW/RW ratio in conjunction with the overall shape of the gladius, including the presence or absence of marginal ribs.

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Queen conch, *Strombus gigas*, in fished and unfished locations of the Bahamas: effects of a marine fishery reserve on adults, juveniles, and larval production

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Abstract.—Marine fishery reserves (MFR's) have been set aside in coastal areas throughout the world with the hope of reversing population decreases commonly observed in many marine resources. In this study, a comparison of population structure of the commercially important gastropod *Strombus gigas*, queen conch, was made between a fished area and an MFR in the Exuma Cays, central Bahamas. There were 31 times more adult conch on the shallow (<5 m) Great Bahama Bank in the MFR, and in a survey at 7 depth intervals (to 30 m) on the island shelf in the Exuma Sound, mean adult density was always higher in the MFR, by as much as 15 times. Shell length and lip-thickness measurements indicated that adults in the MFR migrate with age from bank nursery sites into deeper sound water, whereas those on the bank in the fished area were harvested before reaching water sufficiently deep to protect them from free-diving fishermen. Although sparsely distributed juveniles in shallow-water (<15 m) habitats of the sound were the primary source of adults in the fished area, large juvenile aggregations on the bank also contributed to the deep-water adult stock in the MFR.

Total larval densities in the MFR were frequently an order of magnitude higher than those found in the fished area, and densities of late-stage larvae were 4 to 17 times higher. Because the surface current along the Exuma Cays shelf flows to the northwest, late-stage larvae found inside the reserve must have been spawned outside the reserve; thus the high densities of juvenile and adult conch are the result of natural accumulation of larvae in the area, as well as the result of protection from fishing. Although the fate of larvae dispersed from the reserve is uncertain, it is likely that high numbers of reproductive stock and larvae in the reserve have a significant positive effect on populations in the northern Exuma Sound. Designs of reserves that consider ontogenetic requirements of the target species and strategic locations for larval production, import, export, and metapopulation dynamics will optimize fishery benefits for the many marine vertebrate and invertebrate species that possess pelagic larvae.

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In coastal areas throughout the world, tracts of coastline, reef, and banks known to be important spawning or nursery grounds for economically significant species are being set aside as marine fishery reserves (MFR's). Fishing in such areas is either controlled or prohibited to conserve or enhance production of selected species. Bohnsack (1990) listed 21 potential advantages of fishery reserves including important ecological benefits such as 1) protection of reproductive stocks and genetic diversity, 2) maintenance of the age and social structure of populations, 3) maintenance of areas of undisturbed critical habitat, 4) supplemental restocking of fished areas through emigration, and 5) provision for a larval source for recruitment to surrounding areas. Numerous other advantages of reserves relate to data collection and enforcement of regulations. Surveys of the literature (Roberts and Polunin, 1991; Dugan and Davis, 1993; Rowley, 1992) have yielded evidence that, in most cases, abundance and size of protected species increase within reserves, but there are few data to support the other predicted advantages (see also Roberts and Polunin, 1991; Polunin and Roberts, 1993).

Many fish and invertebrates produce planktonic larvae; therefore, in order to enhance fishery yields in the surrounding waters, an MFR must be located such that its larval production is exported to suitable habitats and to fished areas. Whether or not reserves are sources of recruitment for areas outside the protected waters is debated by environmental scientists, managers, and user groups. There are virtually no data to speak for or against the larval export benefit (Carr and Reed, 1993), although theoretical models incorporating the concepts of metapopulation dynamics indicate that MFR's should provide for larval recruitment to fished areas (Man et al., 1995). Similarly, there is little information on the emigration of

postsettlement fishes and invertebrates from MFR's into fished areas. A recent study (Rakitin and Kramer, 1996), designed to test for emigration of 24 fish taxa from the Barbados Marine Reserve, did not provide conclusive proof that the reserve allowed for exportation of fishes into the surrounding waters. Without solid data, managers will continue to face criticism from fishermen and other special interest groups that reserves are of no advantage to them or the environment.

In this study, a comparison of population structure of the commercially and culturally significant gastropod *Strombus gigas*, queen conch, was made between a fished area and an MFR in the Exuma Cays, an island chain in the central Bahamas (Fig. 1A). The fished area was near Lee Stocking Island,

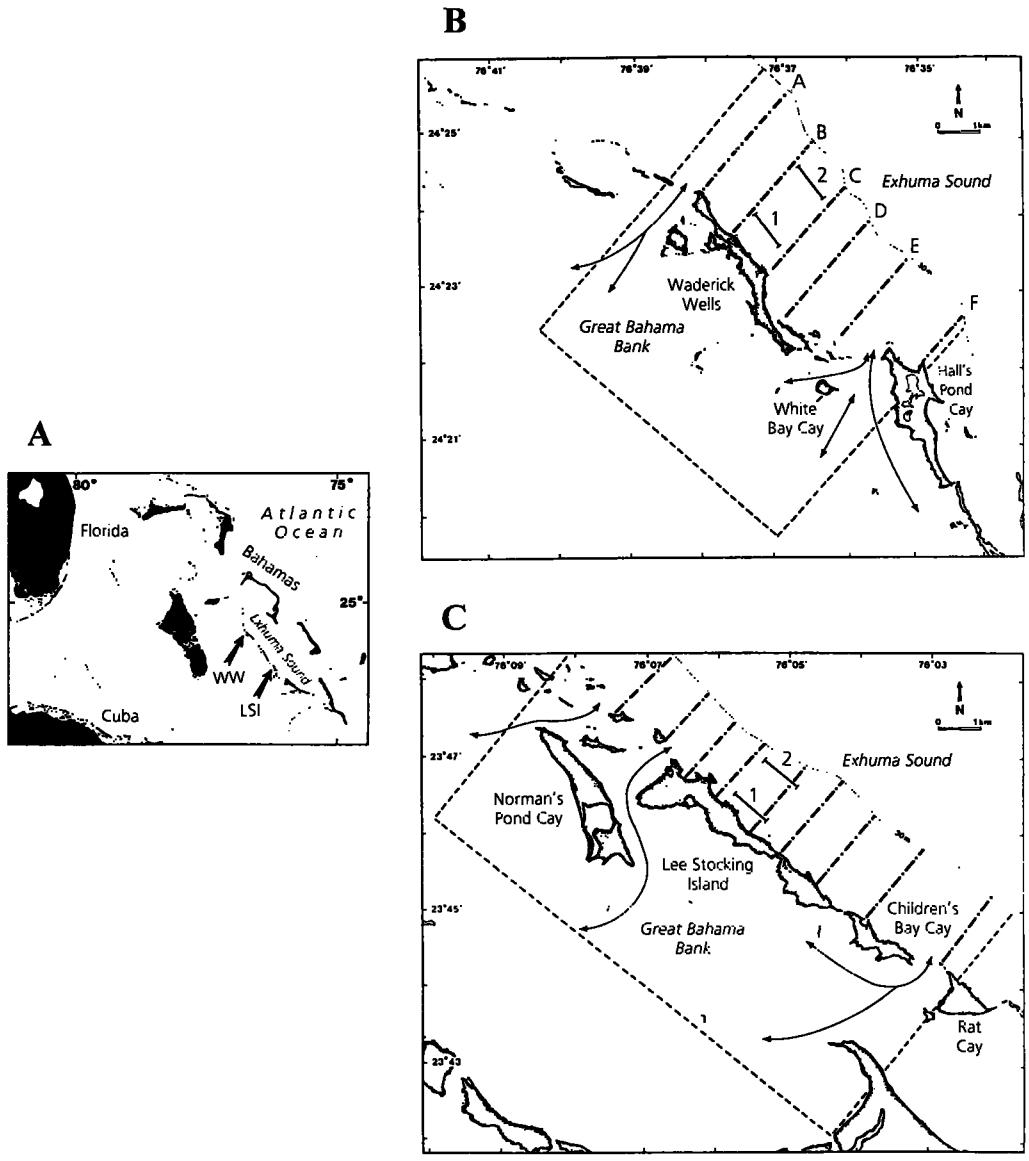

Figure 1

Maps showing 2 study sites in the Exuma Cays, central Bahamas (A). Waderick Wells (WW) (B) is located within the boundaries of a marine fishery reserve, but fishing is allowed near Lee Stocking Island (LSI) (C). In the detailed maps (B, C), dot-dash lines represent survey transects, solid lines with arrows indicate direction and extent of tidal flow, and solid lines labeled 1 and 2 show location of the inshore and offshore plankton tows. Area within the dashed lines and the 30-m isobath comprised the entire survey area.

at the southern end of the chain (Fig. 1C), and the MFR was 87 km north near Waderick Wells in the Exuma Cays Land and Sea Park (Fig. 1B). Our objectives were 1) to test the perceived benefits of an MFR by quantifying differences in densities of adults, juveniles, and larvae; 2) to consider physical-oceanographic mechanisms for such differences with respect to the open nature of the population; 3) to compare abundance patterns with data reported from other regions; 4) to determine sources of adult conch; and 5) to make management recommendations for a species that has been heavily exploited in many Caribbean locations.

Subject species

The natural history of the queen conch is relatively well known. The species is indigenous to subtropical and tropical waters of the western Atlantic from Bermuda and southern Florida to Venezuela and Trinidad (Abbott, 1974). Several egg masses, each containing ~400,000 eggs, are laid by females on clean sand during the summer season (Robertson, 1959; Stoner and Sandt, 1992). Larvae hatch in 3–5 d and live in the upper 5–10 m of the water column for 16–28 d, feeding on phytoplankton (Brownell, 1977; Davis et al., 1993; Stoner and Davis, in press, a). Vertical migration appears to be slight (Barile et al., 1994), and the larvae drift passively on near-surface currents (Stoner and Davis, in press, b). Genetic studies (Mitton et al., 1989; Campton et al., 1992) and analysis of queen conch larval life history and ocean currents in the Caribbean region (Davis et al., 1993) suggest that larvae can travel long distances to colonize seagrass nursery grounds where they settle and feed.

Young conch feed on seagrass detritus and algae (Randall, 1964; Stoner and Waite, 1991) and migrate into deeper water with age (Weil and Laughlin, 1984; Stoner and Schwarte, 1994). At 3.5–4 yr, queen conch reach sexual maturity, cease to grow in shell length, and begin to form the characteristic flared shell lip that thickens with age (Egan, 1985; Appeldoorn, 1988). Longevity is at least 6–7 yr (Berg, 1976) and may reach 26 yr in deep-water habitats (Coulston et al., 1987). Fishing regulations in the Bahamas prohibit the taking of any nonlipped (i.e. juvenile) queen conch and the use of SCUBA gear for any kind of fishing. A general lack of conch at depths >30 m has been attributed to low abundance of plant foods at such depths (Randall, 1964; Adams, 1970).

In 1990, the economic value of queen conch taken from the Caribbean region was estimated at $40 million (US) (Appeldoorn, 1994a). However, as a result of severe overfishing throughout its range (Berg and Olsen, 1989; Appeldoorn, 1994a), queen conch was considered commercially threatened worldwide in 1983 (Wells et al., 1983) and, in 1992, it was added to Appendix II of the Convention on International Trade in Endangered Species (CITES). Fisheries have been closed seasonally or for multiyear periods in areas of Venezuela, Colombia, Belize, Mexico, Cuba, and the U.S. Virgin Islands. Despite closure in Florida (since 1985) and Bermuda (since 1978), stock recovery has been slow (Appeldoorn, 1994a).

Methods

Study sites

The Exuma Cays island chain comprises more than 100 small islands that extend northwest to southeast in the central Bahamas, separating Exuma Sound from the Great Bahama Bank (Fig. 1). The bank is a shallow platform covered with sand and seagrass meadows. In the sound, the island shelf extends from land out 1–3 km to a steep shelf edge beginning at ~30 m depth. At both Lee Stocking Island (LSI) (Fig. 1C), where fishing is allowed, and at Waderick Wells (WW) (Fig. 1B), within an MFR, habitats in the depth range of 2.5–15 m include sand, coral rubble, algal-gorgonian hard-bottom, and seagrass. The hard-bottom is covered with the short turf of the green alga *Cladophoropsis* sp. in many subtidal locations. Beyond 15 m, the habitat is mostly sand and large coral ridges with some hard-bottom. Most of the rocky eastern shore of WW lacks beaches, and water depth close to shore is typically 2 m. At LSI, small sandy beaches lie in protected coves at certain locations between rocky headlands.

Water exchange between the bank and sound occurs through numerous passes that separate the islands, creating extensive tidal flow fields on the bank. At LSI (Fig. 1C), most queen conch reproductive activity occurs in the sound on the island shelf, where adults live in highest densities and juveniles are rare (Stoner and Schwarte, 1994). Larvae are carried through the tidal passes and settle onto the bank (Stoner et al., 1994; Stoner and Davis, in press, b) (Fig. 1, B and C). Discrete juvenile aggregations, with densities of 0.1–1.3 conch/m^2 (most >80 mm shell length), occur on the bank in the same general locations year after year (Wicklund et al., 1991; Stoner and Ray, 1993; Stoner et al., 1996) and may cover 5–600 ha. Most aggregations are located within 5 km of inlets on the Great Bahama Bank in beds of the seagrass *Thalassia testudinum* (Stoner et al., 1994).

The Exuma Cays Land and Sea Park, recognized as a protected area in 1958, extends 40 km along the

Exuma Cays and 13 km across the bank and sound to comprise 456 km^2. A full-time warden enforces park regulations, which strictly prohibit the collection of any plants or animals. This investigation was conducted near the island of Waderick Wells (Fig. 1B) where the park headquarters are located and fishing regulations are best enforced. The study area was well within the park boundaries, 10 km from the southern boundary of the park and 24 km from the northern boundary.

Adult surveys

For a comparison of fished and unfished areas, density surveys for adult queen conch were conducted on the bank and the island shelf, from beach to shelf edge, in the Exuma Sound near LSI between March and September 1991 (Stoner and Schwarte, 1994) and near WW in 1994 in this study. Annual surveys for adult conch conducted at selected sites off LSI, where fishing is allowed, showed little interannual variation in population size (Stoner and Sandt, 1992) and provide justification for the comparison of population densities in different years. Between 1988 and 1991, maximum variation from the mean population size was just 19%; the population was 4% above average in 1991. Adult densities at an important reproductive site at 18 m depth off LSI (Stoner and Sandt, 1992) differed only 8% between 1991 and 1994. Given the relative stability of adult conch populations at LSI and the long adult life (probably >20 years; Coulston et al., 1987), we concluded that surveys from WW and LSI could be compared. In addition, intrasite comparisons of conch density and age structure provided some of the most compelling evidence for the effects of fishing on the recruitment and population size. For direct comparison, survey methods for this study were similar to those used by Stoner and Schwarte (1994).

Near WW in the MFR, the bank survey area extended 7.5 km along the long axis of the island and 5 km southwest from the channels north and south (Fig. 1B), comprising 3,245 ha. Throughout this area, a snorkeler was towed behind a small boat for a total of 47 km while counting the number of adult conch within a 6-m-wide field of view and recording the locations in which adults were abundant. Tows were made along a total of 12 transects which ran perpendicular to WW. These transects started near the western shores of the primary islands and were less than 1 km apart. Latitude and longitude for the beginning and end of each transect were recorded with Global Positioning System (GPS). This resulted in direct observation of a surface area of 28.0 ha. Densities of adult conch were calculated for the transects, and the number of conch was extrapolated for the entire area.

To test the hypothesis that depth distribution of adults differed between the 2 sites, depth-stratified surveys for adult conch were conducted in Exuma Sound along 6 transects which ran perpendicular to WW. Transect A ran northeast from the north tip of WW, and transect F ran northeast from the north end of Hall's Pond Cay (Fig. 1B). Other transects were spaced as uniformly as possible between A and F, 1–2 km apart. Along each transect, estimates of conch density were made at 7 depth intervals: just off the beach (when present), 2.5–5 m, 5–10 m, 10–15 m, 15–20 m, 20–25 m, and 25–30 m. Within each interval, two SCUBA divers swam for 8–30 minutes, depending on depth, holding a line (8 m) between them and counting the number of adult conch that lay beneath the line. One diver carried a calibrated flow meter to calculate the distance traveled. To compensate for the potential influence of current on distance measured, the divers swam from the boat anchor into any discernible current and back, covering two parallel, nonoverlapping paths that normally ran parallel to the isobaths. Thirty-six dives were made during this shelf survey for adult conch density. The mean swim distance was 360 m (SD=6 m). Sampling effort was lowest for the 25–30 m interval because of diving limitations imposed by depth; however, the surface area of this deepest sampling zone was relatively small (Table 1). Again, results were directly comparable with Stoner and Schwarte (1994).

A bathymetric chart of the island shelf east of WW (to 45 m) was created from 250 points for which depth (corrected for tidal state) and position (determined with GPS) were recorded from a small boat. Computer-generated contour lines (1 m) were resolved with normal smoothing algorithms. Surface areas for each contour interval were calculated, and the mean density of conch found during the dive surveys was extrapolated to determine total number for each depth interval.

To examine age distribution and to evaluate potential migration patterns at WW, shell length and shell lip thickness were measured for at least 50 individuals at each depth interval on the shelf and for 213 individuals collected from several locations on the bank. Although young adults laid down lip material faster than older adults and although shells are subject to erosion, shell thickness at the lip provides a relative indication of conch age (Appeldoorn, 1988; Stoner and Sandt, 1992).

To test for differences in size and age distribution associated with depth, frequency distributions of shell length and shell lip-thickness data were analyzed by depth interval with the nonparametric Kolmogorov-Smirnov test. Several aspects of shell

Table 1

Comparison of the total abundance and density of adult queen conch, *Strombus gigas*, in the marine fishery reserve near Waderick Wells and in the fished area near Lee Stocking Island. Estimates for total abundance were extrapolated from bathymetric data and conch density surveys conducted in each habitat and range of depth. Values for adult density are mean ±SE; numbers in parentheses are the number of surveys at each depth.

	Marine fishery reserve			Fished area		
Habitat and depth (m)	Adults (no./ha)	Area (ha)	Total no. of conch	Adults (no./ha)	Area (ha)	Total no. of conch
Bank	53.6	3,245	174,080	1.7	3,997	6,816
Shelf						
0–2.5	0 ±0 (2)	158	0	0 ±0 (4)	161	0
2.5–5	34 ±22 (6)	200	6,871	2.2 ±1.7 (7)	198	444
5–10	49 ±18 (7)	1,035	51,138	7.2 ±4.1 (9)	465	3,353
10–15	270 ±85 (6)	375	101,187	60 ±47 (9)	429	25,800
15–20	104 ±58 (6)	193	20,113	88 ±32 (9)	454	39,902
20–25	148 ±72 (5)	136	20,108	18 ±9 (9)	320	5,843
25–30	122 ±70 (6)	71	8,635	0 ±0 (9)	151	0
Shelf total		2,167	208,053		2,178	75,342
Overall total		5,412	382,133		6,175	82,158

shape, including shell length, are induced by habitat characteristics of juvenile queen conch (Martín-Mora et al., 1995) and are conserved in adults (Stoner and Schwarte, 1994). For example, juvenile conch that develop in shallow seagrass beds of the bank cease to grow in shell length at a smaller size in comparison with conch developing on the shelf in Exuma Sound.

To test for differences in the density of adult queen conch among depth zones and between sites, 2-way analysis of variance (ANOVA) was performed on log-transformed data ($\log_{10}(n+1)$: there were numerous zeros in the data) in accordance with the guidelines of Day and Quinn (1989). Prior to analysis, variances were tested for heterogeneity with Cochran's test ($P>0.05$). The 2-way ANOVA was followed by Tukey's HSD multiple comparison test.

Because the comparison between the MFR near WW and the fished area near LSI constitutes an important aspect of this study, basic results from LSI (modified from Stoner and Schwarte, 1994) are reported in some figures and tables.

Juvenile surveys

To estimate abundance of juvenile queen conch at the two sites, we calculated the areal extent of juvenile aggregations at both WW and LSI. Aggregations of juvenile conch have abrupt boundaries and high densities are found adjacent to habitats without conch (Stoner and Ray, 1993). To estimate the size of aggregations in the study areas, divers were towed systematically over these areas to determine the boundaries within which density was ≥0.1 conch/m^2. Boundaries were marked with buoys, and buoy positions were determined with GPS. The potential error in positions measured with GPS is variable and can be as large as 150 m. However, when the points were plotted on a small-scale chart, they characterized accurately the shapes defined by the buoys in the field, and any error was uniform in direction and magnitude. Absolute position was not critical for the calculation of aggregation sizes. Surface areas of the aggregations were determined with the plots and a digitizing board. Surveys of juvenile queen conch have been conducted each summer since 1988 at LSI and were conducted in 1991 at WW. Juvenile conch were infrequently encountered on the island shelf; consequently, densities there were determined in conjunction with the adult survey.

At LSI, the juvenile surveys were concentrated in the flow field that begins just north of the island and runs south of Norman's Pond Cay onto the Great Bahama Bank and in the flow field that runs between Children's Bay Cay and Rat Cay (5 km) (Fig. 1C). Although most conch were associated with these tidal channels, the entire bank between Rat Cay and the north end of LSI was searched. At WW, the survey area comprised the flow field south of the island which extended onto the bank toward the south end of Hall's Pond Cay (6 km) and the surrounding bank areas (Fig.

1B). These particular tidal flow fields were emphasized because adults on the island shelf probably originated from nurseries in adjacent bank and shelf areas.

To compare juvenile conch abundance at WW and LSI, the percentage of the bank survey area occupied by juvenile aggregations was calculated (ha of aggregation/ha of bank area surveyed). Although this index provides only a crude comparison of juvenile abundance without quantitative data on animal density within the aggregations, our long experience with juvenile aggregations in the Exuma Sound has shown that aggregations rarely have <0.1 or >1.5 conch/m^2. General observations on densities were noted in our 1991 surveys at both sites.

Larval surveys

Surveys for queen conch larvae were conducted during the primary spawning season (June through August) at WW and LSI in order to provide information on the production of larvae in the two areas and to evaluate the supply of late-stage larvae. In 1993, samples were collected on 5 dates (12 June, 30 June, 15 July, 4 August, and 22 August) at each site over the island shelf at 1 inshore station (5-m isobath) and at 1 offshore station (20–30 m isobath) (Fig. 1, B–C). In 1994, samples were collected on 3 dates (22 June, 20 July, and 18 August) at only the offshore stations, where highest concentrations of adults occurred and where highest concentrations of late-stage larvae were collected in 1993. Simultaneous studies of spawning behavior at LSI and WW in 1995 showed that egg-laying is synchronous in the two areas (Stoner and Ray, unpubl. data).

Conical plankton nets (202-µm mesh, 0.5-m mouth diameter) were towed behind a 20-m vessel at 100 m/sec for replicated (n=2) 15-min tows. Because queen conch larvae are found in the upper water column during the day (Stoner and Davis, in press, a), nets were towed in the upper 1–2 m of the water column at inshore sites. At offshore sites, replicated 15-min tows were made for ~5 min at each of the following depths: 1 m, 2–3 m, and 5 m. The volume of water filtered on each tow was calculated from a calibrated flow meter (General Oceanics) secured in the mouth of the net. Samples were preserved in 5% formalin-seawater mixture. Strombid veligers were sorted from the plankton with a dissecting microscope and identified according to Davis et al. (1993). The number of queen conch veligers per 10 m^3 of water was calculated, and subsamples of veligers from each tow were measured for shell length. The veligers were classified as early-stage (≤500 µm), mid-size (500-900 µm), or late-stage (>900 µm). Late-stage larvae were metamorphically competent or nearly so.

Results

Adult surveys

Variation in density and abundance There were an estimated 208,500 adult conch in Exuma Sound near WW within the MFR survey area, which comprised 2,167 ha (Table 1). Two-way ANOVA of the 5 depth intervals from 2.5 to 25 m revealed significant differences both between the two different areas ($F_{1,63}$ =16.62, P<0.001) and among zones ($F_{4,63}$=3.87, P =0.007). The deepest interval (25–30 m) was excluded from analysis because adult conch were never observed at that depth in the fished area. Interaction between the two variables was not significant ($F_{4,63}$=1.48, P=0.218).

Mean adult density was always higher, by as much as 15 times, in the MFR than in the fished area for each depth interval (Table 1). Maximum mean density (270 conch/ha) occurred at 10–15 m in the MFR. This value was three times higher than the highest density observed in the fished area near LSI (88 conch/ha at 15–20 m) and was significantly higher than densities at all LSI depth intervals (Tukey test, P≤0.03) except 15–20 m (P=0.58).

Although nearly half the survey area in the MFR was 5–10 m deep (Table 1), adult densities were relatively low at depths <10 m (0–49 conch/ha) and high (≥104 conch/ ha) at all deeper intervals, even at greatest depth (122 conch/ ha at 25–30 m). No adults were observed at the two beach locations surveyed.

Variation in conch density within depth intervals was high and apparently related to island shelf structure. For example, density at 25–30 m was ≤6 conch/ ha along transects D and E where the slope to the shelf edge increased sharply from 15 m, whereas density was 432 conch/ha farther north in transect C, where the slope to 30 m was more gradual.

The density of adult queen conch on the bank adjacent to WW and Hall's Pond Cay in the MFR (53.6 conch/ha) was 31 times higher than that in the fished area near LSI (1.71 conch/ha). Seventy-four percent of all adult conch encountered on the bank near WW were within 2 km of inlets; this general distribution pattern was also evident at LSI.

There was an estimated total of 174,100 adult queen conch on the bank in the entire MFR survey area (3,245 ha) (Table 1). This was 45.6% of the overall total for the shelf and bank. In the fished area, there were only 6,816 adults in the bank area surveyed (3,997 ha), and this number comprised a relatively small portion of the overall total for the site (8.3%). Most adult conch in the fished area (>87%) were found in depths >10 m, whereas only 39% of adult conch in the MFR were in depths >10 m.

Shell structure Pairwise Kolmogorov-Smirnov tests showed differences in frequency distributions of shell length in the MFR between adult conch on the bank and those at each depth interval ($P \leq 0.002$ in all cases) except 2.5–5 m ($P=0.14$). Adult conch from the sound, always ≥150 mm, tended to be longer than those from the bank (Fig. 2). The length mode for sound conch ranged from 180–189 mm (at 5–10 m and 10–15 m) to 210–219 mm (at 15–20 m and at 25–30 m, where the largest individual [265 mm] was found). Conch at the deepest interval were relatively large, and mean shell length increased 18 mm between the 10–15 m and 25–30 m intervals. A bimodal distribution was observed in the three deepest intervals, with a low frequency of 200–209 mm conch in all cases. Mean shell length for all conch from the sound was 202 mm (SD=21 mm, n=524), compared with 188 mm (SD=20 mm, n=213) for conch on the bank. An intersite comparison showed significant differences in frequency distributions of shell length between the MFR and the fished area for conch living at each depth interval but not for those on the bank (Fig. 2). Adult conch from the shelf in the fished area had longer shells than those from the shelf in the MFR.

Pairwise Kolmogorov-Smirnov tests also showed differences in frequency distributions of shell lip thickness in the MFR between adult conch on the bank and those at each depth interval ($P<0.001$ in all cases) because those on the bank had relatively thin shell lips. All bank adults had shell lips ≤28 mm thick, and 31% were ≤8 mm (Fig. 3). Lip thickness values were >16 mm for most adults in the sound, and <5% of the conch at each of the three depth intervals to 15 m had lip thickness ≤8 mm. Beyond 15 m no thin-lipped conch were measured. Mean lip thickness for all conch from the sound was 24 mm (SD=7 mm, n=524), compared with 12 mm (SD=6 mm, n=213) on the bank.

An intersite comparison showed significant differences in frequency distributions of shell lip thickness for conch living on the bank and at each depth interval ($P \leq 0.001$ in all cases) except for those at 5–10 m ($P=0.08$) (Fig. 3). Compared with conch in the MFR, conch in the fished area tended to have thinner lips in shallow water (bank, and sound <5 m) and thicker lips in deeper water.

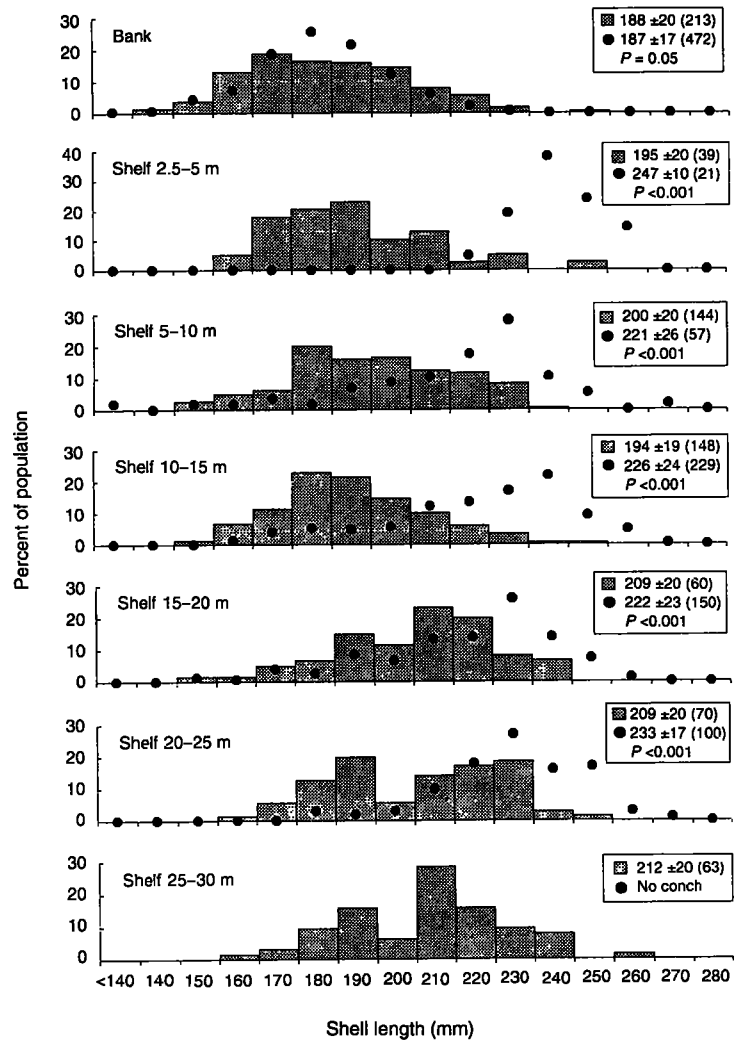

Figure 2

Frequency distribution of shell length of adult conch on the bank and at 6 depth intervals in Exuma Sound on the island shelf near WW in the marine fishery reserve (columns) and in the fished area near LSI (points). Each value on the x-axis represents a range of sizes starting with the lower end of the size interval (e.g. 150–159 mm). Mean shell length (±SD) and sample size in parentheses are also given for each distribution. Values for LSI are adapted from Stoner and Schwarte (1994). P-values are for intersite comparisons (Kolmogorov-Smirnov tests).

Juvenile surveys

Juvenile conch were never observed at depths >15 m in the Exuma Sound at either study area, and they were infrequently observed (mean <6/ha) in shallower water in the MFR (Fig. 4). Highest density of

juveniles in the sound (33.3 juveniles/ha) occurred in the MFR at 5–10 m, but the standard deviation for this depth interval was more than twice the mean (all other densities were 0, except 1 at 5.1 juveniles/ha). In contrast with adults, intersite differences for juvenile densities in Exuma Sound were not significant (Student's t-test, $P>0.2$ for 2.5–5 m, 5–10 m, and 10–15 m).

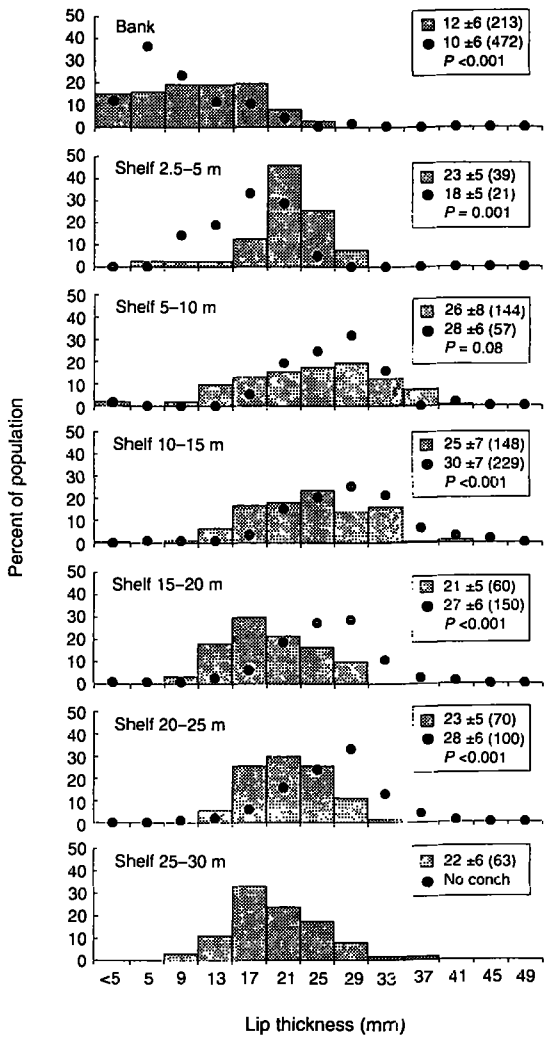

Figure 3

Frequency distribution of shell lip thickness of adult conch on the bank and at 6 depth intervals in Exuma Sound on the island shelf near WW in the marine fishery reserve (columns) and in the fished area near LSI (points). Each value on the x-axis represents a range of sizes starting with the lower end of the size interval (e.g. 5–8). Mean lip thickness (±SD) and sample sizes in parentheses are also given for each distribution. Values for LSI are adapted from Stoner and Schwarte (1994). P-values are for intersite comparisons (Kolmogorov-Smirnov tests).

The majority of juvenile conch at both sites were found on the Great Bahama Bank. On the bank in the fished area, interannual variation in the surface area occupied by juvenile aggregations was high, ranging from 8 to 44 ha in the flow field north of LSI and from 2 to 87 ha in the Children's Bay Cay flow field (Table 2). In the MFR in 1991, juveniles occupied 125 ha. Although data for the MFR are available for only 1 yr, the surface area was nearly twice a large as the average surface area occupied in two flow fields over 6 yr in the fished area. In the MFR, juvenile aggregations covered 3.84% of the bank area surveyed, compared with a mean value of 1.62% in the fished area.

Larval surveys

Densities of queen conch larvae were consistently higher in the MFR near WW than in the fished area near LSI. In 50 plankton tows made at the two sites between 1993 and 1994, densities in the fished area were always <6 larvae/10 m^3 and typically near 1–2 larvae/10 m^3 (Table 3). Densities in the MFR were frequently an order of magnitude higher, reaching a maximum of 55 larvae/10 m^3 in July 1994. Intrasite differences were most notable in the MFR on 22 August 1993 when the offshore station had 184 times the density of veligers as the inshore station. However, results were variable, and during both June cruises in 1993, the inshore station at the MFR had

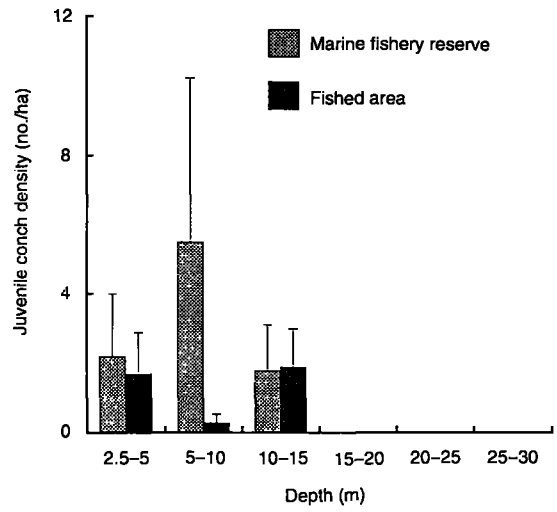

Figure 4

Juvenile conch density at 6 depth intervals in Exuma Sound on the island shelf at the fished area near LSI (Stoner and Schwarte, 1994) and at the marine fishery reserve near WW (this study). Values are mean (+SE).

higher mean larval densities than the offshore station (Table 3).

Early-stage larvae (≤500 µm SL) represented the most abundant size class in collections made at both areas (>90%) (Table 4). Late-stage larvae (≥900 µm SL) were always present in the MFR, except on 22 June 1994, and always occurred at higher densities in the MFR than in the fished area. The highest observed density was 1.9 late-stage larvae/10 m^3 on 4 August 1993. Late-stages were also more abundant offshore than inshore at both sites.

Discussion

Comparisons with earlier investigations

Although direct comparisons of LSI/WW density data with data from other studies are made difficult because of different sampling strategies, incomplete data in some reports, and failures to distinguish between adult and juvenile densities, a review of the literature suggests high regional variability in adult queen conch densities, ranging over three orders of

Table 2

Surface area occupied by juvenile queen conch in two tidal flow fields, one originating north of Lee Stocking Island (LSI), and the second originating between Rat Cay and Children's Bay Cay (CBC) (see Fig. 1C). Surface areas for LSI and CBC were standardized to percent of bank surface area occupied by juvenile aggregations.

	Surface area (ha)			
Year	LSI	CBC	Total	% of bank
1989	31.7	32.2	63.9	1.60
1990	14.5	7.4	21.9	0.55
1991	19.4	1.7	21.1	0.52
1992	8.3	51.7	60.0	1.50
1993	42.2	86.8	129.0	3.23
1994	44.3	49.2	93.5	2.34
Mean	26.7	38.2	64.9	1.62
SD	14.9	31.6	41.8	1.05

Table 3

Larval densities (no. 10/m^3) (mean ±SD) in a marine fishery reserve near Waderick Wells (WW) and in a fished area near Lee Stocking Island (LSI). Samples were collected inshore and offshore for 5 days in 1993 and offshore for 3 days in 1994. *P*- and *t*-values are from Student's *t*-test using pooled variances when data were homogeneous (Cochran's test, $P>0.05$) and from separate variances when data were not ($0.01<P<0.05$).

1993	12 Jun	30 Jun	15 Jul	4 Aug	22 Aug
Inshore					
WW	50.0 ±5.1	43.6 ±5.4	0.65 ±0.33	4.42 ±0.52	0.22 ±0.21
LSI	0.52 ±0.21	2.70 ±0.45	0.63 ±0.44	no data	1.58 ±0.77
t	−13.83	−10.66	−0.06		2.41
P	0.005	0.009	0.96		0.14
Offshore					
WW	36.3 ±2.7	7.26 ±1.12	0.91 ±0.62	1.87 ±0.19	40.4 ±15.4
LSI	0.62 ±0.19	1.00 ±0.10	1.22 ±0.09	0.74 ±0.44	0.43 ±0.24
t	−18.42	−7.85	0.71	−3.33	−3.66
P	0.003	0.02	0.55	0.08	0.17
1994	**22 Jun**	**20 Jul**	**18 Aug**		
Offshore					
WW	27.8 ±5.09	54.7 ±9.35	0.98 ±0.18		
LSI	5.94 ±1.44	0.25 ±0.23	0.06 ±0.08		
t	−5.86	−8.23	−6.73		
P	0.03	0.08	0.02		

Table 4

Densities of queen conch veligers (no. /10 m^3) in three size classes in a marine fishery reserve near Waderick Wells and in a fished area near Lee Stocking Island. Samples were collected inshore and offshore in 1993 and offshore in 1994. Values are mean ±SD; the numbers in parentheses are the number of sampling dates for each site.

	Early-stage (<500 µm)	Mid-size (500–900 µm)	Late-stage (>900 µm)
1993			
Marine fishery reserve			
Inshore	19.7 ±24.9 (5)	0.037 ±0.073 (5)	0.042 ±0.060 (5)
Offshore	15.9 ±18.8 (5)	0.646 ±0.874 (5)	0.768 ±0.701 (5)
Fished Area			
Inshore	1.25 ±1.07 (4)	0.093 ±0.134 (4)	0.011 ±0.008 (4)
Offshore	0.740 ±0.348 (5)	0.018 ±0.017 (5)	0.045 ±0.058 (5)
1994			
Marine fishery reserve			
Offshore	27.4 ±27.0 (3)	0.322 ±0.206 (3)	0.110 ±0.111 (3)
Fished Area			
Offshore	2.05 ±3.33 (3)	0 ±0 (3)	0.029 ±0.025 (3)

magnitude (Table 5). Mean values in the MFR near WW for each depth interval were always ≥34/ha, well above those reported for Bermuda, Florida, Puerto Rico, and the U.S. Virgin Islands. Densities in the MFR in depths >10 m were comparable to those observed before 1984 at Cabo Cruz, Cuba, in the Turks and Caicos Islands, and at a fished area of Venezuela. Only two other studies quantified adult conch densities by depth (Table 6). In Puerto Rico, maximum adult density occurred at 20–25 m, but the value was only 0.05 adults/ha (Torres Rosado, 1987), three orders of magnitude lower than that for our MFR, and two orders of magnitude lower than that at our fished area near LSI. In the U.S. Virgin Islands, adult density was maximum (17.1 adults/ha) at 18–24 m (Friedlander et al., 1994), and nearly identical to densities (18.3 adults/ha) observed in 20–25 m in our fished area.

Highest densities reported in the literature were observed >20 years ago in Cuba and >10 years ago in Venezuela. The highest single density estimate in our study (568 adults/ha) represented only 30–36% of the highest densities reported for Diego Perez, Cuba (1,582/ha), and for a fishery reserve at Islas Los Roques in Venezuela (1,886/ha) (Table 5). This protected area in Venezuela was subsequently depleted of adult conch through illegal fishing (Rodríquez and Posada, 1994), and declines in population density throughout the Caribbean are well documented (Appeldoorn, 1994a). Densities of conch in the Exuma Cays are now among the highest in the region.

Low numbers of adults found in shallow water have been attributed directly to fishing off the Turks and Caicos Islands (Hesse, 1979), Venezuela (Weil and Laughlin, 1984), Puerto Rico (Torres Rosado, 1987), the U.S. Virgin Islands (Friedlander et al., 1994), and the Bahamas (Stoner and Schwarte, 1994). In this investigation there were >31 times the number of adult conch on the bank in the MFR compared with the number in the fished area. Because any adult conch living in water <10 m deep near LSI can be collected easily by abundant free-diving fishermen, we also attribute density differences between our sites at least partly to fishing, although other explanations are also plausible (see below).

Densities of queen conch larvae have been reported in only two published studies. Our estimates of density near WW, commonly >30 veligers/10 m^3, were much higher than these studies. The highest density from a cruise in the eastern Caribbean in 1988 was only 1.2 veligers/10 m^3 (mid- and late-stages) near the Grenadines (Posada and Appeldoorn, 1994), and the highest value found near Puerto Rico in 1993 was only 0.68 veligers/10 m^3 (Appeldoorn and Rodriquez[1]). The highest single value recorded for a site outside the Exuma Sound was 2.0 veligers/10 m^3 (including newly hatched larvae) in the Florida Keys in 1994, with all other values one or two orders of magnitude lower (Stoner et al., in press; Stoner and Mehta, unpubl. data). High larval densities in the Exuma Cays, particularly in the MFR, appear to be directly associated with abundance of spawning stocks.

[1] Appeldoorn, R. S., and L. Rodriquez. 1995. Department of Marine Sciences, University of Puerto Rico, P.O. Box 908, Lajas, Puerto Rico 00667. Unpubl. data.

Table 5

Adult queen conch densities reported throughout the Caribbean and arranged by decreasing latitude.

Location	Density (no/ha)	Depth (m)	Survey date	Reference	Survey methods
Bermuda	0.52	0–20	1988	Berg et al. (1992a)	Towed-diver transects
Florida Keys, United States	0.50	0–25	1987–1988	Berg et al. (1992b)	Stratified towed-diver transects
Bahamas			1983–1984	Smith and van Nierop[1]	Swim transects
Little Bahama Bank	28.50	0–18			
Great Bahama Bank	20.79	0–18			
Cuba			1972–1974	Alcolado (1976)	Swim transects
Diego Perez	1582	3–4			
Cabo Cruz	130	0–5			
Turks and Caicos Islands	255	0–4	1974–1975	Hesse (1979)	Swim transects
Puerto Rico, United States	2.62	0–30	1985–1986	Torres Rosado (1987)	Swim transects
Virgin Islands, United States		—	1981	Wood and Olsen (1983)	Sled transects
St. Thomas	9.7				
St. Croix	7.6				
Virgin Islands, United States			1990	Friedlander et al. (1994)	Scooter transects
St. Thomas	11.79	5–30			
St. John	12.64	5–30			
Los Roques, Venezuela			1981–1983	Weil and Laughlin (1984)	Fixed quadrats
Fished	160[2]	1–4			
Unfished	1886[2]	1–18			

[1] Smith, G. B., and M. van Nierop. 1984. Distribution, abundance, and potential yield of shallow-water fishery resources of the Little and Great Bahama Banks. UNDP/FAO Fish. Dev. Proj. BHA/82/002, p. 1–78.
[2] Assuming conch >210 mm in shell length were adults (Laughlin and Weil, 1983).

Distribution processes in the Exuma Cays

In terms of both density and extrapolated total numbers there were more adult conch in the MFR near WW than in the fished area near LSI. The two sites were similar in terms of habitat, and they lie relatively close together in the same oceanographic basin, yet there were density differences, most notably in the shallow bank waters. We recognize that no unreplicated comparison of two field sites can provide indisputable proof that an MFR is advantageous to a stock unless the analysis includes long time series or data before and after closure of a fishing area, or both (Stewart-Oaten et al., 1986; Osenberg et al., 1994; Underwood, 1994). Unfortunately we know of no biological data for the Exuma Cays Land and Sea Park collected before the fishing closure. This is a common problem associated with studies of MFR's (see Roberts and Polunin, 1991), and future studies should use control sites and replication in both time and space for definitive answers regarding the impact of closing fisheries in reserve areas. On the other hand, it is not surprising when stocks of exploited species increase in closed areas. A more important issue may be whether or not the reserves contribute to long-term conservation of species or whether or not they preserve or enhance stocks in the surrounding waters. Answers to such questions require data

Table 6

Adult queen conch densities reported for two locations in the Caribbean by depth interval. Data for Puerto Rico were collected in 1985–86 (Torres Rosado, 1987) and data for the United States Virgin Islands were collected in 1990 (Friedlander et al., 1994). See Table 1 for comparison with the Exuma Cays sites.

Puerto Rico		Virgin Islands	
Depth (m)	Density (no/ha)	Depth (m)	Density (no/ha)
0–5	0	0–6	5.2
5–10	0.04	6–12	4.2
10–15	0.035	12–18	17.1
15–20	0.035	18–24	10.9
20–25	0.05	24–30	11.0
25–30	0.023		

on mechanistic issues such as reproductive output, recruitment dynamics, and larval import and export. Our data on adult shell size and age, juveniles, and larval size and abundance make this analysis unique and allow considerable insight into distribution mechanisms in the Exuma Cays. An understanding of such mechanisms is critical for making effective management policies.

Site-specific differences in shell size and shape described for queen conch (Stoner and Schwarte, 1994; Martín-Mora et al., 1995) are useful in explaining adult recruitment patterns at WW and LSI. Juveniles in the shelf environment of Exuma Sound grow rapidly, produce shells that are long and slender, and reach sexual maturity (hence terminal length) at a larger size than conch developing on the Great Bahama Bank. On the basis of shell size and shape, low numbers of adults on the bank and near inlets, and high fishing pressure, Stoner and Schwarte (1994) concluded that little migration occurred between bank and sound at LSI and that small numbers of juveniles in shallow regions of the sound were the primary source of deep-water reproductive stock. Adults on the bank were mostly young (i.e. thin-lipped), and most were removed by fishing before they could migrate offshore to the primary reproductive grounds in the deeper shelf environment.

Adults on the bank in the MFR near WW had a length-frequency distribution virtually identical to those on the bank at LSI (i.e. small adults). However, unlike the LSI shelf where large adults dominated the population, adult length-frequency in the shelf environment of WW was bimodal. The smaller WW adults originated on the bank and were able to migrate to deeper shelf waters in the absence of fishing. Therefore, although there was only one primary source of adults for the sound population at LSI, there were two sources at WW, and migration from the unfished bank provides at least a partial explanation for higher densities and the bimodal distribution observed on the adjacent Exuma Sound shelf. Although, in some areas, fishing may result in removal of large individuals and in artificial selection for small conch (Appeldoorn, 1994b), this does not appear to be a problem near LSI, where adults were relatively large.

On the basis of shell lip thickness, it appears that conch were removed from the bank near LSI at an early age, whereas older, thick-lipped conch accumulated on the bank in the MFR near WW. The reverse was evident in deep shelf waters where the average age of conch was higher at LSI than at WW. It is possible that harvesting of young adults from shallow bank and shelf waters near LSI has reduced recruitment to the deep-water spawning population. It has been assumed that, by allowing fishermen to collect conch only by free-diving, a deep-water refuge is secured for conch spawning stock. Although this is true in general, virtually all juveniles and first-year adults in the Exuma Cays live in shallow (<15 m) water and all are available to free-diving fishermen until after reaching adulthood. Protection of habitat used as a migratory pathway is critical in the management of conch stocks.

Patterns of abundance for queen conch juveniles and larvae suggest that differences in recruitment processes, in addition to fishing pressures, may affect differences in the numbers of adult conch between the two study sites. In 1991, juvenile aggregations in the MFR were an order of magnitude larger than those in the fished area, where the aggregations were relatively small in all six annual surveys. The large juvenile aggregations in the MFR can be explained by relatively high densities of competent larvae arriving at the site. In 1993, the mean concentration of late-stage larvae at the offshore shelf stations at the MFR was 17 times higher than the concentration in the fished area. In 1994, the difference was approximately fourfold. The supply of larvae to the MFR nurseries appears to be much higher than the supply to nurseries in the fished area.

Differences in larval supply to a site are affected by three primary processes—production, survival, and transport. Virtually nothing is known about the predators of queen conch larvae or about the survival of queen conch in the plankton. There is little doubt, however, that site differences in larval production, demonstrated by the density of early-stage larvae, reflect local spawning stock size and density. In terms of transport, near-surface flow along the Exuma Cays shelf is to the northwest at LSI, at WW, and at a station midway between the two sites. From June through September 1993, the current on the shelf at WW flowed to the northwest at 1.6–3.4 cm/s (1.4–2.9 km/day (Hickey[2]). Given a larval life of 16–28 d (Davis et al., 1993), late-stage queen conch larvae arriving in the MFR near WW must originate well to the south, and their high densities most likely reflect a natural accumulation of larvae produced by spawning stocks all along the Exuma Cays. This abundance of recruits must also contribute to high densities of juveniles and adults observed in the MFR. Larvae of a closely related, but unfished strombid, *Strombus costatus*, were also highly concentrated in the MFR in 1994 (Stoner, unpubl. data). We conclude, therefore, that the high density of adult conch at WW results not only from reduced fishing

[2] Hickey, B. A. 1995. School of Oceanography, Univ. Washington, Seattle, WA 98195. Unpubl. data.

pressure but also from natural accumulation of larvae. Furthermore, given the surrounding current patterns, the reserve is probably not large enough to hold a self-sustaining conch population; conch at WW are derived from up-stream spawning stocks located outside the reserve. With a northwest current along the Exuma Cays shelf, an MFR located farther to the south might actually allow better downstream conservation of queen conch. However, exact transport distances are unknown, and calculations are complicated by the potential effects of numerous tidal passes and plumes. Because preservation of external sources of larvae will be critical to the maintenance of populations within any park, managers establishing all such reserves must consider the broad metapopulation context (Carr and Reed, 1993; Man et al., 1995).

It is likely that the high densities of larvae exported from the Exuma Park on the northwest current represent a significant recruitment source for conch populations in the northern Exuma Sound. Very large aggregations of juvenile conch (>600 ha) were measured in the northern Exuma Sound near the Schooner Cays in 1993 (Stoner, unpubl. data). These populations appear to have increased since the establishment of the Exuma Cays Land and Sea Park (Higgs[3]). Future modeling of larval transport will be particularly valuable in estimating the actual significance of enhanced larval production in this and other marine fishery reserves. Although the significance of larval export is difficult to prove experimentally (Dugan and Davis, 1993), the value of reserves located upstream may be especially high.

Clearly, the Exuma Cays Land and Sea Park is large enough to protect a large reproductive stock of queen conch in an undisturbed habitat where physical oceanographic features concentrate competent larvae and export them to downstream nurseries and fishing grounds. Because of the potential fishery value of exported larvae, a good understanding of the strategic locations of reserves and of the general oceanographic conditions within the dispersal range of the larvae is necessary. Our observations provide support that fishery reserves can indeed enhance fishery populations in the downstream direction through export of larvae, although only if the sources of larvae for the reserves are maintained. Furthermore, reserves need to incorporate design features that protect habitats required by each life stage. Legal prohibition of the use of SCUBA gear prevents immediate depletion of adult queen conch because those individuals that survive the migration to deep-water constitute an unfished deep-water reproductive stock, even outside a reserve. However, every young adult is vulnerable, and multiple well-placed reserves that protect the tidal inlets, which serve as pathways between nurseries and important reproductive grounds on the shelf, could be particularly valuable. Reserve designs that consider ontogenetic requirements of the target species and strategic locations for larval production, import, export, and metapopulation dynamics will optimize fishery benefits for the many marine vertebrate and invertebrate species that possess pelagic larvae.

[3] Higgs, C. 1994. Department of Fisheries, Ministry of Agriculture, Trade, and Industry, P.O. Box N3028, Nassau, Bahamas. Personal commun.

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Transferrin polymorphism in coho salmon, *Oncorhynchus kisutch*, and its application to genetic stock identification

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Abstract.—The blood protein transferrin is an important source for identifying genetic variation in coho salmon, *Oncorhynchus kisutch*, with starch gel electrophoresis. We present new data for transferrin allele frequencies for 48 samples of coho salmon collected at 34 different locations from Oregon to southern British Columbia. To analyze transferrin allele frequencies from a larger geographic area, data from various sources were compiled for 135 samples from sites from California to southern British Columbia. In a statistical analysis of temporal variation within locations, 26 of 63 pairwise comparisons (41%) showed significant differences between samples ($P<0.05$). An analysis of variance revealed significant between-locale variability and no significant within-locale variability due to whether or not the brood years of the samples were three years apart. Relative gene diversity values were 22.3% between geographic regions, 2.1% between stocks within geographic regions, 3.1% between temporal comparisons, and 72.5% for within-sample variation. Total genetic diversity (H_T) was 0.586, and the average genetic diversity within populations (H_s) equaled 0.425. The samples showed genetic variation that was related to geographic location. Applications of transferrin data to genetic stock identification are discussed in relation to these results.

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The iron binding protein, transferrin (Tf), is a highly polymorphic locus in coho salmon, *Oncorhynchus kisutch*, that exhibits allelic frequency differences between populations (Utter et al., 1970; Hjort and Schreck, 1982; Olin, 1984; Bartley et al., 1992). The transferrin locus is a potentially valuable addition to the set of polymorphic loci currently used for genetic stock identification (GSI) of coho salmon (Milner, 1993). In the past, one drawback of including transferrin in multilocus GSI surveys was the necessity of acquiring a serum sample to resolve allelic variation. However, transferrin allele frequencies can now be obtained from heart tissue (Van Doornik et al., 1995), therefore it is feasible to incorporate variation at this locus into GSI analyses involving coho salmon.

This study was conducted as part of an ongoing research effort to develop a geographically extensive baseline of allele frequencies for coho salmon. Our objectives are to increase the number of polymorphic loci for which allele-frequency data are obtainable, to verify the genetic basis of previously documented and new allelic variation, and to expand the geographic range of our baseline data set. Given adequate geographic coverage and genetic differences among major contributing stocks, allele-frequency data can be used for stock identification of mixed stock fisheries (Milner et al., 1985; Milner, 1993).

The objective of this paper is to examine the potential of transferrin for use in genetic stock identification of coho salmon. Specifically, we 1) report new transferrin allele frequencies for 48 samples collected from 34 coho salmon stocks, 2) compile allele-frequency data for transferrin data from other sources to compare allele frequencies over a larger geographic area, 3) analyze the temporal stability of transferrin allele frequencies, and 4) examine levels and patterns of variation between samples using gene diversity and genetic identity analyses.

Materials and methods

Blood or tissue samples, or both, were collected, as described by Van Doornik et al. (1995), for 48 coho

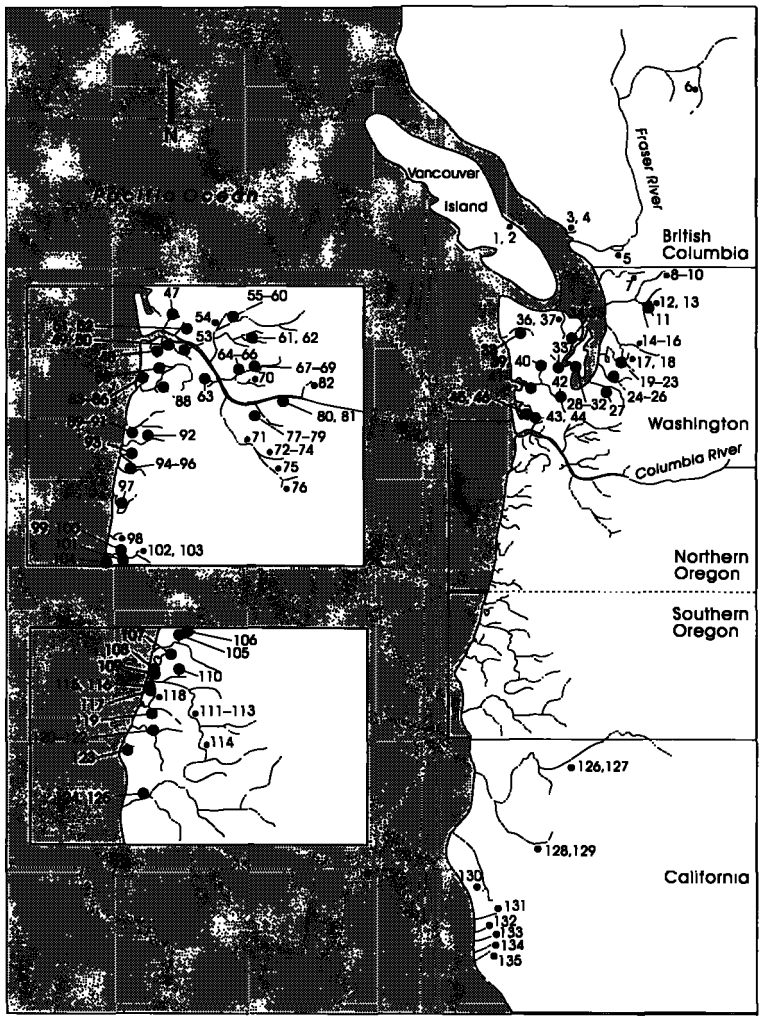

Figure 1

Locations of samples. Numbers refer to sample names identified in Table 1.

salmon samples from 34 locations in northern Oregon (north of Cape Perpetua), the Columbia River, Washington coastal streams, and Puget Sound, Washington (Fig. 1). Starch gel electrophoresis was conducted as described by Aebersold et al. (1987) and Van Doornik et al. (1995).

Observed genotype frequencies were compared with expected Hardy-Weinberg proportions with a chi-square goodness-of-fit test for the 48 samples for which genotype-frequency data were available.

Allele frequencies were compiled from other studies that included 30 or more fish per sample for the transferrin locus to create a data set of 135 samples (Table 1). The log-likelihood ratio statistic (G-test) (Sokal and Rohlf, 1969) was used to compare allele frequencies of these samples that were taken in different years at the same locale. In these analyses, G-tests were performed for each polymorphic locus and the results were summed over all loci to yield an overall G-value and a standardized G-value (G/df). To test for significant differences between samples, an analysis of variance (ANOVA) of arc sine square-root transformed allele frequencies, for $n-1$ alleles, was conducted with SYSTAT statistical software (SYSTAT, 1992). Genetic diversity was partitioned into components defined by regions, samples, and within-sample (temporal variation) according to the method described by Chakraborty (1980) by using the BIOSYS-1 computer program (Swofford and Selander, 1981).

Genetic similarities among samples were estimated with Nei's (1978) unbiased genetic identity and projected as a dendrogram with the unweighted pair-group method with arithmetic averaging (UPGMA) (Sneath and Sokal, 1973) (with BIOSYS-1). Genetic similarities were also analyzed by using

a principal components analysis of the correlation matrix with NTSYS software (Rohlf, 1994).

A noteworthy characteristic of coho salmon populations south of Alaska is their unique propensity to return to spawn at three years of age (Sandercock, 1991). We classified samples from the same locale as "on cycle" if the brood years were three years apart and as "off cycle" when otherwise. We tested for a significant effect of brood-year cycle within a locale on allele frequencies by nesting the brood-year cycle within-locale in the above mentioned ANOVA.

Results

Four alleles were observed with relative mobilities of 106, 103, 100, and 97. The **106* allele was observed at only three locations (Cowlitz, Lewis, and Trinity rivers) at a low frequency ($P<0.03$). Frequencies of the other alleles varied considerably among samples: $0.116 \leq P \leq 1.000$ for the **103* allele, $0.000 \leq P \leq 0.535$ for the **100* allele, and $0.000 \leq P \leq 0.764$ for the **97* allele. Allele frequencies for the 48 new samples analyzed in our laboratory are included in Table 1 (identified as "NMFS").

Of the 48 samples, 3 (6.3%) deviated from expected Hardy-Weinberg proportions: Nehalem Hatchery, brood year 1982 ($P=0.022$); Bonneville Hatchery, brood year 1989 ($P=0.008$); and Minter Creek Hatchery, brood year 1990 ($P=0.039$). Although the total number of significant tests ($n=3$) was only slightly greater than the number expected by chance alone ($n=2.4$), we have no reason to reject the assumptions that the samples represented panmictic populations and the genetic model used to interpret the observed allozyme patterns was correct. Data from an inheritance study have confirmed that the transferrin alleles segregate according to expected Mendelian segregation proportions (Van Doornik, unpubl. data).

Transferrin data compiled from nine sources in addition to those collected for this study are shown in Table 1. The total data set included 135 samples from sites ranging from California to southern British Columbia (Fig. 1). Sample sites were grouped into the following eight geographic regions: Vancouver Island, mainland British Columbia, Puget Sound, coastal Washington, Columbia River, northern Oregon (north of Cape Perpetua), southern Oregon, and California.

Sixty-three pairwise, *G*-tests were made by comparing allele frequencies of samples from the same location but from different brood years. A total of 41% ($n=26$) of the temporal comparisons were statistically significant ($P<0.05$). Despite this substantial temporal variability, the ANOVA indicated significant between-sample variation ($F=21.1$, df=89, $P=0$). (The rare **106* allele was pooled with the **103* allele frequencies for this analysis.) The contribution of brood-year cycle within sample locations to the overall genetic variation was not statistically significant for the **100* allele ($F=2.1$, df=24, $P=0.06$) and the **103* allele ($F=0.9$, df=24, $P=0.60$).

The gene diversity analysis indicated that most of the genetic diversity was found within locations (72.5%). The other components of relative gene diversity were 22.3% between geographic regions, 2.1% between stocks within a geographic region, and 3.1% between temporal comparisons. Relative gene diversity (G_{st}) equaled 27.5%. Total genetic diversity (H_T) was 0.586, and the mean genetic diversity within populations (H_s) equaled 0.425.

A dendrogram of Nei's genetic identity (I) for the compiled data for 135 samples revealed three major clusters at I=0.900 that followed regional geographic patterns (Fig. 2). All samples from Vancouver Island ($n=2$), the Washington coast ($n=8$), Puget Sound ($n=32$), and northern Oregon ($n=22$) formed cluster 1. Cluster 1 is distinguished by samples with moderate frequencies of the **103* ($0.080<P<0.501$) and **97* ($0.250<P<0.77$) alleles. The 21 samples from southern Oregon appeared in all three clusters. Samples from Marlow Creek, Five Mile Creek, Elk Creek, Coos River, North Fork Siuslaw River, and two Umpqua River stock samples (brood year 1981, 1992) also grouped in cluster 1; cluster 3 contained samples from the Rogue River ($n=2$) and Morton Creek; and the remaining 11 southern Oregon samples formed the sole members of cluster 2. Cluster 2 contained samples with relatively high frequencies of the **100* allele ($0.356<P<0.540$). All of the California ($n=10$), Columbia River ($n=36$), and mainland British Columbia ($n=4$) samples grouped together in cluster 3. Cluster 3 consisted of samples with high frequencies of the **103* allele ($0.640<P \leq 1.000$).

The principal components analysis yielded results identical to those from Nei's genetic identity values, and therefore, are not included here.

Discussion

The geographical pattern of genetic variability shown by these data supports several conclusions regarding the genetic population structure of some of these stocks. Results from cluster analysis of the total data set (Fig. 2) indicated that samples from large river systems (Fraser River, Columbia River, Rogue River, and Klamath River) are genetically similar to each other despite the geographical distances separating them. Several studies have shown that coho salmon from small coastal rivers differ from those from large

inland river systems. For example, Hjort and Schreck (1982) examined electrophoretic, morphological, and life-history characteristics of coho salmon in Washington, Oregon, and California. They found, in general, stocks from large rivers (Columbia River, Rogue River, and Klamath River) were more similar to each other than to stocks from smaller rivers. Taylor and McPhail (1985) also found significant differences in body shape

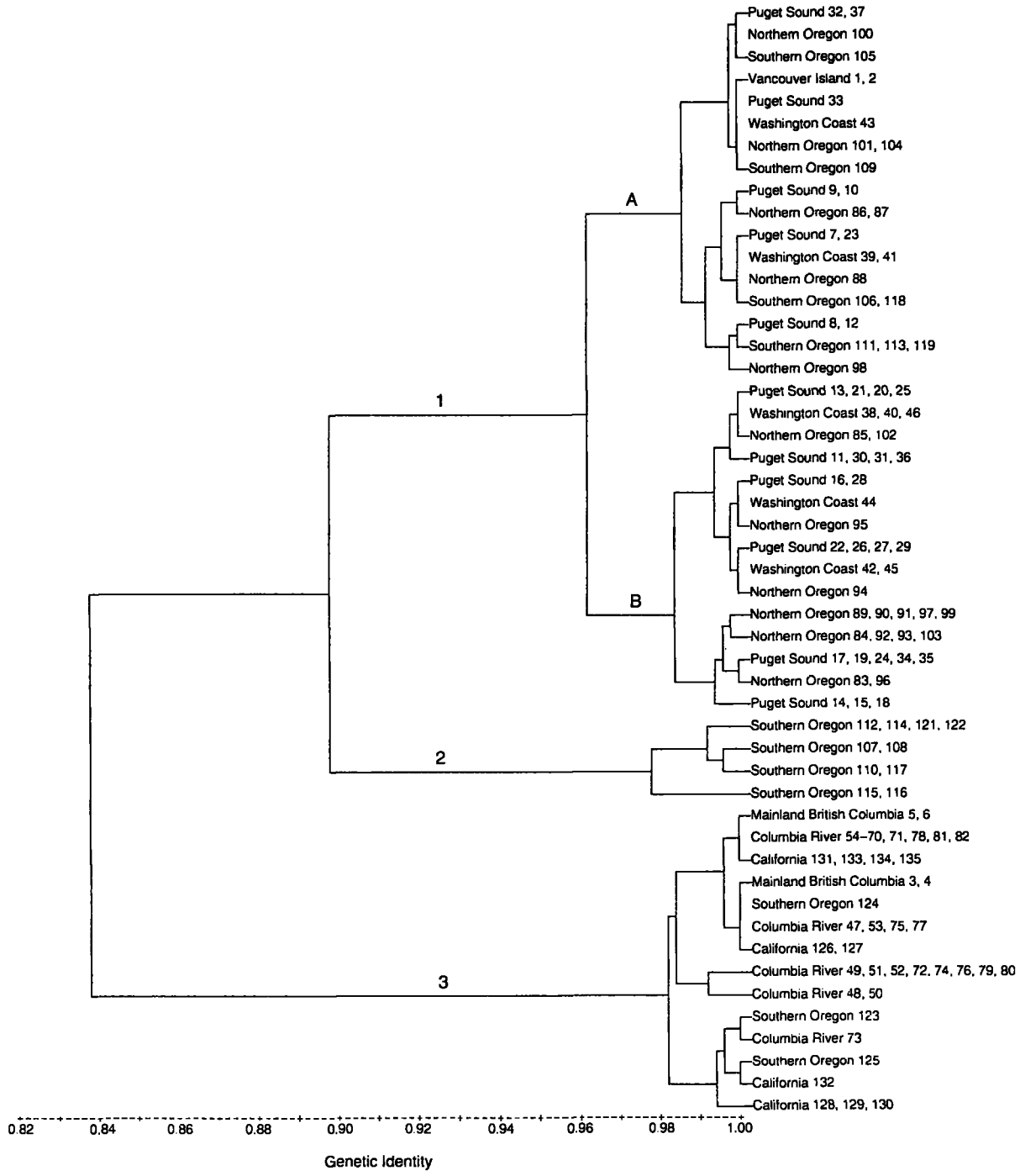

Figure 2

Dendrogram for compilation of 135 samples created with UPGMA clustering of Nei's identity values (Nei, 1978). Numbers refer to sample names identified in Table 1.

Table 1

Sample information, map codes, and allele frequencies for 135 samples of coho salmon, *Oncorhynchus kisutch*, from 81 locations.

Sample number	Name	Sample size	Brood year	Allele frequencies *103	*100	*97	*106	Source
1	Qualicum Hatchery	30	1971	0.367	0.333	0.300	0.000	Utter[1]
2	Qualicum Stock at Capillano Hatchery	91	1976	0.352	0.313	0.335	0.000	Utter[1]
3	Capillano Hatchery	45	1971	0.822	0.089	0.089	0.000	Utter[1]
4	Capillano Hatchery	85	1976	0.847	0.011	0.142	0.000	Utter[1]
5	Hope River, Fraser River	35	1972	1.000	0.000	0.000	0.000	May and Utter[2]
6	Coldwater River at Spius Hatchery	76	1985	0.961	0.039	0.000	0.000	NMFS[3]
7	North Fork Nooksack River	51	1974	0.402	0.196	0.402	0.000	May (1975)
8	Baker River	79	1989	0.544	0.146	0.310	0.000	NMFS[3]
9	Baker River at Skagit Hatchery	87	1989	0.466	0.098	0.437	0.000	NMFS[3]
10	Baker River at Skagit Hatchery	60	1991	0.483	0.125	0.392	0.000	NMFS[3]
11	Skagit Hatchery	40	1974	0.262	0.250	0.488	0.000	May (1975)
12	Clark River at Skagit Hatchery	79	1989	0.544	0.120	0.335	0.000	NMFS[3]
13	Clark River at Skagit Hatchery	57	1991	0.254	0.211	0.535	0.000	NMFS[3]
14	Skykomish River Hatchery	67	1971	0.149	0.104	0.747	0.000	Utter et al. (1973)
15	Skykomish River Hatchery	125	1972	0.116	0.120	0.764	0.000	May and Utter[2]
16	Skykomish River Hatchery	66	1974	0.356	0.053	0.591	0.000	May (1975)
17	Deep Creek, Snoqualmie River	30	1974	0.267	0.117	0.616	0.000	May (1975)
18	Harris Creek, Snoqualmie River	30	1974	0.083	0.167	0.750	0.000	May (1975)
19	Issaquah Hatchery	50	1968	0.220	0.160	0.620	0.000	Utter et al. (1970)
20	Issaquah Hatchery	100	1971	0.235	0.170	0.595	0.000	Utter et al. (1973)
21	Issaquah Hatchery	180	1972	0.278	0.172	0.550	0.000	May and Utter[2]
22	Issaquah Hatchery	88	1973	0.307	0.165	0.528	0.000	May (1975)
23	Issaquah Hatchery	80	1974	0.331	0.162	0.507	0.000	May (1975)
24	Green River Hatchery	54	1968	0.222	0.139	0.639	0.000	Utter et al. (1970)
25	Green River Hatchery	87	1971	0.282	0.155	0.563	0.000	Utter et al. (1973)
26	Green River Hatchery	58	1974	0.353	0.190	0.457	0.000	May (1975)
27	Puyallup Hatchery	60	1974	0.358	0.150	0.492	0.000	May (1975)
28	Minter Creek Hatchery	50	1968	0.410	0.060	0.530	0.000	Utter et al. (1970)
29	Minter Creek Hatchery	84	1971	0.357	0.140	0.503	0.000	Utter et al. (1973)
30	Minter Creek Hatchery	175	1972	0.289	0.200	0.510	0.000	May and Utter[2]
31	Minter Creek Hatchery	79	1974	0.215	0.259	0.526	0.000	May (1975)
32	Minter Creek Hatchery	34	1990	0.338	0.235	0.426	0.000	NMFS[3]
33	George Adams Hatchery	88	1974	0.295	0.341	0.364	0.000	May (1975)
34	Quilcene River Hatchery	60	1968	0.200	0.125	0.675	0.000	Utter et al. (1970)
35	Quilcene River Hatchery	60	1971	0.200	0.125	0.675	0.000	Utter et al. (1973)
36	Dungeness River Hatchery	47	1971	0.287	0.266	0.447	0.000	Utter et al. (1973)
37	Dungeness River Hatchery	80	1985	0.331	0.313	0.356	0.000	NMFS[3]
38	Soleduck River Hatchery	50	1971	0.190	0.220	0.590	0.000	Utter et al. (1973)
39	Simpson Hatchery	127	1972	0.378	0.224	0.398	0.000	May and Utter[2]
40	Simpson Hatchery	40	1992	0.275	0.212	0.513	0.000	NMFS[3]
41	Chehalis Hatchery	51	1971	0.373	0.236	0.411	0.000	Utter et al. (1973)
42	Newaukem River at Green River Hatchery	42	1974	0.393	0.119	0.488	0.000	May (1975)
43	Willapa River Hatchery	50	1971	0.280	0.350	0.370	0.000	Utter et al. (1973)
44	Willapa River Hatchery	37	1990	0.338	0.054	0.608	0.000	NMFS[3]
45	Nemah Hatchery	50	1971	0.300	0.180	0.520	0.000	Utter et al. (1973)
46	Nemah Hatchery	74	1974	0.223	0.216	0.561	0.000	May (1975)
47	Grays River Hatchery	39	1989	0.872	0.038	0.090	0.000	NMFS[3]
48	Klaskanine Hatchery	85	1990	0.653	0.029	0.318	0.000	NMFS[3]
49	Big Creek Hatchery	77	1989	0.812	0.013	0.175	0.000	NMFS[3]
50	Big Creek Hatchery	100	1990	0.675	0.015	0.310	0.000	NMFS[3]
51	Elokomin Hatchery	50	1968	0.800	0.000	0.200	0.000	Utter et al. (1970)
52	Elokomin Hatchery	98	1971	0.786	0.000	0.214	0.000	Utter et al. (1973)
53	Clatskanie River	31	1989	0.855	0.097	0.048	0.000	NMFS[3]
54	Lacamas River at Cowlitz Hatchery	32	1974	0.906	0.063	0.031	0.000	May (1975)

Continued on next page

Table 1 (continued)

Sample number	Name	Sample size	Brood year	Allele frequencies *103	*100	*97	*106	Source
55	Cowlitz Hatchery, Early	70	1989	0.908	0.021	0.043	0.028	NMFS[3]
56	Cowlitz Hatchery, Late	39	1989	0.961	0.013	0.000	0.026	NMFS[3]
57	Cowlitz Hatchery	50	1971	1.000	0.000	0.000	0.000	Utter et al. (1973)
58	Cowlitz Hatchery	38	1983	0.974	0.013	0.013	0.000	Gall[4]
59	Cowlitz Hatchery	52	1983	0.894	0.077	0.190	0.010	Gall[4]
60	Cowlitz Hatchery	100	1990	0.955	0.025	0.020	0.000	NMFS[3]
61	Toutle River Hatchery	50	1968	1.000	0.000	0.000	0.000	Utter et al. (1970)
62	Toutle River Hatchery	100	1971	0.980	0.000	0.020	0.000	Utter et al. (1973)
63	Scappoose Creek	40	1989	0.938	0.038	0.025	0.000	NMFS[3]
64	Lewis Hatchery, Early	78	1989	0.923	0.071	0.006	0.000	NMFS[3]
65	Lewis Hatchery, Late	79	1989	0.962	0.025	0.000	0.013	NMFS[3]
66	Lewis Hatchery, Late	86	1990	0.913	0.029	0.058	0.000	NMFS[3]
67	Speelyai Creek Hatchery	50	1968	0.990	0.000	0.010	0.000	Utter et al. (1970)
68	Speelyai Creek Hatchery	99	1971	1.000	0.000	0.000	0.000	Utter et al. (1973)
69	Speelyai Creek Hatchery	96	1990	0.938	0.010	0.052	0.000	NMFS[3]
70	Rock Creek, East Fork Lewis River	31	1974	0.935	0.000	0.065	0.000	May (1975)
71	Clackamas River	30	1989	1.000	0.000	0.000	0.000	NMFS[3]
72	Eagle Creek at Clackamas Hatchery	50	1983	0.800	0.010	0.190	0.000	Gall[4]
73	Eagle Creek Hatchery	75	1989	0.713	0.167	0.120	0.000	NMFS[3]
74	Eagle Creek Hatchery	96	1990	0.792	0.005	0.203	0.000	NMFS[3]
75	North Fork Clackamas Dam	40	1990	0.900	0.013	0.087	0.000	NMFS[3]
76	Fish Creek, Clackamas River	42	1983	0.774	0.000	0.226	0.000	Gall[4]
77	Sandy River Hatchery	50	1983	0.880	0.000	0.120	0.000	Gall[4]
78	Sandy River Hatchery	75	1989	0.947	0.013	0.040	0.000	NMFS[3]
79	Sandy River Hatchery	100	1990	0.770	0.055	0.175	0.000	NMFS[3]
80	Bonneville Hatchery	49	1983	0.806	0.031	0.163	0.000	Gall[4]
81	Bonneville Hatchery	79	1989	0.949	0.013	0.038	0.000	NMFS[3]
82	Willard Hatchery	80	1989	0.944	0.038	0.019	0.000	NMFS[3]
83	Nehalem River at Nehalem Hatchery	87	1981	0.213	0.109	0.678	0.000	Olin (1984)
84	Nehalem River at Nehalem Hatchery	79	1992	0.209	0.019	0.772	0.000	NMFS[3]
85	Nehalem Hatchery	84	1982	0.226	0.185	0.589	0.000	NMFS[3]
86	Nehalem Hatchery	73	1990	0.445	0.130	0.425	0.000	NMFS[3]
87	Cronin Creek, Nehalem River	36	1981	0.486	0.028	0.486	0.000	Olin (1984)
88	Fishhawk Creek at Nehalem Hatchery	63	1981	0.413	0.198	0.389	0.000	Olin (1984)
89	Trask Hatchery	79	1981	0.285	0.025	0.690	0.000	Olin (1984)
90	Trask Hatchery	117	1991	0.265	0.021	0.714	0.000	NMFS[3]
91	Trask River at Trask Hatchery	79	1992	0.291	0.032	0.677	0.000	NMFS[3]
92	Bogus Creek, Nestucca River	79	1983	0.215	0.017	0.766	0.000	Gall[4]
93	Hawk Creek, Neskowin River	47	1981	0.181	0.053	0.766	0.000	Olin (1984)
94	Salmon River Hatchery	71	1981	0.317	0.141	0.542	0.000	Olin (1984)
95	Salmon River Hatchery	86	1982	0.343	0.116	0.541	0.000	NMFS[3]
96	Salmon River at Salmon River Hatchery	80	1992	0.237	0.094	0.669	0.000	NMFS[3]
97	Siletz River at Salmon River Hatchery	77	1992	0.227	0.026	0.747	0.000	NMFS[3]
98	Beaver Creek	46	1981	0.500	0.250	0.250	0.000	Olin (1984)
99	Alsea River at Fall Creek Hatchery	85	1981	0.259	0.041	0.700	0.000	Olin (1984)
100	Alsea River at Fall Creek Hatchery	44	1992	0.386	0.273	0.341	0.000	NMFS[3]
101	Meadow Creek, Alsea River	41	1981	0.341	0.354	0.305	0.000	Olin (1984)
102	Fall Creek at Fall Creek Hatchery	50	1983	0.240	0.170	0.590	0.000	Gall[4]
103	Fall Creek at Fall Creek Hatchery	68	1992	0.176	0.059	0.765	0.000	NMFS[3]
104	Yachats River	35	1981	0.271	0.314	0.415	0.000	Olin (1984)
105	North Fork Siuslaw River	70	1983	0.371	0.236	0.393	0.000	Gall[4]
106	Elk Creek, Siuslaw River	47	1981	0.457	0.181	0.362	0.000	Olin (1984)
107	Maple Creek	41	1983	0.427	0.402	0.171	0.000	Gall[4]
108	Tahkenitch Lake at Fall Creek Hatchery	77	1992	0.377	0.409	0.214	0.000	NMFS[3]
109	Five Mile Creek	41	1981	0.329	0.341	0.330	0.000	Olin (1984)
110	Johnson Creek	49	1981	0.400	0.500	0.100	0.000	Olin (1984)

Continued on next page

Table 1 (continued)

Sample number	Name	Sample size	Brood year	Allele frequencies *103	*100	*97	*106	Source
111	Umpqua River at Rock Creek Hatchery	74	1981	0.478	0.179	0.343	0.000	Olin (1984)
112	Umpqua River at Rock Creek Hatchery	50	1983	0.570	0.410	0.020	0.000	Gall[4]
113	Umpqua River at Rock Creek Hatchery	69	1992	0.522	0.188	0.290	0.000	NMFS[3]
114	South Fork Umpqua River at Butte Falls Hatchery	70	1992	0.529	0.357	0.114	0.000	NMFS[3]
115	Eel Lake at Butte Falls Hatchery	120	1981	0.280	0.535	0.185	0.000	Olin (1984)
116	Eel Lake at Butte Falls Hatchery	63	1992	0.286	0.492	0.222	0.000	NMFS[3]
117	Tenmile Lake	50	1981	0.466	0.489	0.045	0.000	Olin (1984)
118	Marlow Creek	50	1981	0.375	0.182	0.443	0.000	Olin (1984)
119	Coos River at Cole River Hatchery	65	1992	0.546	0.169	0.285	0.000	NMFS[3]
120	Coquille River	84	1983	0.280	0.535	0.185	0.000	Gall[4]
121	Coquille River at Butte Falls Hatchery	57	1992	0.509	0.412	0.079	0.000	NMFS[3]
122	Coquille River at Butte Falls Hatchery	73	1981	0.570	0.410	0.020	0.000	Olin (1984)
123	Morton Creek	48	1981	0.643	0.204	0.153	0.000	Olin (1984)
124	Rogue River	65	1983	0.869	0.077	0.054	0.000	Gall[4]
125	Rogue River at Cole River Hatchery	57	1992	0.702	0.281	0.018	0.000	NMFS[3]
126	Klamath River at Irongate Hatchery	92	1981	0.852	0.031	0.117	0.000	Olin (1984)
127	Klamath River at Irongate Hatchery	81	1983	0.852	0.031	0.117	0.000	Gall[4]
128	Trinity River Hatchery	83	1983	0.813	0.181	0.000	0.006	Gall[4]
129	Trinity River Hatchery	111	1985	0.831	0.164	0.000	0.005	Bartley (1987)
130	Huckleberry Creek, South Fork Eel River	52	1985	0.837	0.163	0.000	0.000	Bartley (1987)
131	Pudding Creek	47	1985	0.914	0.057	0.029	0.000	Bartley (1987)
132	Caspar Creek	82	1985	0.730	0.230	0.040	0.000	Bartley (1987)
133	Russian Gulch	31	1985	1.000	0.000	0.000	0.000	Bartley (1987)
134	Little River	51	1985	0.929	0.071	0.000	0.000	Bartley (1987)
135	Albion River	30	1985	0.944	0.056	0.000	0.000	Bartley (1987)

[1] Utter, F. M. 1979. Memorandum dated January 19, 1979 to Dr. Keith Sandercock, Canadian Dep. of the Environment, Vancouver, B.C. Subject: Transferrin frequencies of coho salmon from Qualicum and Capillano Hatcheries, 3 p.
[2] May, B., and F. M. Utter. 1974. Biochemical genetic variation of the genus *Oncorhynchus* in Pacific Northwest populations: a progress report and program summary, 12 p. Available: Washington Dep. Fisheries, P.O. Box 43151, Olympia, WA 98504–3151.
[3] Samples analyzed in our laboratory.
[4] Gall, G. A. E. 1991. Allele frequencies of selected stocks of California, coastal Oregon, and Columbia River coho salmon, 59 p. Available: Dep. Animal Sci., Univ. California, Davis, CA 95616-8521.

of juvenile coho salmon between fish from coastal rivers and those from large inland river systems. They concluded that these differences are coastwide and are at least partially genetically determined.

It is possible that there is some selective pressure on the transferrin alleles occurring in large rivers, because all the samples from the Fraser, Columbia, Rogue, and Klamath rivers have high frequencies of the **103* allele, and low frequencies of the **97* allele.

Samples from California clustered with Columbia River samples. California stocks may have been affected by imported stocks: most of California's hatchery stocks originated from eggs imported from Oregon (Bartley et al., 1992), primarily from hatcheries on the Columbia River (Brown et al., 1994).

In other areas, however, stocks appear to follow a regional pattern of genetic differences, despite transfers of fish between geographical areas. For example, the Bonneville and Klaskanine Hatcheries on the Columbia River have received hatchery stocks from northern and southern Oregon (Oregon Dep. Fish and Wildlife[1]), yet still remain most similar genetically to other Columbia River samples (Fig. 2). Again, this could be due to selective factors unique to a given area.

Our findings are similar to results from related genetic studies of coho salmon. Noting allele frequencies at 26 enzyme loci, Wehrhahn and Powell (1987) also found significant differences between samples from Vancouver Island and the southern coastal region of mainland British Columbia. In a study of mitochondrial DNA variation in coho salmon from Oregon, Currens and Farnsworth[2] found that Colum-

[1] Oregon Department of Fish and Wildlife. 1991. Lower Columbia River coho salmon, evaluation of stock status, causes of decline, and critical habitat—Part 2. Report to ESA Administrative Record, 43 p., plus appendices. Available: Oregon Dep. Fish Wildl., P.O. Box 59, Portland, OR 97207.

[2] Currens, K. P., and D. Farnsworth. 1993. Mitochondrial DNA variation in Oregon coho salmon. Report to Oregon Department of Fish and Wildlife, 12 p. Available: Oregon Dep. Fish Wildl., P.O. Box 59, Portland, OR 97207.

bia River samples clustered separately from northern Oregon coastal samples. However, the two southern Oregon coastal samples that they examined (Rogue River and Coquille River) clustered with the Columbia River samples, rather than with samples from the Oregon coast. This result is similar to ours, except that the Coquille River did not cluster with Columbia River samples in our analysis.

Another important discovery was the relatively high level of temporal variation for transferrin allele frequencies. Accurate stock identification from allele-frequency data requires that allele frequencies remain relatively stable over time. Because most coho salmon south of Alaska return to spawn at 3 years of age (Sandercock, 1991), it is possible that allele frequencies for a particular stock could show marked differences between brood years. Waples and Teel (1990) found that for salmon populations where 90% of a brood year returned to spawn in the same year, the probability of finding a significant test for temporal differences increased dramatically.

Our test for temporal allele stability assumed there was no influx of nonnative fish into the gene pool; however, it is unlikely that this assumption was valid. All comparisons were made between samples obtained from hatcheries, and many of these hatcheries have imported and released fish that were not native to the hatchery location. For example, from 1952 to 1991, 20.2% of the coho salmon released at the Minter Creek Hatchery were not native to Minter Creek (Washington Dep. Fish and Wildlife[3]).

Another assumption that we made when testing temporal stability was that no natural selection occurred. Previous studies have found some evidence that transferrin alleles are influenced by natural selection. Suzumoto et al. (1977) observed that fish that have the **97* transferrin allele are less susceptible to bacterial kidney disease (BKD). Pratschner (1978) found that the **103/*103* phenotype had greater resistance to furunculosis, whereas the **97/*97* phenotype was most resistant to vibriosis. A study by McIntyre and Johnson (1977) indicated that fish with a **103/*103* phenotype had a faster growth rate than those with a **103/*97* phenotype, but the escapement rate for the two different phenotypes was equal. However, results of a study by Winter et al. (1980) conflicted with both Suzumoto et al. (1977) and Pratschner (1978). Their results indicated that only certain stocks show a genetically influenced resistance to BKD, furunculosis, and vibriosis. They concluded that "the importance of transferrin genotypes in resistance to disease is stock specific." The extent to which these factors affect transferrin allele frequencies and how they relate to GSI analyses are uncertain. If certain alleles are being selected for, according to location-specific factors, then allele frequencies could be more stable over time for a given location, even after nonnative stocks are introduced into an area. However, if selection factor(s) were to change, allele frequencies would change significantly over time, which would help to explain the large percentage of significant temporal comparisons that we found.

We found at least as much temporal variation between samples analyzed in our own lab as we did between samples analyzed in two different laboratories. Therefore, we ruled out the possibility that temporal variation was due to differing techniques or to differing interpretations of data, or both, in two different laboratories.

These results suggest that before the transferrin locus is used in GSI analysis, temporal variation of allele frequencies between brood years will need to be considered. However, temporal variation does not necessarily preclude the use of the transferrin locus in GSI analysis. In a study of temporal variation in lake trout, *Salvelinus namaycush*, Grewe et al. (1994) found that although there were significant differences in allele frequencies between year classes, the accuracy of their mixed-stock contribution estimates was not substantially affected. Waples (1990) suggested that to obtain maximum precision of estimates, temporally spaced samples should be pooled, unless the temporal differences are too large to be attributable to sampling error and to genetic drift. Of course, if the baseline data include only the brood years known to be contributing to the mixed-stock, temporal variation will not be a problem.

The mean heterozygosity value we calculated (0.425) was indicative of a high level of heterozygosity for the transferrin locus. This was one of the highest mean heterozygosity values we have observed for any polymorphic locus in coho salmon (Van Doornik, unpubl. data). It is also one of the highest mean heterozygosity values in comparison with other studies of salmonids. For example, the highest mean heterozygosity found by Wehrhahn and Powell (1987) in their study of 26 coho salmon loci from 95 sites in British Columbia was 0.0099 for the locus *LDH-B2** (transferrin was not included in this study). The largest mean heterozygosity value, in a study of 25 loci of 86 populations of chinook salmon, was 0.420 for the locus *PGK-2** (Utter et al., 1989).

As shown by the results from the ANOVA, there were significant differences between samples. The relative gene diversity values showed that there was

[3] Washington Department of Fish and Wildlife. 1994. Historical releases of juvenile salmon into Washington waters, coho salmon. Available: Washington Dep. Fish Wildl., 600 Capitol Way N., Olympia, WA 98501-1091. (Interactive database).

a high degree of genetic differentiation between samples from different geographic regions (22.3%). However, the level of differentiation between samples within regions was actually less than the level of temporal variation. This could be due to the extensive number of stock transfers within regions that have taken place for coho salmon. Therefore, we concluded that although the transferrin locus may be used to discriminate between samples from different geographic regions, caution must be used when attempting to use this locus to discriminate between samples from within a region.

It is important to realize that these results and conclusions are based on data from only one locus. Accurate GSI procedures rely upon baseline data from many polymorphic loci. Our current protocol for obtaining baseline genetic data includes using more than 60 loci that have been shown to be polymorphic for coho salmon. A large baseline of genetic information, from potential source populations and from enough loci with significant allele-frequency differences between stocks, to identify the contributing stocks is generally required for GSI methods to be successful (Milner et al., 1985).

Our results provide further evidence that identifiable regional genetic differences can be detected among coho salmon populations. GSI investigations of coho salmon will be more precise when data from the transferrin locus is used in conjunction with allozyme data and perhaps DNA-type variation (Park et al., 1993). As these data show, the transferrin locus exhibits significant allele-frequency differences between stocks from different geographical areas and has the potential to increase the discriminating power of GSI analyses for coho salmon.

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Abstract.—A catch-length model was constructed to estimate abundance of crab populations for which no survey data are available. The model incorporates stochastic growth by length and gradual recruitment over length and assumes constant catchability. Required data include catch by length and shell condition, fishing effort, growth increment per molt by length, and annual natural mortality rate. Model application to red king crab populations in Bristol Bay and off Kodiak Island, Alaska, generally provides accurate estimates of trends of relative population abundances. The accuracy of absolute abundance estimates depends on knowledge of natural mortality. The model provided a good fit to the catch by length and shell condition for both populations. In comparison to population abundances estimated directly from surveys, the catch-length model performed best with instantaneous natural mortality set equal to 0.4 and with fishing effort and catch-length/shell composition weighted equally in the calculation of residual sum of squares.

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A catch-length analysis for crab populations*

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Molting is one of the most important biological differences between crabs and fishes. The hard structure of crabs is replaced during molting, which makes direct ageing of crabs extremely difficult. The molting process of an individual crab is short, normally a few days, resulting in punctuated growth. Molting frequency of red king crab (RKC, *Paralithodes camtschaticus*) depends on body size and varies over time (Balsiger, 1974). Thus, ability to age crabs indirectly by conventional length-frequency analysis is questionable. Without age information, a conventional catch-age analysis cannot be applied to crab populations.

An alternative to a catch-age analysis is a catch-length analysis which combines information on fishing effort, catch at length, growth, and natural mortality to estimate recruitment and population abundance. During the past decade, much progress has been made to improve catch-length analysis. Lai and Gallucci (1988) examined the effects of parameter variation on length-cohort analysis, Fournier and Doonan (1987) developed a length-based production model, and Schnute (1987) derived a general size-structured population model. Sullivan et al. (1990) constructed a catch-length analysis which incorporates stochastic growth and separates recruitment into year and length components. However, most catch-length analyses were developed or applied to fish populations. Some size-frequency analyses have been conducted for decapods (Jones, 1979; Caddy, 1987; Fogarty and Idoine, 1988), but to our knowledge, few catch-length analyses have been applied to crabs.

Some commercially important crab populations are assessed annually by trawl surveys, and population abundances can be directly estimated from assessment data. Previously, we developed a length-based population model using such crab survey data to estimate population parameters and to improve abundance estimates (Zheng et al., 1995). However, for many crab populations the only usable data available are fishing effort and catch at length. Thus, a logical choice is to estimate abundance of crab populations using these data.

Our purpose in this study is to develop a catch-length analysis to estimate population size for unsurveyed crab populations. We modified the length-based population model developed by Zheng et al. (1995) for application to fishing effort and catch-at-length data that are routinely collected from many

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crab pot fisheries. The model incorporates stochastic growth, in which individual crabs molt with an annual molting probability and gradual recruitment over length. We applied our catch-length analysis to RKC populations in Bristol Bay and off Kodiak Island, Alaska. Bristol Bay RKC have supported one of the most valuable fisheries in the United States. The Kodiak RKC fishery was also very valuable before it collapsed in the early 1980's, and the population has failed to recover since then. We selected these stocks because both populations have been intensively studied during the last three decades and because data are available to estimate biological parameters such as growth and mortality. Moreover, the availability of annual trawl or pot survey data allowed us to compare population abundances estimated from the catch-length analysis and from surveys to determine the reliability of the catch-length analytical methods that we developed.

Methods

Data requirement

Data required for the model include annual length-frequency of commercial catches by shell condition, total annual catch and effort, the mean and variance in growth increment per molt, and natural mortality. Catch-length frequency and total fishing effort are available for most crab populations in Alaska. In this study we defined fishing effort as total annual pot lifts, i.e., the product of the total number of pots fished and the number of times each pot was deployed and retrieved in the fishery. The mean and variation in growth increment per molt can be estimated from tagging data, which are available for some crab populations.

In our study, we estimated the mean and variation in growth increments per molt for Bristol Bay and Kodiak RKC from studies by Balsiger (1974), Powell (1967), and Weber and Miyahara (1962). The model was fitted to RKC fishery data for Bristol Bay from 1974 to 1993 and for Kodiak from 1964 to 1982. Owing to low abundance, the Bristol Bay fishery was closed in 1994, and the Kodiak fishery has been closed since 1983. The RKC fisheries in Alaska harvest only male crabs, and the minimum legal carapace length (CL) is 135 mm for Bristol Bay RKC and 147 mm for Kodiak. Accordingly, we modeled only legal male crabs. The length frequency of catches was summarized by 5-mm intervals, and the largest length group included crabs ≥165 mm CL for Bristol Bay and ≥182 mm CL for Kodiak.

For comparisons, area-swept estimates of Bristol Bay legal male abundance were obtained from trawl surveys conducted by the National Marine Fisheries Service (NMFS) (Stevens et al.[1]). Standardized catch per unit of effort (CPUE) from pot surveys and from tag and recovery data for Kodiak legal male crabs was provided by Peterson et al. (1986). We estimated mean catchability of the Kodiak pot survey using the Petersen mark-recapture equation and annual commercial catch, tag, and recovery data from 1973 to 1979. This allowed us to estimate annual legal male abundances by dividing relative abundance (standardized survey CPUE) by the catchability. These abundance estimates derived from survey data were not used in catch-length analyses but were instead compared to final results of catch-length analyses.

Population model

The population model is similar to the length-based model for Bristol Bay RKC developed by Zheng et al. (1995). Mean growth increment per molt for length class i, G_i, is assumed to be a linear function of mean carapace length ι of the length class just before molting:

$$G_i = a + b\iota, \tag{1}$$

where a and b are the intercept and slope. Parameters a and b were estimated from Weber and Miyahara (1962) to be 13.140 and 0.018 for Bristol Bay, whereas we estimated them from Powell's (1967) data as 41.047 and –0.159 for waters off Kodiak Island.

For flexibility, we chose a gamma distribution to describe the variation in growth increment per molt:

$$g(x \mid \alpha_i, \beta) = x^{\alpha_i - 1} e^{-x/\beta} / \left(\beta^{\alpha_i} \Gamma(\alpha_i)\right), \tag{2}$$

where x is growth increment per molt, α_i and β are parameters, and $\alpha_i = G_i / \beta$. The expected proportion of crabs molting from length class i' to length class i is equal to the integral of the gamma function over the length interval $[i_1, i_2)$ of the receiving length class i:

$$P_{i',i} = \int_{i_1 - \iota}^{i_2 - \iota} g(x \mid \alpha_i, \beta)\, dx, \tag{3}$$

where ι is the mean length of length class i'. For the last length class L, $P_{L,L} = 1$. The variation in growth increment per molt, β, for both populations was set to 0.75, which produced a transitional matrix similar to that estimated by Balsiger (1974) for Bristol Bay RKC.

[1] Stevens, B. G., R. A. MacIntosh, J. A. Haaga, and J. H. Bowerman. 1993. Report to industry on the 1993 eastern Bering Sea crab survey. Alaska Fish. Sci. Center., Natl. Mar. Fish. Serv., NOAA, Seattle, WA, Proc. Rep. 93-14, 53 p.

The molting probability for a given length class and time t is modeled by a logistic function:

$$m_{i,t} = 1 - \frac{1}{1+\phi_t e^{-\omega_t l}}, \tag{4}$$

where ϕ_t and ω_t are parameters, and l is the mean length of length class i. Different logistic functions were used to describe the molting probabilities during different periods. The molting probabilities during different years were grouped to produce a good fit. Three groups were selected for the Bristol Bay RKC: group 1 includes 1974–76, 1980, 1987–88, and 1992–93; group 2 covers 1981–86; and group 3 includes 1977–79 and 1989–91. Two groups were made for the Kodiak RKC: group 1 includes 1964–65, 1972, and 1980–82 and group 2 includes 1966–71 and 1973–79.

Recruitment into the exploitable population is separated into two components: 1) total recruits for year t entering the exploitable population, R_t, and 2) the proportion of recruits belonging to each length class, U_i. This is expressed by

$$R_{i,t} = R_t U_i, \tag{5}$$

where U_i is described by a gamma distribution for flexibility, such as in Equations 2 and 3, with parameters α_r and β_r.

To reduce the number of parameters, we assumed that new-shell and old-shell crabs have the same natural mortality and probability of molting the following year (Zheng et al., 1995). The annual abundance of new-shell crabs is the combined result of growth, mortality, and recruitment:

$$N_{i+1,t+1} = \sum_{i'=1}^{i+1}\left[P_{i',i+1}\left(\begin{array}{l}(N_{i',t}+O_{i',t})e^{-M} - \\ \sum_p\left[(CN_{i',t,p}+CO_{i',t,p})e^{(T_{t,p}-1)M}\right]\end{array}\right)m_{i',t}\right] \times + R_{i+1,t+1}, \tag{6}$$

where $N_{i,t}$ and $O_{i,t}$ are the respective abundances of new-shell and old-shell crabs in length class i on 1 July in year t; $CN_{i,t,p}$ and $CO_{i,t,p}$ are the commercial catches of new-shell and old-shell crabs in length class i, year t, and fishing period p; M is instantaneous natural mortality; and $T_{t,p}$ is the period from 1 July to the mid-point of fishing period p in year t. All recruits are new-shell crabs. Old-shell crabs are crabs that did not molt the previous year:

$$O_{i+1,t+1} = \left(\begin{array}{l}(N_{i+1,t}+O_{i+1,t})e^{-M} - \\ \sum_p\left[\begin{array}{l}(CN_{i+1,t,p}+ \\ CO_{i+1,t,p})e^{(T_{t,p}-1)M}\end{array}\right]\end{array}\right)(1-m_{i+1,t}). \tag{7}$$

The new-shell and old-shell crabs in the last length class were lumped together.

There was only one fishing period each year for the Bristol Bay RKC fishery and for the Kodiak RKC fishery prior to 1974. A second fishing period that targeted large crabs occurred for the Kodiak fishery each year from 1974 to 1982. The catch in the second fishing period was about 10% of that in the first period. We did not use the fishing efforts in the second period because the efforts targeted only a small proportion of the population and were relatively small.

For the first fishing period, the catch by length was estimated as

$$\begin{aligned} CN_{i,t,1} &= TC_{t,1}s_{i,1}N_{i,t}/TB_{t,1}, \\ CO_{i,t,1} &= TC_{t,1}s_{i,1}O_{i,t}/TB_{t,1}, \end{aligned} \tag{8}$$

where $TC_{t,1}$ is total annual observed catch for the first fishing period, and $TB_{t,1}$ is estimated exploitable abundance on 1 July in year t, i.e.

$$TB_{t,1} = \sum_i\left[s_{i,1}(N_{i,t}+O_{i,t})\right], \tag{9}$$

and $s_{i,1}$ is the selectivity coefficient in length class i for the first fishing period. Parameters $s_{1,1}$ and $s_{2,1}$ were estimated for each population, and selectivity coefficients for length class 3 or larger were set to one.

The annual fishing effort for the first fishing period was

$$f_t = TC_{t,1}/(qMB_{t,1}), \tag{10}$$

where q is catchability coefficient for the fishery and $MB_{t,1}$ is mean exploitable abundance during the first fishing period in year t and approximated as

$$MB_{t,1} = TB_{t,1}e^{-T_{t,1}M} - 0.5TC_{t,1}. \tag{11}$$

During the second fishing period for the Kodiak RKC fishery, there were minimum size limits of 168 mm CL from 1974 to 1977, and 157.5 mm CL from 1978 to 1982. Two parameter values, θ_{s1} and θ_{s2}, were estimated for the two minimum size limits:

$$s_{i,t,2} = (e^{(i-i')^2\theta_{st}} - 1)/s_{L,t,2}, \tag{12}$$

where ι is the mean length of length class i, and ι' and L are the mean lengths of the first and last length classes. This selectivity function was chosen, based on the differences of the catch-length frequencies between the first and second fishing periods.

The catch by length for the second fishing period was estimated as

$$CN_{i,t,2} = TC_{t,2}\, s_{i,t,2}(N_{i,t}\, e^{-T_{t,1}M} - CN_{i,t,1})/TB_{t,2},$$
$$CO_{i,t,2} = TC_{t,2}\, s_{i,t,2}(O_{i,t}\, e^{-T_{t,1}M} - CO_{i,t,1})/TB_{t,2}, \quad (13)$$

where $TC_{t,2}$ is total annual observed catch for the second fishing period and $TB_{t,2}$ is estimated exploitable abundance just after the first fishing period in year t, i.e.

$$TB_{t,2} = \sum_i \left[s_{i,t,2} \begin{pmatrix} (N_{i,t} + O_{i,t})e^{-T_{t,1}M} \\ - CN_{i,t,1} - CO_{i,t,1} \end{pmatrix} \right]. \quad (14)$$

Parameter estimation

Model parameters were estimated under the assumption of log normally distributed measurement or observation errors for length compositions of catches and annual fishing efforts. In Alaska, catch data are legally required for sales transactions between fishermen and processors, and it is generally believed that total annual crab catches in Alaska are fairly accurately reported. Thus, no measurement error was imposed on total annual catch for the catch-length analysis. A nonlinear least squares approach was used to minimize the residual sum of squares (RSS) of length compositions of catches and annual effort:

$$RSS = \sum_{i,t,p} \left[\begin{array}{l} \left(\ln(CN_{i,t,p} + c) - \ln(\tilde{C}N_{i,t,p} + c)\right)^2 + \\ \left(\ln(CO_{i,t,p} + c) - \ln(\tilde{C}O_{i,t,p} + c)\right)^2 \end{array} \right] \quad (15)$$
$$+\lambda^2 \sum_t \left[\left(\ln(f_t + 1) - \ln(\tilde{f}_t + 1)\right)^2 \right],$$

where $\tilde{CN}_{i,t,p}$ and $\tilde{CO}_{i,t,p}$ are observed catches for new-shell and old-shell crabs in length class i, year t, and fishing period p; f_t is observed fishing effort in year t for the first fishing period each year; λ is an error weighting factor for fishing effort relative to catch composition; and c is a constant set equal to 0.01×10^6 crabs to avoid taking the logarithm of zero and to reduce the impact of extremely small catches on parameter estimation. Generally, c should be relatively small compared to total catch, but estimation may fail to converge for a very small c.

The subroutine DBCLSF of IMSL FORTRAN (IMSL, 1991) was used to perform nonlinear least-squares parameter estimation through a modified Levenberg-Marquardt algorithm and a finite-difference Jacobian. All parameters were bounded to be nonnegative.

The following model parameters were estimated for each population: recruits for each year, except the first year; total abundance in the first year; parameters α_r and β_r; molting probability parameters ϕ_t and ω_t; selectivity parameters $s_{1,1}$, $s_{2,1}$, θ_{s1} and θ_{s2}; and catchability coefficient q. Starting in the second year, the abundances by length, sex, and shell condition were computed recursively from 1) the abundances by length and shell condition in the first year, 2) annual recruitment, 3) catch, and 4) model parameters. To reduce parameters further, we used the observed frequencies of length and shell classes from first-year catch data to approximate the true catch frequencies. Thus, we had to estimate only total abundance of male crabs for the first year.

Initial values of parameters were approximated by using catch data. A 40% harvest rate was used to convert total catch in the first year into total abundance and the sum of the new-shell catch in the first four length classes each year into recruitment (Zheng et al., 1995). Initial values were interactively updated; the estimated parameters for the first run were used as the initial parameters for the second run, and so on, until no further reduction of total RSS could be made.

Because we did not know the ratio between the variance of catch by length and the variance of fishing effort, we could not use a maximum likelihood approach. Instead, we used seven error weighting factors (λ): 0, 1, 2, 3, 5, 7, and 10 to conduct alternative catch-length analyses and compared the results for different weighting factors.

We did not estimate natural mortality but used several natural mortalities for comparisons. Kruse and Collie[2] and Collie[3] used 0.3 as instantaneous natural mortality for the Bristol Bay and Kodiak le-

[2] Kruse, G. H., and J. S. Collie. 1991. Preliminary application of a population size estimation model to the Bristol Bay stock of red king crabs. Alaska Dep. Fish Game, Comm. Fish. Div., Reg. Information Rep. 5J91-09, 25 p.

[3] Collie, J. S. 1991. Estimating the abundance of king crab populations from commercial catch and research survey data. Rep. to Alaska Dep. Fish Game. Univ. Alaska, Fairbanks, Rep. 91-03, 27 p.

gal male RKC. Besides 0.3, we also used M of 0.2, 0.4, and 0.5 in our analyses for both populations. In addition, variable natural mortalities—0.2 for periods of 1974–79 and 1985–93, 0.7 for 1980 and 1983–84, and 1.2 for 1981–82—were used for the Bristol Bay population for comparisons based on our previous work with this stock (Zheng et al., 1995).

Results

Bristol Bay red king crab

Model parameter estimates for Bristol Bay RKC depend on natural mortality and weighting factor (Table 1). Higher natural mortality generally resulted in a higher total abundance in the first year and higher annual recruitment. Higher weights applied to fishing effort produced larger total RSS, whereas an intermediate weight resulted in the highest RSS contributed by the fishing effort (Table 1). For a weighting factor of one, total RSS were similar and ranged from 23.4 to 24.8 for all fits (Table 1). Catchability coefficient was negatively associated with natural mortality. Selectivity coefficients were less than one for the first length class for all fits and equal to about one for all other length classes.

The abundances of Bristol Bay legal male RKC estimated from the trawl surveys conducted by NMFS changed dramatically during the last two

Table 1

Summary of parameter estimates by the catch-length analysis for the Bristol Bay red king crab, *Paralithodes camtschaticus*, population for eight fits. Recruits are in thousands of crabs. Variable M is 0.2 for 1974–79 and 1985–93, 0.7 for 1980 and 1983–84, and 1.2 for 1981–82. Total RSS (RSS_{tot}) is equal to the RSS of length compositions of catches (RSS_c) and annual effort (RSS_e).

	M=0.3 λ=0	M=0.3 λ=1	M=0.3 λ=3	M=0.3 λ=10	M=0.2 λ=1	M=0.4 λ=1	M=0.5 λ=1	M=var λ=1
α_r	232.743	244.608	194.611	188.020	222.013	208.456	182.513	223.248
β_r	0.6127	0.5824	0.7249	0.7546	0.6407	0.6761	0.7664	0.6355
ϕ_1	138,820	76,821	105,956	20,075	99,974	257,671	388,794	182,935
ω_1	0.0805	0.0750	0.0763	0.0658	0.0770	0.0832	0.0864	0.0812
ϕ_2	5,193.0	5,136.2	5,157.8	2,699.4	5,424.3	2,818.5	1,797.6	4,666.4
ω_2	0.2000	0.2000	0.2000	0.2000	0.2000	0.2000	0.2000	0.2000
ϕ_3	385,353	4,634,955	3,093,737	579,222	1,537,110	10,721,570	5,192,095	2,621,660
ω_3	0.0773	0.0944	0.0935	0.0836	0.0876	0.1001	0.0954	0.0906
q	NA	0.0023	0.0022	0.0024	0.0028	0.0019	0.0016	0.0024
$S_{1,1}$	0.9834	0.9008	0.8289	0.9379	0.9520	0.7820	0.7412	0.8329
$S_{2,1}$	0.9974	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
N_{74}	19,732.5	21,360.0	20,537.7	18,295.4	17,630.4	25,811.1	31,131.7	18,345.1
R_{75}	15,852.5	16,650.6	16,700.4	16,446.1	14,052.6	19,849.8	23,623.7	14,647.9
R_{76}	14,501.8	14,250.6	13,648.1	13,131.0	12,358.8	16,829.6	19,824.2	12,922.0
R_{77}	24,927.0	22,896.5	17,450.5	13,745.3	18,518.2	27,286.2	32,225.9	21,283.3
R_{78}	34,971.4	34,473.4	27,690.5	22,081.5	26,614.2	40,847.3	47,167.4	33,598.9
R_{79}	24,073.3	25,932.3	27,849.9	28,343.4	23,378.7	29,761.8	33,153.0	27,839.3
R_{80}	18,409.0	19,090.3	22,253.7	21,837.6	19,488.9	20,820.4	22,445.6	25,626.7
R_{81}	1,958.6	2,096.8	2,299.2	3,230.2	1,995.5	2,243.9	2,437.9	3,178.3
R_{82}	354.1	997.2	1,452.6	1,111.6	787.7	1,404.6	1,986.8	1,502.9
R_{83}	547.6	149.8	286.6	229.0	135.9	157.0	174.2	774.0
R_{84}	1,084.5	1,333.0	2,111.7	2,411.7	1,094.2	1,694.5	2,240.7	1,559.8
R_{85}	1,343.6	1,602.3	2,208.4	2,350.4	1,292.2	2,059.8	2,749.6	1,345.3
R_{86}	2,582.5	2,830.2	3,071.4	3,297.8	2,318.2	3,559.0	4,622.2	2,405.0
R_{87}	4,437.1	5,201.8	4,268.0	2,782.2	3,815.0	6,867.2	9,075.5	4,066.3
R_{88}	5,317.7	5,223.7	3,535.5	2,759.2	3,793.1	6,895.0	9,125.6	4,131.9
R_{89}	7,244.1	6,304.6	4,104.7	3,043.8	4,785.9	8,000.4	10,285.6	5,269.1
R_{90}	4,616.4	4,792.3	5,413.8	5,681.4	4,034.9	5,866.9	7,268.1	4,194.0
R_{91}	4,134.6	4,396.6	5,020.9	4,858.1	3,704.9	5,424.8	6,758.2	3,894.6
R_{92}	1,420.0	1,527.6	1,713.1	1,357.2	1,293.8	1,879.8	2,322.0	1,382.3
R_{93}	3,489.0	3,489.4	4,126.9	4,234.4	2,953.3	4,182.8	5,090.3	3,393.6
RSS_{tot}	19.957	24.659	35.028	45.685	24.844	23.999	23.782	23.356
RSS_c	19.957	20.999	30.030	42.629	21.437	20.595	20.461	19.839
RSS_e	0.000	3.660	4.998	3.056	3.407	3.404	3.321	3.517

decades (Stevens et al.[1]). The abundances peaked in the late 1970's and then declined more than 30-fold during the early 1980's (Fig. 1). A moderate recovery occurred in the late 1980's and early 1990's; then abundances decreased again during the last three years. The estimated abundances by different weighting factors with natural mortality of 0.3 generally reflected this trend of crab abundance with different accuracies, although modeled estimates were generally lower than the survey abundances (Fig. 1). The commercial CPUE was adjusted to the same scale as abundances to facilitate comparison, but it did not track well with the abundance trend estimated from the trawl surveys. The CPUE's were much higher in 1974 and 1975 and much lower in 1977 and 1978 than expected from the survey data. The CPUE's from 1984 to 1993 fluctuated around a low level, whereas the abundance increased and then decreased during the same period (Fig. 1). The estimated abundances from catch-length analyses with $\lambda = 0$ and $\lambda = 1$ were very similar, but the abundances in recent years tended to increase beyond a reasonable level without constraints on fishing effort or the recruitment in the terminal year for $\lambda = 0$. The upper limit of recruitment in the terminal year (1993) with $\lambda = 0$ was set to that estimated with $\lambda = 1$ to stabilize estimates. High weighting factor, $\lambda = 3$ or $\lambda = 10$, forced the abundance estimates close to the trend of CPUE. Overall the estimated abundance with $\lambda = 1$ most closely followed the trend of survey abundances (Fig. 1).

The estimated abundances with different instantaneous natural mortality rates followed the trend of survey abundances, and higher natural mortalities resulted in higher abundance estimates (Fig. 2). Generally, $M = 0.4$ produced absolute abundance estimates closer to the trawl survey than other natural mortalities. Variable natural mortality, expressed as three different levels, produced abundance estimates between those with M of 0.2 and 0.5, providing improvement in abundance estimates only during the early 1980's when high natural mortality occurred (Fig. 2).

The observed catches by length were compared to estimated catches by length from the model fit with $\lambda = 1$, with constant M of 0.3 and 0.5, and with three levels of M (Fig. 3). All three fits of the model produced similar catches by length and fit the observed data very well.

The observed and estimated fishing efforts have a similar overall trend but differed by up to 50% in some years (Fig. 4). As expected, larger weighting factors resulted in estimates of fishing effort closer to the observed level.

To explore further the effects of parameters λ and M on model results, we compared estimated length compositions of recruits and molting probabilities for the two most disparate fits (Fig. 5). There was very little variation in length compositions of recruits among different fits. The difference in molting probabilities was less than 15% between any two fits for any given length class within the same time period (Fig. 5) and was less than 5% among most fits for a given length class. The average molting probabilities from all fits for the first group of years were similar to the average molting probabilities estimated by Zheng et al. (1995) from the survey data with one exception. The molting probabilities for the period 1980–

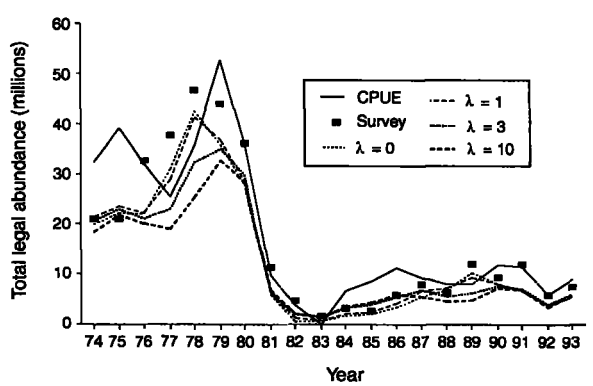

Figure 1

Comparison of estimates of total legal male abundance for Bristol Bay red king crab, with $M = 0.3$ and with different weighting factors (λ). The fishery CPUE (mean catch of legal male crabs per pot lift) was scaled to the same level as abundances. Also shown are NMFS trawl survey estimates of abundance.

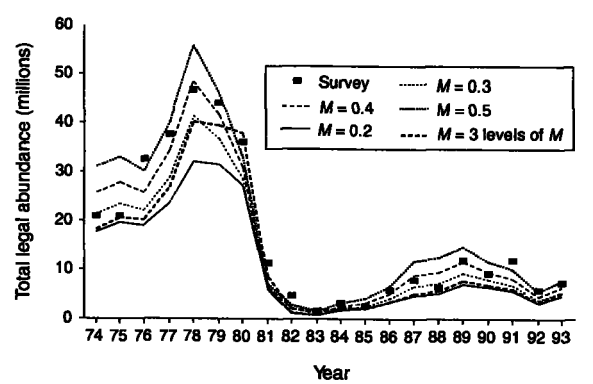

Figure 2

Comparison of estimates of total legal male abundance for Bristol Bay red king crab modeled with weighting factor $\lambda = 1$ and with either constant or variable M at three levels: 0.2 for 1974–79 and 1985–93, 0.7 for 1980 and 1983–84, and 1.2 for 1981–82. Trawl survey estimates of abundance are also shown for comparison.

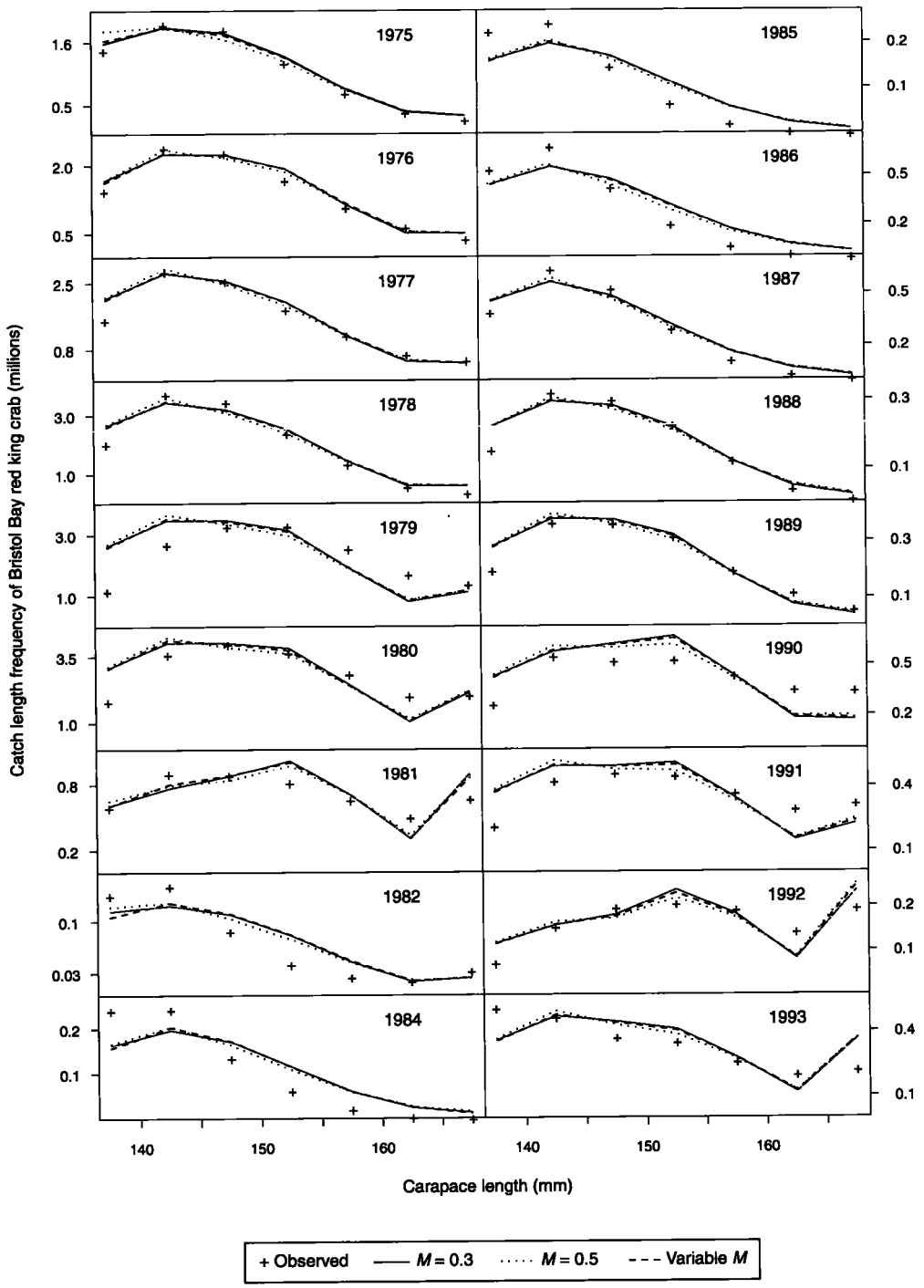

Figure 3

Comparison of observed and estimated length frequencies of Bristol Bay red king crab catches modeled with weighting factor $\lambda = 1$, constant M of 0.3 and 0.5, and with three levels of M (0.2 for 1974–79 and 1985–93, 0.7 for 1980 and 1983–84, and 1.2 for 1981–82).

86 were estimated to be zero, which is biologically unrealistic. The zero molting probabilities were primarily caused by few large new-shell crabs in the catch during this period. The average molting probabilities from all fits during 1977–79 and 1989–91 were slightly higher than those estimated by Zheng et al. (1995).

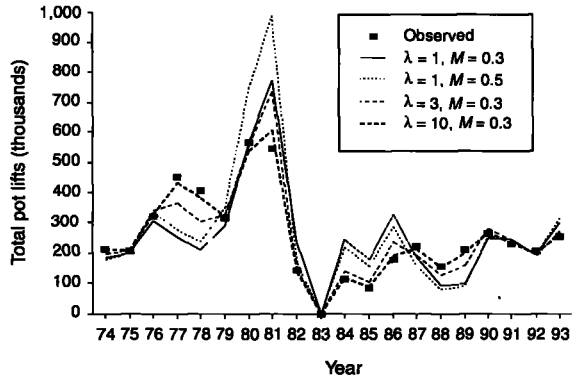

Figure 4

Comparison of observed and estimated fishing efforts of the Bristol Bay red king crab fishery modeled with weighting factor λ = 1 and constant M of 0.3 and 0.5 and with weighting factor λ = 3 and 10 and constant M of 0.3.

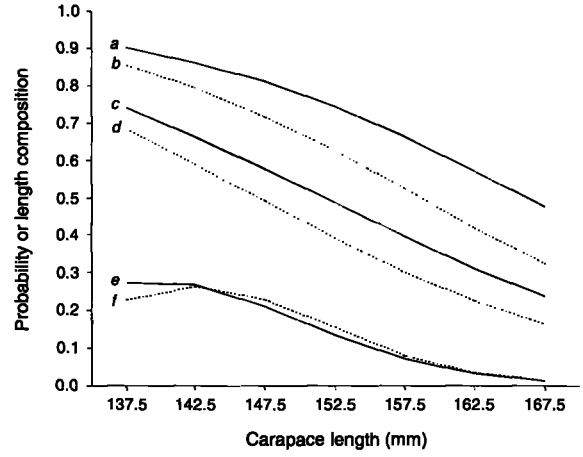

Figure 5

Comparisons of length compositions of recruits (*e*: λ=0 and M=0.3, *f*: λ=10 and M=0.3), molting probabilities during periods 1974–76, 1980, 1987–88, and 1992–93 (*c*: λ=5 and M=0.3, *d*: λ=1 and M=0.3), and during periods 1977–79 and 1989–91 (*a*: λ=1 and M=0.5, *b*: λ=0 and M=0.3) from the two most disparate fits among all model fits for Bristol Bay red king crab.

Kodiak Island red king crab

As in the case of Bristol Bay RKC, the abundance in the first year and annual recruitment of red king crab off Kodiak Island were mainly affected by natural mortality and the weighting factor (Table 2). For all fits, the recruitment in 1965 was much higher than those in other years. With λ = 1, total *RSS* decreased slightly with increasing natural mortality, whereas the *RSS* contributed by fishing effort increased (Table 2). Higher weighting factors resulted in higher total *RSS* (Table 2). For the first fishing period, selectivity coefficients for the first length class were about 0.5, and no selectivity was detected for the other length classes (Table 2). For the second fishing period, catches concentrated on large-size crabs.

The estimated legal male abundances of Kodiak RKC peaked in 1965 and fell to a very low level in the late 1960's (Fig. 6). The population moderately recovered in the early and middle 1970's but declined again in the late 1970's and completely collapsed after 1982. Model estimates of abundance with M = 0.3 and different weighting factors basically followed the same trends as the fishery CPUE and the abundances estimated by pot surveys (Fig. 6). Note that no survey data were available until 1973 (Peterson et al., 1986). Like the results for Bristol Bay RKC, the abundance estimates with λ = 1 followed the trend of survey abundances best among all fits. The scaled CPUE was very close to survey abundance estimates from 1973 to 1977 but were much lower from 1978 to 1981.

Similar to Bristol Bay RKC, the estimated abundances for Kodiak RKC with different natural mortalities had a similar trend over time, and a higher natural mortality produced higher abundance estimates (Fig. 7). The estimated abundances with natural mortality of 0.2 were lower than survey abundances for most years, whereas the abundances estimated with natural mortality of 0.5 were generally higher. With M = 0.4, the closest abundance estimates to survey abundances were produced among all fits (Fig. 7).

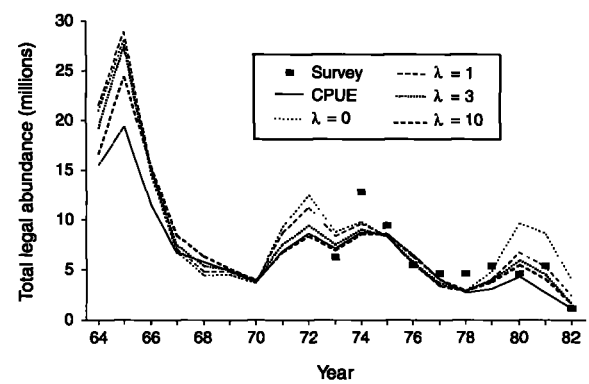

Figure 6

Comparison of estimates of total legal male abundance for Kodiak red king crab with M of 0.3 and different weighting factors (λ). The fishery CPUE was scaled to the same level as abundances.

Table 2

Summary of parameter estimates by the catch-length analysis for the Kodiak red king crab population for seven fits. Recruits are in thousands of crabs. Total *RSS* (RSS_{tot}) is equal to the *RSS* of length compositions of catches (RSS_c) and annual effort (RSS_e).

	M=0.3 λ=0	M=0.3 λ=1	M=0.3 λ=3	M=0.3 λ=10	M=0.2 λ=1	M=0.4 λ=1	M=0.5 λ=1
α_r	81.727	35.562	39.570	34.371	39.576	33.364	37.299
β_r	1.7562	3.4703	3.2294	3.6075	3.2052	3.6289	3.2795
ϕ_1	147,272	135,590	134,336	246,181	121,736	142,585	656,736
ω_1	0.0674	0.0679	0.0684	0.0732	0.0671	0.0683	0.0769
ϕ_2	258,686	5,900,997	5,859,429	6,001,626	5,215,578	5,681,410	3,532,557
ω_2	0.0787	0.0982	0.0981	0.0981	0.0972	0.0982	0.0952
q	NA	0.0045	0.0047	0.0048	0.0050	0.0038	0.0029
$S_{1,1}$	0.5520	0.4481	0.4649	0.4560	0.4538	0.4466	0.4460
$S_{2,1}$	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
θ_{s1}	1.0e-6	1.0e-6	1.0e-6	0.0003	1.0e-6	0.0002	0.0004
θ_{s2}	1.0e-6	1.0e-6	1.0e-6	1.0e-6	1.0e-6	1.0e-6	1.0e-6
N_{64}	20,944.8	21,537.4	19,273.2	16,664.7	18,173.0	25,863.5	32,485.1
R_{65}	17,684.0	18,482.6	18,412.5	17,298.9	16,460.5	20,938.2	24,625.0
R_{66}	4,592.4	5,330.7	6,662.2	8,951.2	4,873.5	5,831.0	6,222.7
R_{67}	2,796.0	3,078.2	3,647.5	5,127.5	2,798.5	3,417.3	3,878.6
R_{68}	3,316.6	3,619.0	4,046.4	4,529.1	3,164.2	4,274.9	5,632.4
R_{69}	3,461.8	3,621.5	3,525.1	3,125.5	3,045.6	4,492.4	6,385.9
R_{70}	2,121.7	2,158.9	2,043.8	2,029.3	1,795.0	2,707.4	3,880.0
R_{71}	8,046.7	7,480.9	6,209.6	5,328.2	5,918.3	9,819.2	15,043.5
R_{72}	8,586.0	7,634.8	6,320.9	5,610.1	6,186.2	9,740.1	14,467.9
R_{73}	4,095.6	4,263.0	4,037.3	3,766.8	3,574.5	5,190.1	6,710.2
R_{74}	5,185.5	5,405.2	5,448.1	5,466.6	4,647.3	6,423.0	8,182.8
R_{75}	4,116.1	4,407.9	4,809.2	5,360.7	3,835.2	5,143.3	6,362.9
R_{76}	2,266.6	2,464.4	2,753.0	3,264.4	2,152.7	2,859.6	3,463.3
R_{77}	1,416.1	1,495.0	1,599.8	1,835.6	1,323.9	1,702.9	2,033.7
R_{78}	1,837.0	1,816.9	1,723.0	1,573.6	1,645.5	2,034.8	2,493.3
R_{79}	4,074.1	3,510.5	3,232.3	3,008.8	3,210.3	3,956.7	5,256.6
R_{80}	8,327.1	5,879.3	5,147.0	4,672.7	5,410.7	6,762.5	9,835.9
R_{81}	6,295.2	4,101.1	3,556.5	3,271.2	3,825.8	4,814.7	6,714.1
R_{82}	1,889.0	1,888.9	1,400.1	1,474.6	1,773.6	2,230.5	2,315.5
RSS_{tot}	35.584	41.165	46.751	53.170	42.361	39.801	36.519
RSS_c	35.584	39.828	43.379	51.876	40.908	38.176	34.181
RSS_e	0.000	1.337	3.372	1.294	1.453	1.625	2.338

The observed catches by length were compared to estimated catches by length from the model fit with λ = 1 and with constant M of 0.3, 0.4, and 0.5 (Fig. 8). All three fits of the model produced similar catches by length and fitted the observed data very well, except data for 1965 and 1982. The poor fit in 1965 was mainly caused by the observed catch-length composition in the initial year (1964). The rapid expansion of fishing grounds during this period made the catch-length compositions inconsistent between these two years. The catch in 1982 was extremely low in comparison to the past annual catches.

The fishing effort was very high during the mid-1960's and the early 1980's (Fig. 9). Like Bristol Bay RKC, larger weighting factors produced estimates of fishing effort closer to the observed effort. With λ = 1, a constant M of 0.3 fitted the fishing effort much better than a constant M of 0.5 (Fig. 9).

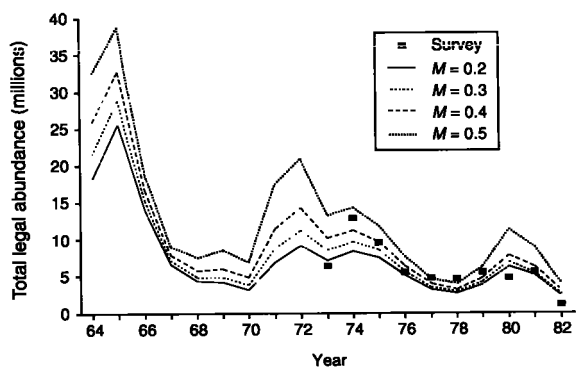

Figure 7

Comparison of estimates of total legal male abundance for Kodiak red king crab modeled with weighting factor λ = 1 and different values of M.

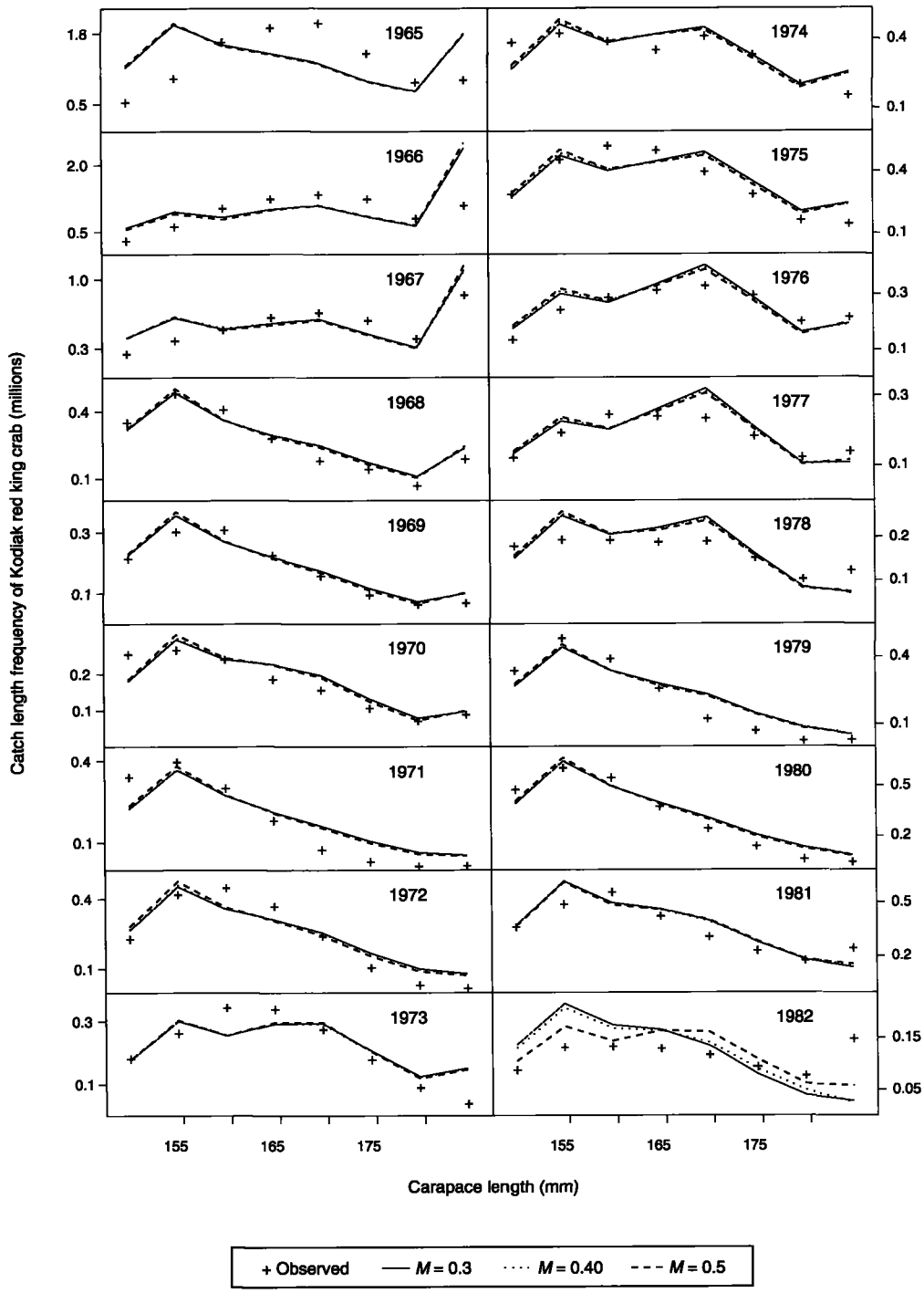

Figure 8

Comparison of observed and estimated length frequencies of Kodiak red king crab catches modeled with weighting factor $\lambda = 1$ and with a constant M of 0.3, 0.4, and 0.5.

Similar to Bristol Bay RKC, there was very little difference in length compositions of recruits among all fits (Fig. 10). The difference in molting probabilities was generally less than 10% between any two fits for any given length class (Fig. 10) and was less than 2% among most fits for a given length class. Molting probabilities for the first group of years were much higher than the second group.

Discussion

Two alternative models have been developed for RKC populations. A measurement error model using catch and survey data was developed to smooth out measurement errors in abundance estimates of legal male crabs composed of two groups: recruits and post-recruits (Collie and Kruse, in press; Kruse and Collie[2]; Collie[3]). The expanded version of the measurement error model is a length-based population model that incorporates stochastic growth and gradual recruitment over length and that estimates abundances of mature crabs of both sexes (Zheng et al., 1995). The length-based model also provides a means to study stock-recruitment relationships and can be used to evaluate harvest strategies. The catch-length analysis we developed in this study is a simplified version of the length-based model constructed by Zheng et al. (1995) and is meant to be applied to crab populations for which no surveys are conducted. The length-based model estimates abundance by producing the best fit to length-frequency data from the survey, and the catch-length analysis estimates abundance by producing the best fit to length-frequency and fishing-effort data from the commercial fleet. The catch-length analysis generally provides accurate estimates of trends of relative population abundances and gives reasonable estimates of absolute abundances provided that M can be approximated.

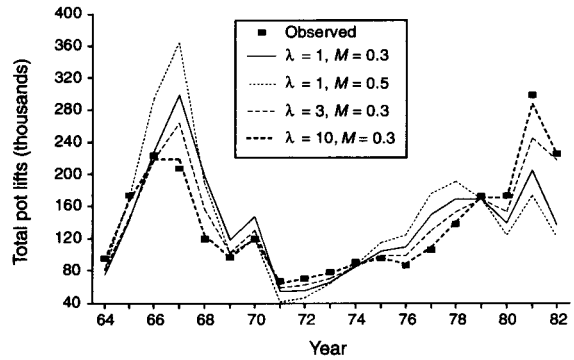

Figure 9

Comparison of observed and estimated fishing efforts of the Kodiak red king crab fishery modeled with weighting factor $\lambda = 1$ and constant M of 0.3 and 0.5 and with weighting factor $\lambda = 3$ and 10 and constant M of 0.3.

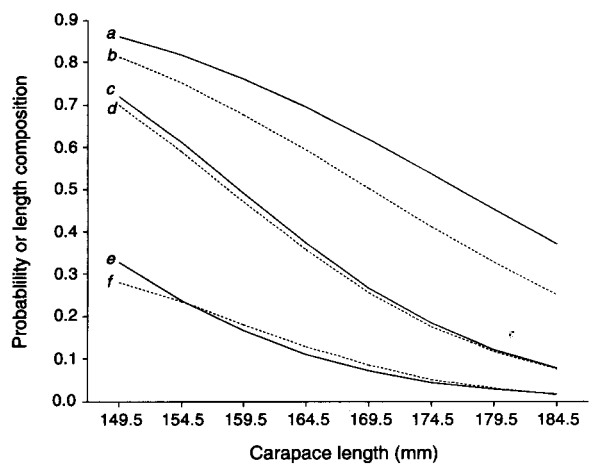

Figure 10

Comparisons of length compositions of recruits (e: λ=0 and M=0.3, f: λ=10 and M=0.3), molting probabilities during periods 1966–71 and 1973–79 (c: λ=1 and M=0.2, d: λ=1 and M=0.5), and during periods 1964–65, 1972, and 1980–82 (a: λ=1 and M=0.5, b: λ=0 and M=0.3) from the two most disparate fits among all model fits for Kodiak red king crab.

The legal male crab abundances estimated from the survey data for both populations were assumed to be absolute and were used to gauge the reliability of the catch-length analysis. A systematic approach was used to survey both populations with complete coverage of areas occupied by large-size crabs (Peterson et al., 1986; Stevens et al.[1]). The length frequency of crabs caught by the survey gears in Bristol Bay and Kodiak indicated that the selectivity of legal male crabs is about equal to one. Catchability of survey gears is difficult to estimate. Zheng et al. (1995) assumed the catchability of the trawl survey for Bristol Bay legal male RKC to be one, and Collie and Kruse (in press) showed that catchabilities of legal male RKC for both populations are close to one. Therefore, our assumption of absolute crab abundances from the survey estimates is reasonable. If this assumption is invalid, the survey abundances still represent relative population abundances, but we cannot use them to compare different levels of natural mortality in the catch-length analysis.

The most important parameter affecting total abundance estimates from the catch-length analysis is M, which has to be estimated separately from the analysis. Published natural mortalities for RKC vary greatly from one study to another and are probably a function of time and length (Schmidt and Pengilly, 1993; Zheng et al., 1995). A constant M of 0.3 was assumed for both Bristol Bay and Kodiak legal male RKC (Kruse and Collie[2]; Collie[3]; NPFMC[4]). Our re-

[4] NPFMC (North Pacific Fishery Management Council). 1990. Environmental assessment for Amendment 1 to the fishery management plan for the commercial king and Tanner crab fisheries in the Bering Sea/Aleutian Islands. North Pacific Fishery Management Council, Anchorage, AK, 27 p.

sults indicate that a constant M of 0.4 provides population abundance estimates closest to the abundances estimated by survey data for both RKC populations. Unlike the results from Zheng et al. (1995), variable M over time improved only slightly the abundance estimates from catch-length analysis. Because it is difficult to estimate M for crab populations, we suggest that a sensitivity study should be conducted to examine the effect of M on estimated abundances. Although M affects absolute abundance greatly, relative abundance is fairly robust to changes in M. Thus, if we are mainly interested in recruitment or population trends, such as those used in fishery oceanography, then uncertainty of M is not a big concern. On the other hand, if we wish to manage an unsurveyed crab stock with a fixed exploitation rate strategy, M must be known fairly accurately in order to avoid consistent over- or under-harvest.

In contrast to M, weighting factor λ primarily affects the estimated trend of a population. By weighting fishing efforts heavily, the population trend most closely resembles the fishery CPUE. The CPUE for crab pots depends not only on exploitable crab abundance, but also on many other factors, such as pot size, soak time, bait, tidal cycle, and vessel characteristics. Pot size is limited by regulations in Alaska and has not changed much over time. Soak time is probably the most important factor but generally is not collected for crab fisheries. Tidal information is available, but the relationship between tidal condition and CPUE may be too complex to be used for effort standardization. Vessel characteristics can be used to adjust for temporal changes in fleet composition, but Johnson (1991) found that vessel characteristics do not effect the relationship between crab density and CPUE for the Kodiak RKC fishery from 1969 to 1982. The CPUE defined as catch per pot lift, which is available for most crab fisheries in Alaska, could explain only partial variation in crab densities. Therefore, heavy weighting of fishing effort would distort the true trend of crab abundance, whereas without fishing effort information the abundances in recent years have tended to be over-estimated. An error-weighting factor of one generally gave a good fit for both RKC populations.

Red king crab tend to aggregate by forming pods much in the same way that some fishes form schools. When crab abundance decreases, the area of distribution shrinks, and crab density in the remaining area is still relatively high. The overall geographic distribution of Bristol Bay RKC has gradually shrunk since crab abundances peaked in the late 1970's. Such aggregate or schooling behavior may produce depensatory catchability (Clark, 1974). When population abundances are low, depensatory catchability can easily result in overestimates of population abundances and overfishing if a constant catchability is assumed. On the other hand, when population abundances are high, abundances may be underestimated because of gear saturation (Bannerot and Austin, 1983). We modified Equation 10 in a manner described by Bannerot and Austin (1983) to compare the results between constant and density-dependent catchabilities. Overall, both relative and absolute abundances estimated under a constant catchability assumption fitted closer to the survey abundances for both populations than those fitted under an assumption of density-dependent catchability. It is conceivable that our fishery CPUE data may not have sufficient information to estimate density-dependent catchability.

As with conventional catch-age or cohort analyses, without auxiliary information there is great uncertainty in estimating the abundance in the terminal year by catch-length analyses. The accuracy of estimated absolute abundance in the terminal year depends on how accurately we can estimate fishing mortality. However, by incorporating fishing effort data, even with large measurement errors, it has been possible to estimate relative abundance trends rather well in most recent years. In cases where fishing effort is not available, an upper limit should be set for recruitment in the terminal year to avoid biasing the trend of relative abundances upward in the most recent years.

The selectivity coefficient for the first length class was estimated to be less than one for all scenarios; thus legal crabs with sizes close to the size limit appear to have a lower catchability. Legal male crabs have been mature for at least one or two years and theoretically should fully recruit to the fishing gear. But the observed catch-length frequency shows that length compositions of the first length class were smaller than those of the second length class for both fisheries and for all years except 1993. This selectivity may be partially caused by throwing back some barely legal-size crabs that were incorrectly measured by fishermen. The catch-length analysis may sometimes fail to estimate selectivity because selectivity coefficients and recruitment parameters may be confounded. A low proportion of recruitment to the first length class of new-shell crabs can cancel the effect of selectivity. We suggest that the selectivity coefficient for the first length class be interactively set to different values less than one during estimation until RSS cannot be further minimized. In recent years, observers have been placed on crab catcher and floater processors in Bristol Bay, and length frequency of the catch has been measured before sorting. In the future, comparison of the time series of length-frequency data on presorted and retained catches could

be used to estimate selectivity, and then selectivity could be fixed in catch-length analyses.

The trend of legal male abundances for Kodiak RKC is similar to that for Bristol Bay RKC, except that the Kodiak stock peaked 13 years prior to Bristol Bay. The high estimated abundance for the Kodiak population in the early 1960's may partly reflect expansion of the fleet to new fishing grounds (Spalinger[5]), whereas the peak abundance for the Bristol Bay population in the late 1970's resulted from strong recruitment (Zheng et al., 1995). Both populations decreased dramatically from their peak abundances within a few years and then fluctuated at low levels over time. When these two populations are examined over the same time scale, the trends are quite different. The abundance for the Bristol Bay population increased greatly from the early to late 1970's, whereas the abundance for the Kodiak population gradually decreased during the same period. The abundances for both populations decreased from 1980 to 1982. Since 1982 the Bristol Bay population has recovered a little, whereas the Kodiak population has completely collapsed and has not been able to support a fishery (Spalinger[5]).

Acknowledgments

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Allozyme variability in two samples of swordfish, *Xiphias gladius* L., in the North Pacific Ocean

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The swordfish, *Xiphias gladius* L., is a cosmopolitan species found in all tropical and temperate oceans (Nakamura, 1983). It is an esteemed food fish and subject to a multinational fishery throughout its range of distribution (Sakagawa, 1989). In 1991 the Pacific catch was 29,245 metric tons (t) or about 44% of the total global catch of 67,142 t (FAO, 1993).

A variety of population structures have been proposed for Pacific swordfish. From one to four stocks have been proposed on the basis of fishery data from all of the Pacific Ocean (Bartoo and Coan, 1989; Skillman, 1989; and Sosa-Nishizaki and Shimizu, 1991). Grijalva-Chon et al. (1994) examined restriction-fragment-length polymorphisms (RFLP) of mitochondrial DNA (mtDNA), and their results supported the hypothesis of one stock in the North Pacific.

Allozyme analyses have been used extensively to study population structure in fishes, especially in fishery resources, because of their relative simplicity (Utter et al., 1974, 1987; Ihssen et al., 1981). Several studies of mtDNA have demonstrated increased resolution for detecting population substructure (Ferris and Berg, 1987), and the methods used in them have complemented each other because they involve different modes of inheritance: with protein electrophoresis, phenotypic data from nuclear loci and from alleles transmitted by sexual reproduction can be analyzed, whereas with the mtDNA method, fragments of haploid DNA that are (usually) maternally inherited and evolve rapidly can be analyzed (Allendorf et al., 1987). The nuclear allelic variants involve sexual exchange among individuals, and one can infer the population fitness or reproductive success through genetic variation (Nevo, 1978). In the case of a fishery resource, fishing mortality alters the frequency of adaptative traits (Nelson and Soulé, 1987).

The intent of this study was to examine the genetic variation at protein-coding loci in swordfish in a preliminary way to test whether swordfish in two localities in the North Pacific were genetically homogeneous.

Materials and methods

Samples of white muscle, liver, and heart from 44 individuals from the N–NE Hawaiian Islands and from 50 individuals from Mexico off Baja California were used to study the allozymic variation (see Grijalva-Chon et al. [1994] for sampling and storage details).

Samples of approximately 5 g of tissue were homogenized in equal volumes of a solution consisting of 0.1 M Tris-HCl pH 8, NAD+, NADP, and polyvinylpyrrolidone (100:0.1:0.1:1, v:w:w:w), with an electric homogenizer (Tissumizer Tekmar). In the case of liver, 0.5 mL of toluene was added. Homogenized samples were centrifuged at 20,000 ×g for 20 minutes at 4°C, and supernatants transferred into capped tubes and stored at –70°C.

The allozyme analysis comprised 15 enzyme systems that encoded 26 presumptive loci (Table 1). In general, the method described by Aebersold et al. (1987) was followed, with the exception that agar was not used in the staining procedure. The support media were 12% starch gels (Sigma S4501).

The criteria of Grant and Utter (1980) and Grant et al. (1984) were followed for zymogram interpretation. Locus nomenclature followed that of Shaklee et al. (1990), which designates the loci in ascending order beginning with number 1 for the most cathodal locus. Alleles for polymorphic loci were designated by using relative electrophoretic mobilities: the most common allele at each locus was designated to be 100.

Data were analyzed with BIOSYS-1 (Swofford and Selander, 1981). A locus was considered poly-

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Table 1

Protein systems and loci resolved in North Pacific swordfish. Buffers: A = Continuous Tris-citratre II, pH 8.0 (Selander et al., 1971); B = Tris-maleate, pH 7.4 (Selander et al., 1971); C = Tris-EDTA-borate, pH 8.0 (Shaw and Prasad, 1970); D = Tris-citrate, pH 8.0 (Tracey et al., 1975); E = Aminopropyl-morpholine, pH 6.1 (Clayton and Tretiak, 1972). Stains: 1 = Shaw and Prasad (1970); 2 = Schaal and Anderson (1974); 3 = Rosa-Velez (1986). E.C.= Enzyme Commission number.

Enzyme or protein	E.C.	Locus	Tissue	Buffer	Stain
Lactate dehydrogenase	1.1.1.27	*LDH-1**	Heart	A	1
		*LDH-2**	Heart		
Glucose-6-phosphate isomerase	5.3.1.9	*GPI-1**	Heart	A	1
		*GPI-2**	Heart		
Malic enzyme	1.1.1.40	*MEP**	Heart	A	2
Phosphoglucomutase	5.4.2.2	*PGM**	Muscle	A	2
Aspartate aminotransferase	2.6.1.1	*AAT-1**	Liver	A	2
		*AAT-2**	Liver		
Glucose-6-phosphate dehydrogenase	1.1.1.49	*G6PDH**	Heart	B	2
Xanthine dehydrogenase	1.1.1.204	*XDH**	Liver	C	2
Glutamate dehydrogenase	1.4.1.3	*GDH**	Liver	C	2
Acid phosphatase	3.1.3.2	*ACP-1**	Liver	D	1
		*ACP-2**	Liver		
Octanol dehydrogenase	1.1.1.73	*ODH**	Liver	D	1
Sorbitol dehydrogenase	1.1.1.14	*SDH-1**	Liver	D	2
		*SDH-2**	Liver		
Glycerol-3-phosphate dehydrogenase	1.1.1.8	*G3PDH**	Liver	D	2
General protein	—	*PROT-1**	Heart	D	3
		*PROT-2**	Heart		
		*PROT-3**	Muscle		
		*PROT-4**	Muscle		
Esterase	3.1.1.-	*EST**	Liver	E	1
Glyceraldehyde-3-phosphate dehydrogenase	1.2.1.12	*GAPDH-1**	Heart	E	2
		*GAPDH-2**	Heart		
		*GAPDH-3**	Heart		
		*GAPDH-4**	Heart		

morphic if the frequency of the most common allele did not exceed 0.95. The mean heterozygosity over all loci was computed following Nei's (1978) unbiased formula. The Hardy-Weinberg equilibrium hypothesis was tested for all polymorphic loci by means of a chi-square (χ^2) test, by pooling genotypes when more than two alleles were observed. Lavene's correction for small sample size and Yates's correction for continuity were applied (Swofford and Selander, 1981). Exact significance probabilities were calculated only to check concordance with the χ^2 test.

Genetic distance (Nei, 1978) between localities was computed. Also, the inbreeding coefficient, F_{is}, and the standarized variance in allelic frequencies, F_{st}, were calculated to measure the amount of divergence among subpopulations (Wright, 1965). The null hypothesis $F_{is}=0$ was tested by means of $\chi^2=F_{is}{}^2n$, with $k(k-1)^2$ degrees of freedom, where k denotes number of alleles (Li and Horvitz, 1953). The null hypothesis $F_{st}=0$ was tested by means of $\chi^2=F_{st}{}^2n$, with $(s-1)(k-1)$ degrees of freedom, where s denotes the number of geographic localities and k the number of alleles (Workman and Niswander, 1970). The heterogeneity of allelic frequencies at polymorphic loci among geographic localities was tested with the log-likelihood ratio test (G-test) with Yates's correction for continuity (Zar, 1984). The number of migrants per generation was estimated by $N_em = (F_{st}{}^{-1}-1)/4$ (Hartl, 1988).

Results

Four out of twenty-six loci were polymorphic: *ODH**, *GPI-1**, *PROT-2**, and *PROT-3**. Table 2 summarizes the genetic variation fish from both localities. The average number of alleles per locus was 1.19 (Mexico), and 1.31 (Hawaii). The observed heterozygosity per locus ranged between 0.000 and 0.341 (Table 3), with a mean of 0.010 in Mexico, and 0.026 in Hawaii. The mean gene diversity for the pooled data was 0.020.

Isocitrate dehydrogenase (IDH) revealed variation in a preliminary survey. Richardson et al. (1986) showed, however, that this enzyme may mimic a genetic polymorphism where in fact it is exhibiting age-related modification. The tissues samples were held

for 1 to 1.5 years at –70°C before analysis. Because of this, IDH was eliminated from the analysis.

Only one locus was out of Hardy-Weinberg equilibrium: *GPI-1** showed heterozygote deficiency in the Mexican sample (Table 3). This result was reflected in the F_{is} value for that locus (Table 4). The genetic distance between populations was very low: it varied between 0.000 and 0.014, with a mean of 0.0007 over all loci.

Table 2

Genetic variation of North Pacific swordfish. Standard errors are in parentheses.

	Mexico	Hawaii
No. of individuals	50	44
No. of loci examined	26	26
No. of polymorphic loci	2	2
Percentage of polymorphic loci	7.69	7.69
No. of alleles per locus	1.19 (0.08)	1.31 (0.11)
Average heterozygosity		
Observed	0.010 (0.005)	0.026 (0.014)
Expected	0.013 (0.006)	0.027 (0.013)

Table 4

Genetic distance, *G*-test for allelic frequencies heterogeneity, and *F*-statistics at polymorphic loci of North Pacific swordfish. * = 0.01 < $P \leq 0.05$; ** = 0.001 < $P \leq 0.01$; and *** = $P \leq 0.001$. *D* = genetic distance; *G* = *G*-test.

	D	*G*	F_{is}	F_{st}
*ODH**	0.001	0.615	–0.054	0.026 (*)
*GPI-1**	0.000	1.837	0.338 (***)	0.008
*PROT-2**	0.002	1.489	–0.082	0.030 (*)
*PROT-3**	0.014	4.851 (*)	–0.183	0.066 (***)
Totals		8.792 (*)	–0.013	0.039 (**)

Table 3

Allelic frequencies, heterozygosity, and Hardy-Weinberg expectations of phenotypes at four polymorphic loci. Number of individuals are in brackets. Differences in sample sizes were due to inactivation of enzymes. ns= not significant; ** = $P \leq 0.01$.

					Heterozygosity			Phenotype frequencies		
Locus	Locality	Allelic frequencies			Observed	Expected	Phenotype	Observed	Expected	Chi-square
		*100	*114							
*ODH**	Mexico	0.949	0.051		0.103	0.099	A	0	0.780	0.000 (ns)
	[39]						AB	4	3.844	
							B	35	35.078	
	Hawaii	1.000	0.000		0.000	0.000	A	0		
	[42]						AB	0		
							B	42		
		*75	*100	*119						
*GPI-1**	Mexico	0.070	0.930	0.000	0.060	0.132	B	45	43.212	9.296 (**)
	[50]						BC	3	6.576	
							C	2	0.212	
	Hawaii	0.024	0.963	0.012	0.073	0.072	A	0	0.000	0.000 (ns)
	[41]						AB	1	0.975	
							AC	0	0.025	
							B	38	38.037	
							BC	2	1.951	
							C	0	0.012	
		*100	*175							
*PROT-2**	Mexico	0.990	0.010		0.020	0.020	A	0	0	0.000 (ns)
	[50]						AB	1	1	
							B	49	49	
	Hawaii	0.917	0.083		0.167	0.155	A	0	0.253	0.000 (ns)
	[42]						AB	7	0.494	
							B	35	35.253	
		*100	*175							
*PROT-3**	Mexico	0.980	0.020		0.040	0.040	A	0	0.010	0.000 (ns)
	[50]						AB	2	1.980	
							B	48	48.010	
	Hawaii	0.829	0.171		0.341	0.287	A	0	1.123	0.619 (ns)
	[41]						AB	14	11.753	
							B	27	28.123	

The analysis of heterogeneity of allelic frequencies showed relatively small but significant differences (Table 4), with the total G=8.79 (P<0.05). The weighted average of F_{is} was –0.013, not different from zero (P>0.05), and the weighted average of F_{st} was 0.039, different from zero (P<0.001). Considering the F_{st} value, the estimated number of migrants per generation was 6.2.

Discussion

North Pacific swordfish exhibit low heterozygosity. The heterozygosity in swordfish, 0.020, is low compared with the averages of 0.055 (Smith and Fujio, 1982) and 0.064 (Ward et al., 1994) reported for marine fishes. For bony fishes in general, Nevo (1978) and Winans (1980) reported 0.051 and 0.048, respectively. The Pacific blue marlin, *Makaira nigricans*, another billfish, showed a mean heterozygosity of 0.06 (Shaklee et al., 1983).

Both *PROT-2** and *PROT-3** were polymorphic in the Hawaiian population; however, the latter was responsible for the significant differences in allelic frequencies. Although *PROT-3** drove the final result in the analysis of allelic frequencies, *ODH** and *PROT-2** also contributed in a significant way to the amount of divergence as denoted by F_{st}.

The locus *IDH** showed a high number of heterozygous organisms in the Hawaiian samples during the preliminary analysis, but that result was doubtful considering the delicate nature of that enzyme (Richardson et al., 1986). Future studies should use tissues that are as fresh as possible.

The observed heterogeneity in allelic frequencies among the two samples was an unexpected result. Recently, Grijalva-Chon et al. (1994) reported no differences in genotypic frequencies in a restriction analysis of mtDNA of North Pacific swordfish and could not reject the null hypothesis of a single population. Chow (1994) carried out PCR-RFLP analysis on the control region of mtDNA and found no differences in the haplotype frequencies between western (Japan) and eastern (Baja California) Pacific specimens of swordfish.

A widespread opinion is that mtDNA analysis is a more sensitive approach for defining population structure than are allozymes (Ferris and Berg, 1987). In fact, many studies using mtDNA analysis in several species have confirmed preliminary results of stock identification or have shown differences that other methods have not detected (e.g. Avise et al., 1986; Kornfield, 1986; Hanzawa et al., 1987; Kornfield and Bogdanowicz, 1987; Ward et al., 1989).

Recently, incongruent results have been reported with mtDNA and allozymes. Ferguson et al. (1991) did not find evidence of population structure in brook char, *Salvelinus fontinalis*, using mtDNA analysis. Allozymatic variation showed, however, a significant divergence among sampled localities. Stott et al. (1992) concluded that American plaice, *Hippoglossoides platessoides*, comprise a single population in the Canadian Atlantic coast; mtDNA analysis gave less resolution than did allozymes. Also, Ward et al. (1994) reported that yellowfin tuna, *Thunnus albacares*, from the Pacific Ocean form at least two groups or populations according to allozyme analysis, comprising five polymorphic loci and contrasting with the homogeneity suggested by mtDNA restriction analysis.

Results obtained here could be explained by a recent population "bottleneck," which would have had a bigger effect on mtDNA than on nuclear genes (Ferris and Berg, 1987). However, it is very difficult to fix the time of such a bottleneck from allozyme data because, where a specific genetic distance value is obtained, the divergence time interval is very wide (Hillis and Moritz, 1990).

Another possible explanation lies in the population sex ratio. Birky et al. (1989) pointed out that extranuclear genes may show a more subdivided population than do nuclear genes, but this feature can be reversed if females are in excess. The sex ratio in our samples indicate a skew toward females (4.8:1 in samples from Mexico and 2.7:1 from Hawaii), and data from several fishing campaigns in Baja California during 1992 and 1993 indicate consistently high female:male ratios (~5.8:1, Castro-Longoria[1]). The observed sex ratio in Baja California waters, however, is not sufficiently skewed to explain the observed difference. In accordance with Birky et al. (1989), the number of females must always be more than seven per male for nuclear genes to show more subdivision than extranuclear genes.

Because the gene flow suggested by N_em was higher than the required value to prevent differentiation due to genetic drift, the third alternative explanation could be some kind of selection. In our case, the hypothesis is that selection supported a significant heterogeneity in the face of genetic flow. The proof of this hypothesis is beyond the scope of this paper. In accordance with Lewontin (1991), it is not possible to discriminate between selectionism and neutralism with static-type data such as ours.

For fishery management purposes, it is important to establish clearly the presence or absence of genetic differentiation of fishery resources among geo-

[1] Castro-Longoria, R. 1994. Universidad de Sonora, CICTUS, Rosales y Niños Héroes s/n., Hermosillo, Sonora, México. Personal commun.

graphic areas. It is widely agreed that the absence of genetic differences, as suggested by allozyme analysis, cannot be attributed to genetic identity at the DNA level (Utter et al., 1987). When differences are evident from allozyme analysis, however, the possibility of population differentiation exists to some degree. According to our results, the genetic population structure of swordfish in the North Pacific is more complicated than previously shown by Chow (1994) and Grijalva-Chon et al. (1994). From the fishery resources management point of view, it is necessary to corroborate the status of swordfish populations throughout the Pacific Ocean both with a DNA-based character set and with allozyme analysis. Moreover, future studies should include a sampling strategy that analyzes temporal variation.

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Demographic variability in seafood consumption rates among recreational anglers of Santa Monica Bay, California, in 1991–1992

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Abstract.—Contaminated fish in Santa Monica Bay, California, have raised concerns about health risks from local seafood consumption. In preparation for a new health risk analysis, a field study was undertaken to determine local angler consumption rates, consumption characteristics, and angler catch. During 1991–92, biologists interviewed 1,244 anglers on piers, party boats, private boats, and beaches; 555 provided consumption-rate estimates. In contrast to previous studies, non-English as well as English speaking anglers were interviewed. The median seafood consumption rate of 21 g/day for local anglers was less than the national average. Consumption-rate distributions were highly skewed, upper-decile consumption rates being several times higher than median rates. Upper-decile consumption rates were more useful than median rates in delineating demographic and species-specific differences in consumption rates. Angler consumption rates of potentially contaminated species and angler awareness of health risks varied by ethnic group; therefore communication of health risks should target habits and languages of high-risk anglers.

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State and Federal regulatory agencies currently use seafood consumption rates in evaluations of health risks from contaminated seafood organisms (Murray and Burmaster, 1994). The United States Environmental Protection Agency (USEPA) estimates that United States recreational anglers consume a median of 30 g/day of fish and shellfish from national waters (USEPA, 1990). Regional medians range from 26 to 37 g/day (Puffer et al., 1981, 1982; Landolt et al., 1985, 1987; Humphrey, 1988; Murray and Burmaster, 1994; SDCDHS[1]). However, extrapolation of national or nonlocal rates to local angling populations can underestimate health risks (Humphrey, 1988). Consumption rates may vary between studies because angler populations differ demographically and in species preference or because rate-determination methods differ. In this study we examine the influence of variability in angler demography, species preference, and rate-determination

[1] SDCDHS (San Diego County Department of Health Services). 1990. San Diego Bay health risk study. Report prepared for Port of San Diego, San Diego, CA. San Diego County, Dep. Health Serv., San Diego, CA, 322 p.

method on seafood consumption rates in a diverse local angling population in Santa Monica Bay, California.

Santa Monica Bay is an embayment of the southern California coast that borders the Los Angeles metropolitan area, one of the largest urban areas in the United States. The presence of chemically contaminated seafood organisms in Santa Monica Bay has raised public concern about the health risk of eating seafood species caught in the Bay (Pollock et al.[2]; SCCWRP et al.[3], SCCWRP[4]). In particular, white croaker, *Genyonemus lineatus*, a species commonly caught by local recreational anglers, is contaminated in some areas of the Bay (Pollock et al.[2]; SCCWRP et al.[3]). Warnings advising restricted consumption of white croaker have been posted since 1985 (Stull et al., 1987; Pollock et al.[2])

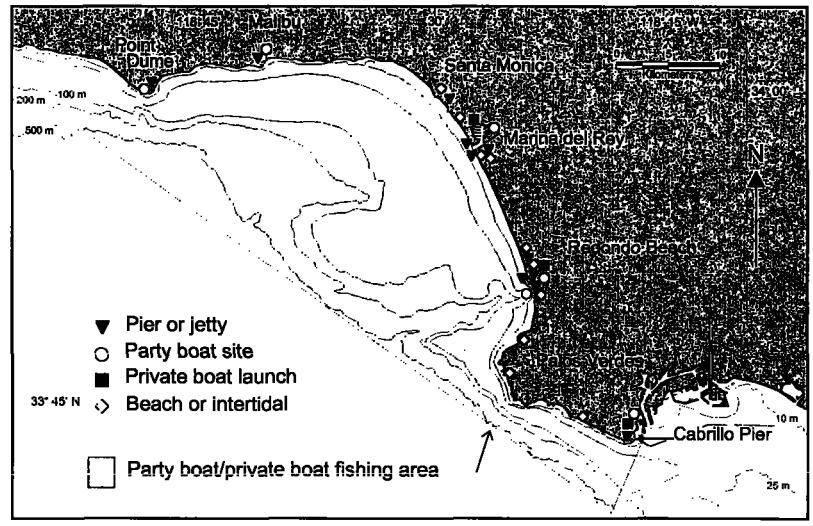

Figure 1

Recreational angler fishing sites sampled in the Santa Monica Bay Seafood Consumption Study, September 1991 to August 1992.

The only study of angler seafood consumption habits for the Los Angeles metropolitan area (including Santa Monica Bay) was conducted in 1980 (Puffer et al., 1981, 1982). The study surveyed more than 1,000 anglers but interviewed only those that spoke English. The median consumption rate of Los Angeles anglers in that study was higher (37 g/day) than the national median (which was 18.7 g/day) (Puffer et al., 1981).

Considering contaminant levels in fish collected in 1987, the State recommended restricted consumption of some species at certain fishing sites in southern California (including Santa Monica Bay) (Pollock et al.[2]). In anticipation of a new risk analysis for the area,[5] a study of seafood consumption habits of Santa Monica Bay recreational anglers was conducted in the early 1990's.[6] The objectives of this study were to describe the demographic and consumption characteristics of Santa Monica Bay anglers, to identify groups with high consumption rates, and to determine the most abundantly caught and consumed species in the early 1990's.

Materials and methods

Field survey

The study area consisted of Santa Monica Bay and adjacent areas, extending from Point Dume to Cabrillo Pier (Fig. 1). It included waters inshore of the 500-m isobath from Point Dume to Cabrillo Pier. We conducted 113 field survey trips at 29 sites on 99 days from 3 September 1991 to 30 August 1992. Interviewers surveyed anglers at piers and jetties (11 sites), party boats (5 sites), private boats (3 sites), and beach and intertidal zones (11 sites) (Fig. 1).

Previous studies indicated that more anglers fish during the summer than during the winter (Stull et al., 1987; NFSP, 1992). Thus, we separated the sampling period into summer (September 1991 and June through August 1992) and nonsummer (October 1991 through May 1992) periods. We conducted survey

[2] Pollock, G. A., I. J. Uhaa, A. M. Fan, J. A. Wisniewski, and I. Witherell. 1991. A study of chemical contamination of marine fish from Southern California. II: Comprehensive study. Calif. Environ. Protection Agency, Office Environ. Health Hazard Assess., Sacramento, CA, 393 p. (161 p. + append.)

[3] SCCWRP (Southern California Coastal Water Research Project), MBC Applied Environmental Sciences, and University of California, Santa Cruz, Trace Organics Facility. 1992. Santa Monica Bay seafood contamination study. Report prepared for Santa Monica Bay Restoration Project, Monterey Park, CA. Southern Calif. Coastal Water Res. Project, Long Beach, CA, 179 p.

[4] SCCWRP (Southern California Coastal Water Research Project). 1994. Contamination of recreational seafood organisms off Southern California. *In* J. N. Cross, C. Francisco, and D. Hallock (eds.), Southern California coastal water research project annual report 1992–1993, p. 100–110. Southern Calif. Coast. Water Res. Project, Westminster, CA.

[5] Santa Monica Bay Restoration Project, Monterey Park, CA, is funding this risk-analysis study.

[6] SCCWRP and MBC (1994) (Footnote 9 in the text) provides a detailed account of sampling protocols, analytical methods, and results of this study.

trips to pier-and-jetty, party-boat, and private-boat sites on two week days and two weekend days per month in summer and on one week day and one weekend day per month in nonsummer.

To minimize sampling bias, we used a stratified-random design to schedule and conduct the survey trips. Fishing modes, regions, sites, and sampling times were selected randomly to maximize spatial coverage of the Bay. For each month, we selected a sampling sequence at random for four regions and sites within each region, using a random numbers table; we surveyed each site in the selected sequence. If a site could not be sampled, we sampled the next site on the list. Sampling was conducted without replacement within a month and with replacement between months.

We chose survey-trip times at random for the three major fishing modes. Interviewers surveyed pier-and-jetty anglers in the morning (0800–1200 h), afternoon (1200–1600 h), or evening (1600–2000 h) with roving surveys. They surveyed party-boat anglers on half-day boats within the study area (full-day boats generally fished outside the area) in the morning (0700–1200 h) or afternoon (1230–1730 h). Private-boat anglers were interviewed at boat launches or hoists in the morning (1000–1400 h) or afternoon (1400–1800 h). Interviewers conducted 1-h beach survey trips before pier-and-jetty surveys and conducted 2-h rocky intertidal surveys on randomly selected afternoons (1300–1700 h) during low tides.

Interviewers tried to interview all anglers at a site. However, if too many anglers were present, they systematically selected every second or third angler. Interviewers censused (counted and characterized) anglers at each site and asked all (or a subset of the anglers) questions from a specially designed questionnaire. All interviewers spoke English; at least one interviewer per survey spoke Spanish; and others spoke Vietnamese, Chinese, or Pilipino. They interviewed a designated household head if two or more individuals from a household were present. Interviewers asked anglers 35 questions regarding their background, their fishing history, the types of fish they had eaten, their consumption habits, their methods of preparing fish, their awareness of health risk warnings, and their response to warnings (Table 1). Anglers chose the ethnic-group category best representing their background from a list used in the most recent United States census report (USBC, 1990).

Interviewers identified to species any fish possessed by anglers and measured its fork length to the nearest centimeter. They showed photographs of important species in order to enable anglers to identify other species consumed during the previous month. The species included bocaccio (*Sebastes paucispinis*), barred sand bass (*Paralabrax nebulifer*), kelp bass (*Paralabrax clathratus*), white croaker, queenfish (*Seriphus politus*), California corbina (*Menticirrhus undulatus*), chub (=Pacific) mackerel (*Scomber japonicus*), and California halibut (*Paralichthys californicus*). Interviewers also carried a balsa-wood model of a 150-g generic fish fillet (based on a fillet of that size obtained from a supermarket [the USEPA standard meal size; USEPA, 1989]). They asked anglers to estimate their meal size for each species (in hand or in photographs) in relation to the fillet model. The fillet model gave the angler a three-dimensional image of the standard meal size.

Data analysis

Questionnaire responses were numerically coded and entered into a computer database for analysis. We calculated consumption rates by two methods. The primary method used the angler's estimates of meal size based on a 150-g fillet model. The other method used consumable-portion sizes of fish possessed by an angler. For the latter method, we converted lengths of fish measured in the field to total and consumable-portion weights. These were estimated for each fish from weight-length regressions[7] and from consumable-portion information.[8] In both methods, we multiplied the amount consumed per meal or the consumable portion by the number of times an angler consumed that species during the previous four weeks. This gave a monthly consumption rate (in grams per month). We divided this rate by 28 days to get daily consumption rates (in grams per day). For the consumable-portion method, we divided the consumable portion by the number of consumers in the household. We did not do this for the fillet-model estimates because we obtained only information on the angler's meal size.

Consumption rate data were summarized by parametric (means, standard deviations, and 95% confidence limits) and nonparametric statistics (median and upper decile or 90th percentiles). We tested for consumption-rate differences among ethnic and income groups using a Kruskal-Wallis one-way analysis of variance on ranked data. We tested for differences between fillet-model and consumable-portion estimates of consumption rates using a Wilcoxon's sign-rank test or paired *t*-test, as appropriate.

[7] S. J. Crooke, Calif. Dep. Fish Game, Long Beach, CA, provided weight-length relationship information.

[8] W. Jacobson, U.S. Dep. Commer., Natl. Ocean. Atmos. Admin., Natl. Mar. Fish. Serv., Los Angeles Reg., Long Beach, CA, provided consumable-portion information.

Table 1

Information collected by a questionnaire administered to recreational anglers during the Santa Monica Bay seafood consumption study, September 1991 to August 1992.

No.	Information
1	Interviewer(s)
2	Date
3	Location
4	Interview time (begin and end)
5	Fishing technique used by angler — hook-and-line (number of poles), other
6	Observed gender of angler
7	Permission or not to interview angler
8	Angler previously or not interviewed for this study
9	Length of time angler fished at location during day of interview (number of hours)
10	Additional time angler expected to fish during day of interview (boat anglers excluded)
11	Number of years or months angler fished in Santa Monica Bay
12	Seasons angler fished
13	Number of times angler fished at location during past four weeks
14	Angler's fishing experience elsewhere in Santa Monica Bay during past four weeks (number of times, fishing mode, site)
15	Number of times angler consumed fish caught in Santa Monica Bay during past four weeks
16	Number of fish caught during day of interview
17	Permission or not to examine angler's catch
18	Species caught:
	a correct species name, angler's name for species
	b fish length (cm)
	c fate of fish (eat, throw back, give away, other)
	d parts of fish consumed (whole gutted, fillet/steak, whole with intestines, other)
	e how much consumed (relative to fillet model)
	f preparation method (fry, broil/barbecue, bake/boil/steam, raw/smoked/ceviche, soup, other)
19	Specific species (shown in photos): (a–f, same as in question 18)
20	Was angler aware of fish consumption health warnings for Santa Monica Bay?
21	How was angler informed of the health warnings (posted signs, TV, newspapers or magazines, anglers/friends, other)?
22	Did angler respond to warnings? (If yes, how? Eat less of all or specific species? Stopped eating all or specific species?)
23	Importance of warnings to angler
24	Angler's town and zip code of residence
25	Angler's occupation
26	Angler's age
27	Angler's racial or ethnic background
28	Number of angler's family members fishing at site that day
29	Others in angler's household: number, ages, participation in and frequency of consumption of catch from Santa Monica Bay, relative amounts eaten (compared with fillet model)
30	Angler's family income
31	Permission to call angler
32	Best time of day to call angler
33	Angler's phone number
34	Angler's name
35	Interviewer observations (quality of interview, survey type, comments, language used in interview)

Results

Angler characteristics and catch

During the survey year, interviewers counted 2,376 anglers and approached 1,740 for interviews. Of those approached, they did not interview 149 (9%) because of language barriers and 347 (20%) because they refused information. They interviewed 1,244 anglers; of these, 555 provided sufficient information for consumption-rate calculations (Table 2). Of these 555 consumers, 232 (42%) were interviewed on party boats, 210 (38%) on piers and jetties, 106 (19%) on private boats, and 7 (1%) at beach and intertidal areas. Hence, we did not consider beach and intertidal areas as a major fishing mode. On the average, they interviewed 52% of the anglers at a site. By mode, the mean percentage interviewed at a site was 59%

Table 2

Sampling success in surveys of recreational anglers by fishing mode and time of week, Santa Monica Bay seafood consumption study, September 1991 to August 1992.

Fishing mode and period	No. survey trips	Anglers: Counted No.	Approached No.	Approached %[1]	Interviewed No.	Interviewed %[2]	Used in study No.	Used in study %[3]
Piers								
Weekday	16	313	333	106	221	66	97	44
Weekend	16	571	453	79	299	66	113	38
Total	32	884	786	89	520	66	210	40
Party boats								
Weekday	16	365	264	72	190	72	101	53
Weekend	16	612	366	60	260	71	132	51
Total	32	977	630	64	450	71	233	52
Private boats								
Weekday	16	131	87	66	75	86	29	39
Weekend	16	350	217	62	183	84	77	42
Total	32	481	304	63	258	85	106	41
Beach								
Weekday	8	14	8	57	7	88	5	71
Weekend	5	8	7	88	4	57	1	25
Total	13	22	15	68	11	73	6	55
Intertidal								
Weekday	4	12	5	42	5	100	0	0
Grand total	113	2,376	1,740	73	1,244	71	555	45

[1] % approached = (no. approached/no. counted) × 100; number of anglers approached for interviews was higher than number initially counted when late-arriving anglers on pier were interviewed.
[2] % interviewed = (no. anglers approached/no. interviewed) × 100.
[3] % used in study (i.e. providing consumption information) = (no. used/no. interviewed) × 100.

at piers and jetties, 54% on private boats, 50% on beaches, 47% on party boats, and 42% at beach and intertidal sites.

Santa Monica Bay anglers comprised several demographic groups. Most were males (93%), 21–40 yr old (54%), and white (43%), with annual household incomes of $25,000–$50,000 (39%) (Fig. 2). Anglers were 8–86 yr old and less than 10% were younger than 21 years. Because we interviewed only household heads, we probably underestimated numbers of anglers below 21 years; therefore, we excluded these from the age-frequency summary (Fig. 2). The following ethnic groups were noted: white, black, Hispanic, and Asian (including Japanese, Koreans, Chinese, Filipinos, Vietnamese, Cambodians, Indonesians, Pakistanis, and Pacific Islanders). The second most abundant ethnic group was Hispanic, followed by Asian, and black (Fig. 2). "Others" included a native American, an Iranian, and an Egyptian, as well as anglers not providing ethnic information. Hispanics were the predominant group on piers and jetties, whereas whites were the predominant group on party boats and private boats (Fig. 3). Most (60%) anglers with incomes below $10,000 fished on piers and jetties. Most (46%) anglers had fished 5 yr or less in Santa Monica Bay, whereas 7% had fished more than 30 yr. Most (63%) anglers fished all year but 19% fished only in summer. About (33%) had not fished during the month (28 days) before the interview, but of those that had, most had fished 3–5 times per month and for 2–5 h at a time.

Interviewed anglers possessed at least 67 species of fish, two species of crustaceans, two species of mollusks, and one species of echinoderm from the study area. The most abundant species were chub mackerel, barred sand bass, kelp bass, white croaker,

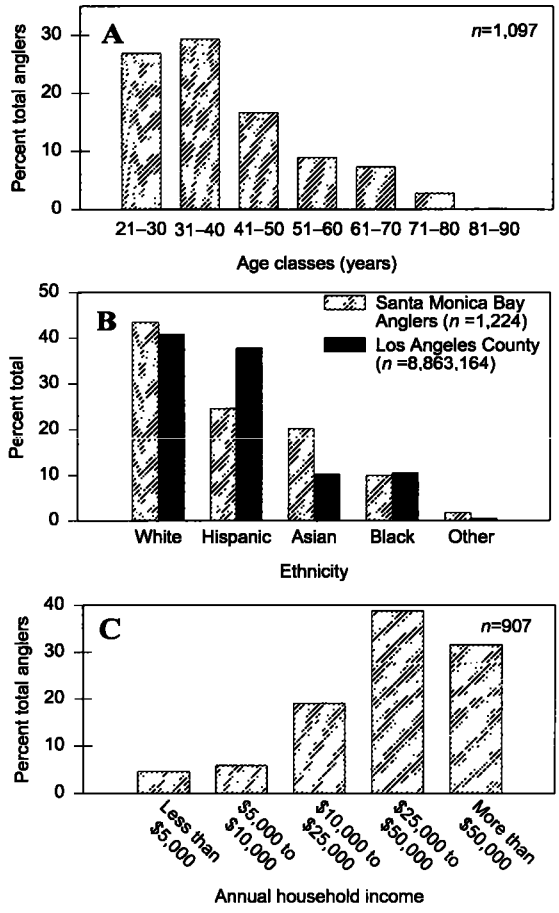

Figure 2

Characteristics of recreational anglers interviewed in the Santa Monica Bay seafood consumption study, September 1991 to August 1992: (**A**) age distribution (anglers older than 20 yr); (**B**) ethnic distribution (anglers and general population of Los Angeles County in 1990 [USBC, 1990]); and (**C**) annual household income distribution (nonrespondents not included).

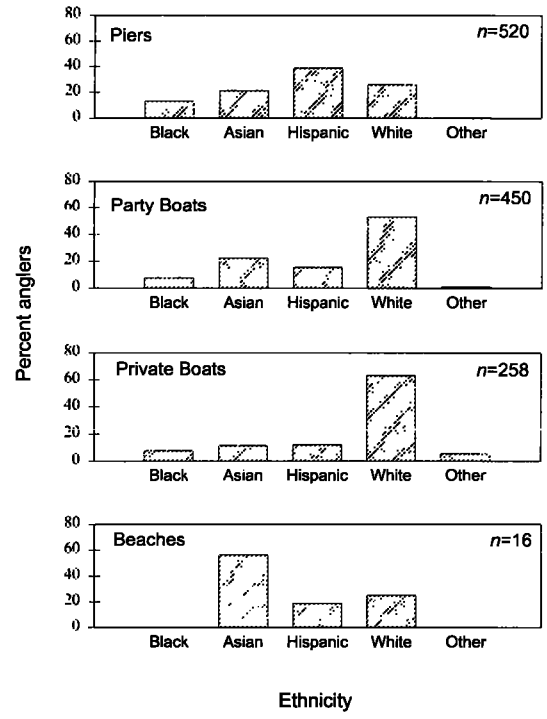

Figure 3

Ethnic distribution of recreational anglers by fishing mode, Santa Monica Bay seafood consumption study, September 1991 to August 1992.

Pacific barracuda (*Sphyraena argentea*), and Pacific bonito (*Sarda chiliensis*) (Table 3). Most anglers could not give the correct common name (Robins et al., 1991) (e.g. Pacific barracuda, chub mackerel) for fish species but generally could give the correct generic common names (e.g. barracuda, mackerel).

Only 45% of the respondents had eaten fish from the Bay within four weeks of the interview, and most anglers had caught fish on the interview day. More party-boat (76%) and private-boat (74%) anglers had caught fish on the interview day than had pier-and-jetty anglers (47%). About 63% of the anglers intended to eat their catch. Private-boat anglers were most likely (70%) and pier-and-jetty anglers least likely (58%) to eat their catch. Pacific bonito, Pacific barracuda, and California halibut were the species most frequently eaten if caught, whereas white croaker, chub mackerel, and queenfish were the species most frequently thrown back.

About 65% of the anglers ate fish steaks or fillets, whereas 33% ate their fish whole but gutted; only 1% ate whole ungutted fish. Whites, blacks, and Hispanics usually ate fish steaks or fillets, whereas Asians ate whole gutted fish with equal frequency. About 47% of the anglers fried their fish, 27% used a variety of cooking methods, and 17% broiled or barbecued their fish. Frying was the most common method of cooking fish for all ethnic groups. However, a combination of methods was important for all groups other than the Hispanic. Broiling and barbecuing was also an important cooking method for whites but less so for the other groups. We did not ask anglers if they consumed fish with or without skin.

Consumption rates

Consumption-rate distributions were strongly right-skewed (Fig. 4). From fillet-model estimates, Santa Monica Bay anglers had a median consumption rate

Table 3

Species most commonly caught by recreational anglers with different fishing modes, Santa Monica Bay seafood consumption study, September 1991 to August 1992.[1]

		Number of organisms				
Common name	Scientific name	Piers or jetties	Party boat	Private boat	Beach or intertidal	Total
chub mackerel	*Scomber japonicus*	476	356	215	0	1,047
barred sand bass	*Paralabrax nebulifer*	1	308	79	0	388
kelp bass	*Paralabrax clathratus*	1	250	76	0	327
white croaker	*Genyonemus lineatus*	167	3	149	0	319
Pacific barracuda	*Sphyraena argentea*	4	202	53	0	259
Pacific bonito	*Sarda chiliensis*	25	124	101	0	250
sea mussel, unidentified	*Mytilus* spp., unidentified	0	0	0	100	100
Pacific purple urchin	*Strongylocentrotus purpuratus*	0	0	0	90	90
jacksmelt	*Atherinopsis californiensis*	64	2	8	0	74
California scorpionfish	*Scorpaena guttata*	3	34	28	0	65
bocaccio	*Sebastes paucispinus*	0	46	16	0	62
California halibut	*Paralichthys californicus*	12	23	27	0	62
halfmoon	*Medialuna californiensis*	0	32	24	0	56
opaleye	*Girella nigricans*	31	0	12	9	52
rockfish, unidentified	*Sebastes* spp., unidentified	0	34	3	0	37
squarespot rockfish	*Sebastes hopkinsi*	0	29	0	0	29
surfperches, unidentified	*Embiotocidae* spp.	18	0	9	0	27
black perch	*Embiotoca jacksoni*	5	0	21	0	26
starry rockfish	*Sebastes constellatus*	0	18	6	0	24
yellowfin croaker	*Umbrina roncador*	16	0	1	3	20
other species combined		95	67	69	11	242
total		918	1,528	897	213	3,556
rockfishes, combined[2]	*Sebastes* spp., combined	4	166	28	0	198

[1] A complete list of observed species is given in SCCWRP and MBC (Footnote 9 in the text).
[2] Rockfishes combined included 15 identified and one unidentified species, some of which (i.e. boccacio, squarespot rockfish, rockfish unidentified, and starry rockfish) are included in the top 20 species shown in this table as separate species and others as other species combined. Because rockfishes are commonly combined in catch summaries, the catch of the group as a whole is also shown separately.

of 21 g/day and an upper-decile rate of 107 g/day (Table 4). Thus about 10% of the anglers had consumption rates more than five times the median (Fig. 4; Table 4).

Consumption rate distributions for ethnic and income groups were also strongly right-skewed. Median consumption rates for ethnic groups ranged from 16 g/day (Hispanics) to 24 g/day (blacks) (Table 4). Although median consumption rates among ethnic groups were not homogeneous (Kruskal-Wallis; H=10.759; df=3; P=0.0131), none differed significantly from each other (Dunn's method). Upper-decile consumption rates ranged from 64 g/day (Hispanics) to 137 g/day (Asians) (Table 4). Although anglers with annual household incomes less than $5,000 had higher median consumption rates (Table 4), these did not differ significantly from the others (Kruskal-Wallis; H=1.776; df = 4; P=0.7768). Upper-decile consumption rates by income group ranged from 48 g/day ($5,000–$10,000) to 129 g/day (>$50,000) (Table 4).

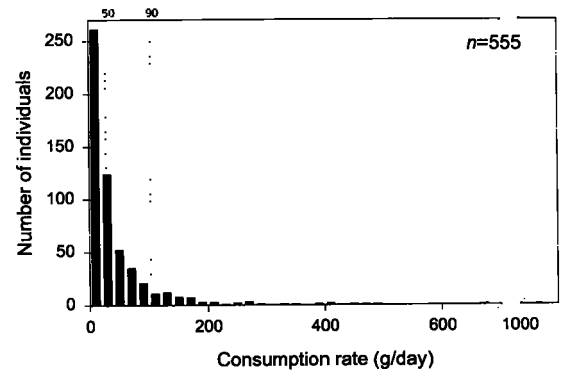

Figure 4

Distribution of seafood consumption rates (all fish species combined) for recreational anglers interviewed in the Santa Monica Bay seafood consumption study, September 1991 to August 1992. Median (50th percentile) and upper decile (90th percentile) are noted with vertical dotted lines.

Table 4

Angler consumption rates of all fish species by ethnic, income, and seasonal groups, Santa Monica Bay seafood consumption study, September–August 1992. CL = ± confidence limit (95%). UD = upper decile (90th percentile).

Category	Number of anglers	Consumption rate (g/day)			
		Mean	CL	Median	UD
Ethnicity[1]					
White	218	58	19	21	116
Hispanic	137	28	6	16	64
Black	57	49	19	24	99
Asian	135	60	20	21	137
Income[2]					
<$5,000	20	42	18	32	64
$5,000–$10,000	27	41	29	21	48
$10,000–$25,000	90	40	9	21	80
$25,000–$50,000	149	47	11	21	113
>$50,000	130	59	21	21	129
Fishing season					
Summer (June–September)	295	55	16	21	113
Nonsummer (October–May)	260	44	8	21	107
Total (all anglers)	555	50	9	21	107

[1] The eight anglers that gave no response to the ethnicity question were not included here. Ethnic categories are those used by USBC (1990).
[2] The 139 anglers that gave no response to the income question were not included here.

Consumption rates of anglers fishing in summer and nonsummer months did not differ significantly (Mann-Whitney rank sum test; T=72,857; n(small)= 260; n(large)=295; P=0.7597). Median consumption rates were 21 g/day for both groups (Table 4).

Median consumption rates of the most commonly caught species were similar (11–16 g/day) but upper-decile rates were more variable (27–80 g/day) (Table 5). Some individuals greatly exceeded average consumption rates for chub mackerel (Fig. 5). Median consumption rates were highest (16 g/day) for barred sand bass, kelp bass, combined rockfish species (*Sebastes* spp.), Pacific bonito, Pacific barracuda, and California halibut (Table 5). Upper-decile consumption rates were highest for kelp bass, barred sand bass, and combined rockfishes (80, 78, and 63 g/day, respectively). Rates of consumption of specific species varied by ethnic group (Table 5). Species with highest median and upper-decile consumption rates, respectively, by ethnic group were as follows: jacksmelt, *Atherinopsis californiensis*, and barred sand bass (white); barred sand bass and chub mackerel (Hispanic); rockfishes and chub mackerel (Asian); and Pacific bonito and California halibut (black).

Consumption rates estimated by the fillet-model and by the consumable-portion methods did not differ significantly for all species, chub mackerel, or kelp bass (Table 6). However, consumable-portion estimates were significantly higher for barred sand bass, Pacific bonito, Pacific barracuda, and California hali-

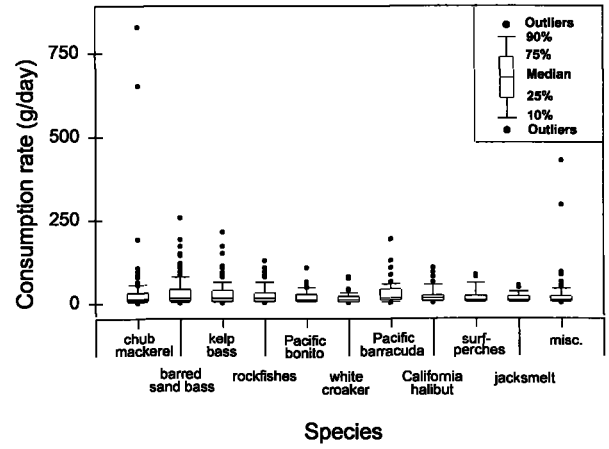

Figure 5

Seafood consumption rates (by fish species) for recreational anglers interviewed in the Santa Monica Bay seafood consumption study, September 1991 to August 1992.

Table 5

Consumption rates (g/day) by fish species for Santa Monica Bay anglers of different ethnic groups, September 1991 to August 1992. n = number of anglers. Md = median (50th percentile) consumption rate in g/day. UD = upper decile (90th percentile) consumption rate in g/day.

	White			Hispanic			Asian			Black			All[1]		
Fish species	n	Md	UD	n	Md	UD	n	Md	UD	n	Md	UD	n	Md	UD
chub mackerel	31	16	48	53	12	43	49	16	98	12	11	24	147	13	54
barred sand bass	72	19	86	20	16	32	35	11	54	16	16	58	144	16	78
kelp bass	75	16	55	14	11	37	34	12	80	16	19	64	140	16	80
rockfishes	50	16	43	13	8	24	28	23	64	10	16	32	101	16	63
Pacific bonito	24	11	30	23	11	36	23	11	44	4	28	54	77	11	44
white croaker	10	11	11	41	11	32	5	5	51	14	13	37	72	11	32
Pacific barracuda	42	21	54	8	11	36	16	11	55	4	24	79	71	16	54
California halibut	39	11	43	5	11	23	9	11	26	8	21	86	62	16	51
surfperches	7	21	44	4	11	14	6	11	32	3	8	59	20	11	27
jacksmelt	5	32	40	9	8	11	5	11	40	4	16	21	23	11	32

[1] Individuals giving no response to the ethnicity question were included in "All" but were not treated as a separate group.

Table 6

Results of Wilcoxon signed-rank test comparing angler seafood consumption rates estimated with fillet-model and consumable-portion methods, Santa Monica Bay seafood consumption study, September 1991 to August 1992. n = number of samples. T_s = smaller sum of ranks. W = difference between sums of ranks.

		Median consumption rate (g/day)		Absolute value		
Species	n	Fillet-model	Consumable-portion	T_s	W	P
chub mackerel	62	10.7	10.7	844	265	0.3547
barred sand bass	46	10.7	18.6	322	437	0.0017
kelp bass	55	10.7	11.8	729	82	0.7344
rockfish spp.	49	8.2	2.1	294	637	0.0016
Pacific bonito	33	10.7	22.5	90	381	<0.0001
white croaker	29	10.7	2.5	78	279	0.0027
Pacific barracuda	35	10.7	26.1	76	478	<0.0001
California halibut	6	10.7	55.7	0	21	0.0313
surfperch spp.	13	8.2	2.1	0	91	0.0017
jacksmelt	14	9.3	2.1	14	77	0.0171
all species[1]	406	10.7	8.2	40,639	1,343	0.7767

[1] Includes the above species and additional single species with both fillet-model and consumable-portion estimates.

but, and significantly lower for rockfishes, white croaker, surfperches, and jacksmelt.

Overall consumption rates were estimated for anglers with fish and for anglers that had consumed a species shown in a photograph during the previous month (Tables 4 and 5). However, consumable-portion estimates included only anglers with fish. Hence, fewer (406) anglers provided information for both estimates (Table 6). In addtion, we compared only individual species that had both consumable-portion and fillet-model estimates. Hence, the overall median (Table 6) was lower than the overall consumption rate according to all species consumed by an angler during the month (Table 4).

Health concerns

Anglers who consumed white croaker, a potentially contaminated species, were mostly male (92%), Hispanic (57%), 21 to 30 years old (26%), and with household incomes of from $10,000 to $25,000 (17%) (Fig. 6). Although more Hispanics consumed white croaker, blacks had the highest median (13 g/day) and Asians the highest upper-decile (51 g/day) consumption rates of this species (Table 5). Most anglers caught white croaker at piers (particularly Cabrillo Pier), fished all year, had fished less than six years, and had eaten this species at least once during the past four weeks. They generally ate the fish whole but gutted, ate about 150 g at a time, and generally fried their catch.

About 77% of anglers were aware of health warnings regarding consumption of Santa Monica Bay fish, most respondents citing television and newspaper or magazine articles as the major source of these warnings (Table 7). Of the anglers who were aware, 50% had altered their seafood consumption habits. The greatest percentage (46%) of these had stopped consuming some species. Most anglers of all ethnic groups were aware of the warnings. Black and Hispanic anglers generally became aware via television, whereas newspapers and magazines were the major source of health warnings for Asian and white anglers. Most Asian and white anglers altered their consumption behavior, but most black and Hispanic anglers did not. Of those responding, the pattern was similar for all ethnic groups: most stopped eating some species and somewhat fewer ate less of all species. White croaker consumers generally became aware of health warnings from a variety of media sources. Although most thought the warnings were very important, half did not alter their consumption habits (Fig. 7).

Discussion

Santa Monica Bay anglers in the early 1990's included relatively more whites and Asians and fewer Hispanics than the overall Los Angeles County popu-

Table 7

Response to health-risk awareness warnings by recreational anglers of different ethnic groups, Santa Monica Bay seafood consumption study, September 1991 to August 1992.

	Ethnic group					
Concern	Black	Asian	Hispanic	White	Other	Total
Number of respondents						
Total number	124	251	306	541	22	1,244
Number aware of warnings	95	185	179	473	10	942
Number affected by warnings	43	104	78	244	3	472
Warning awareness (percent respondents)						
Percent aware	77	74	58	87	45	76
Percent not aware/no response	23	26	42	13	55	24
Source of warnings (percent of aware)[1]						
Percent by television	61	46	64	51	20	53
Percent by newspaper or magazines, or both	45	47	30	58	30	49
Percent by posted signs	33	38	32	31	60	33
Percent by anglers or friends, or both	20	19	14	27	20	22
Percent by other	6	10	7	12	10	10
Response to warnings (percent of aware)						
Percent affected by warnings	45	56	44	52	30	50
Percent not affected	55	44	56	48	70	50
Type of response (percent of affected)						
Percent stopped eating some species	37	52	44	46	0	46
Percent ate less of all species	37	26	28	20	67	25
Percent stopped eating all species	19	13	18	21	0	19
Percent ate less of some species	7	9	10	12	33	11

[1] Respondents could say "yes" to more than one category; hence, percentages may sum to more than 100%.

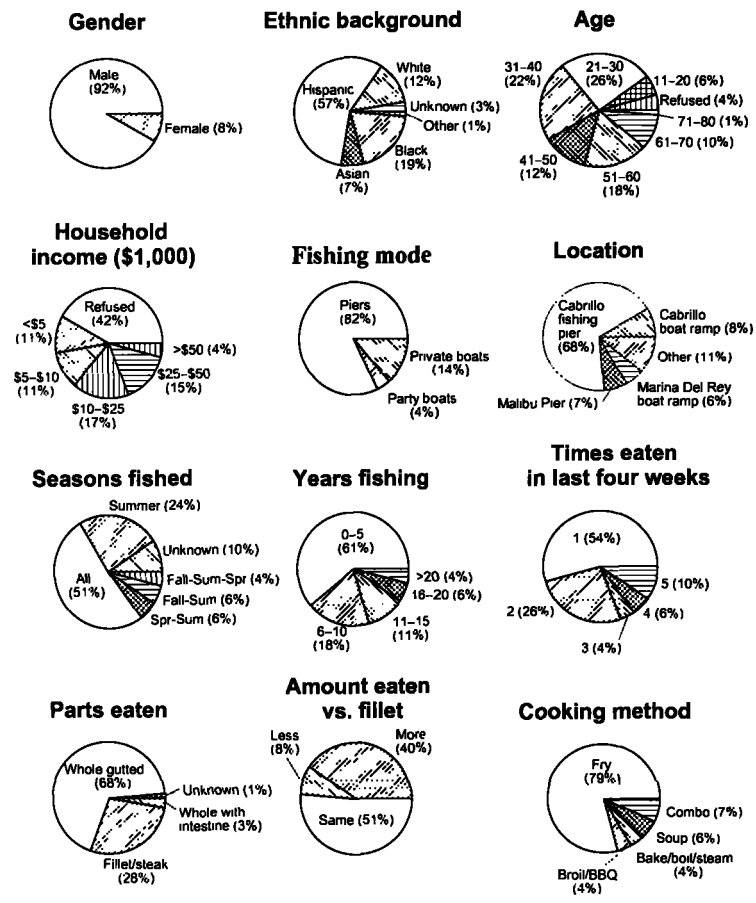

Figure 6

Characteristics of recreational anglers who consumed white croaker, *Genyonemus lineatus*, in the Santa Monica Bay seafood consumption study, September 1991 to August 1992. Sample size = 72 anglers.

lation (Fig. 2) (USBC, 1990; SCCWRP and MBC Applied Environmental Sciences[9]). Surprisingly, the gender, age, and ethnic characteristics of Santa Monica anglers in 1991–92 had not changed much since 1980 (Puffer et al., 1981, 1982).

Santa Monica Bay anglers commonly caught white croaker, chub mackerel, and Pacific bonito in 1980 (Puffer et al. 1981, 1982) and 1991–92. However, they caught fewer white croakers in 1991–92. Local anglers in 1991–92 caught similar species to southern California anglers in 1989, who primarily caught barred sand bass, Pacific bonito, and chub mackerel (NFSP, 1992). In all three surveys, similar survey methods were used and anglers were interviewed at piers and jetties, party boats, and private boats.

In seafood consumption studies, estimated rates are commonly based on consumable portions (Puffer et al., 1981, 1982; Landolt et al., 1985, 1987; SDCDHS[1]). However, in some studies (e.g. Murray and Burmaster, 1994) fillet-model estimates have been used. Of the two methods, we preferred the fillet-model method because the angler gave specific information on meal size. With the consumable-portion method, the number of household consumers influenced the estimated meal size. With consumable-portion estimates, we assumed that household consumers would eat the entire consumable portion and would catch similar-size fish on other fishing days. This resulted in unreasonably high estimates for large and less

[9] SCCWRP (Southern California Coastal Water Research Project) and MBC Applied Environmental Sciences. 1994. Santa Monica Bay seafood consumption study. Report prepared for Santa Monica Bay Restoration Project, Monterey Park, CA. Southern Calif. Coastal Water Res. Project, Westminster, CA, 199 p. (101 p. + appendices.)

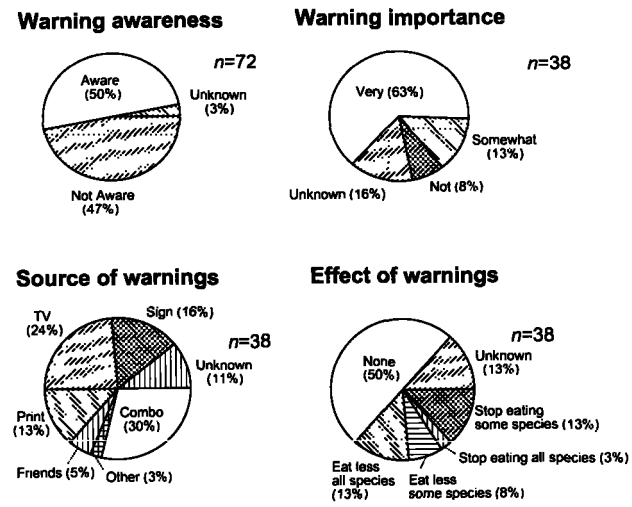

Figure 7

Responses to health risk warnings by Santa Monica Bay anglers who consumed white croaker, *Genyonemus lineatus*, in the Santa Monica Bay seafood consumption study, September 1991 to August 1992.

abundant species (e.g. California halibut). Consumable-portion method estimates were generally higher than fillet-model estimates for larger species and lower for smaller species. With the consumable-portion method, estimated rates were calculated only for species in an angler's possession at the time of the interview. In contrast, the fillet-model method also provided consumption-rate estimates for species not caught on the interview day.

Fillet-model medians varied less between species than did consumable-portion medians (Table 6) because the fillet-model method used fewer measurement units for meal size. The angler estimated meal size in relation to the model size (e.g. 0.5, 1.0, or 2.0 times the model). Thus, if the angler consumed a meal equal in size to the model twice a month, his or her consumption rate would be 10.7 g/day. The consumable-portion medians were more variable, in part because the consumable-portion weights had more divisions (i.e. grams).

Consumption-rate distributions were strongly right-skewed. Hence medians and upper-deciles provided more appropriate summaries than did arithmetic means and 95% confidence limits. The skewed distributions indicate that relatively few anglers had high consumption rates, whereas many had low consumption rates. All demographic groups examined had right-skewed consumption-rate distributions. This was true for all species or individual species. Similar consumption-rate distributions for Michigan anglers were lognormal (Murray and Burmaster, 1994). An upcoming paper[10] will describe statistically the consumption rate distributions from the present study.

In 1989, southern California anglers took 1.85, 1.66, and 1.13 million fishing trips on piers and jetties, private boats, and party boats, respectively (NFSP, 1992). Percentages of total anglers by fishing mode (piers, private boats, and party boats, respectively) were 40, 36, and 24% in 1989 and 42, 21, and 37% in the present study. Pier anglers represented about the same percentage of the population in both surveys. However, the present study differed in having more party-boat than private-boat anglers. Thus, there may be relatively fewer private-boat anglers in Santa Monica Bay than in southern California as a whole. Because the NFSP estimates were from fishing trips, some anglers may have repeated trips. Hence, the trips do not accurately represent the numbers of different anglers (which we needed for consumption rates).

We used only data collected in our study to calculate consumption rates. Where we summarized data for the whole study population, we combined data for each fishing mode (i.e. piers, party boats, and private boats). We did not adjust these estimates for

[10] Hill, M. D., and D. M. Lee. 1996. Estimated distributions of average daily fish consumption rates among Southern California marine anglers. Calif. Environ. Protection Agency, Sacramento, CA. In prep.

possible differences in numbers of anglers using each mode. We did not know how many anglers annually used each mode and could not estimate the numbers without conducting a special study. However, some weighting occurred naturally owing to the different numbers of anglers fishing (and hence being interviewed) in each mode. Given the limitations and available resources of the study, we believe that this natural weighting provided the best estimate of angler population size for each mode.

The median consumption rate (21 g/day) for Santa Monica Bay anglers was 70% of the national median of 30 g/day (USEPA, 1990). Only 45% of the anglers provided sufficient information for determination of consumption rates. Thus, relatively fewer Santa Monica Bay anglers may rely on their catch as a major food source. In 1980 the median consumption rate of Los Angeles anglers (estimated by the consumable-portion method) was higher (37 g/day) than the national median (which was 18.7 g/day) (Puffer et al., 1981). In that study, upper-decile consumption rates were 225 g/day; upper-decile consumption rates in this study were 107 g/day. Thus, seafood consumption rates among local anglers have decreased substantially (median 43% and upper-decile 52%) since 1980. This may be the result of health-risk warnings (posted since 1985) regarding DDT and PCB contamination of some species (Stull et al., 1987).

Santa Monica Bay anglers generally consumed the most commonly caught species at the highest rates. These species included barred sand bass, Pacific barracuda, kelp bass, combined rockfish species, and California halibut, all of which have low PCB and DDT levels (Pollock et al.[2]; SCCWRP et al.[3]). However, anglers also consumed white croaker at relatively high rates even in areas where it has high levels of PCB and DDT (Pollock et al.[2]; SCCWRP et al.[3]; SCCWRP[4]). Hispanic anglers were the primary consumers of white croaker, commonly catching it at Cabrillo Pier (where it is contaminated) (Pollock et al.[2]). However, although more Hispanics consumed white croaker, blacks and Asians had higher consumption rates for this species.

Although current advisories warn anglers not to consume white croaker in Santa Monica Bay and Los Angeles–Long Beach Harbor (Pollock et al.[2]), clearly many anglers still eat this species. Many anglers aware of the warnings did not alter their consumption rates, reasoning that if there was a health risk, they would experience ill effects within a day of eating the fish. Thus, agencies should improve communication of the risks by using a variety of media and languages. For Santa Monica Bay they should communicate risks in English and Spanish (at minimum) via television, newspapers and magazines, and posted signs, emphasizing piers and private boat launches where anglers catch white croaker for consumption.

Conclusions

In 1991–92, median seafood consumption rates for Santa Monica Bay anglers were lower than the national median. Consumption-rate distributions were skewed strongly to the right; upper-decile rates were often considerably higher than medians. Upper-decile rates varied more among demographic groups and species than did median rates; thus upper-decile rates are valuable in identifying high-risk groups. Overall, Asian and high-income anglers had the highest upper-decile consumption rates. Certain ethnic groups consumed more of the potentially contaminated species (e.g. white croaker). The lack of a strong response to health warnings by anglers indicates that health advisories should communicate the health risks from eating contaminated fish to specific ethnic groups at high-risk sites. Overall, consumption rates determined by consumable-portion and fillet-model methods were similar, but some species-specific rates did differ.

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The use of minisatellite DNA variation for stock identification of chum salmon, *Oncorhynchus keta*

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Abstract.—Geographic variation in minisatellite DNA was examined in 42 stocks of chum salmon, *Oncorhynchus keta*, from the eastern and western Pacific by restricting genomic DNA with *Hae*III and hybridizing it with two minisatellite probes. Regional differentiation in allelic frequencies at the two minisatellite loci was observed; Japanese stocks were distinct from Russian and Yukon River stocks, and stocks from those two regions were distinct from stocks in southeast Alaska and British Columbia. No significant annual variation was observed in allelic frequencies at the two loci for three stocks. Simulated mixed fishery samples of 100 Japanese chum salmon were resolved with a baseline of nine Japanese stocks with an average error of 0.5% per mixture stock. Similarly, simulated mixtures of Yukon River chum salmon resolved with a baseline of five stocks resulted in an average error of 0.6% per mixture stock. Fraser River chum salmon mixtures were resolved with an average error of 3% per mixture stock. With Asian and North American stocks pooled into two groups, accuracy of classification for individual fish to continent of origin was 78% for 323 Asian fish, and 94% for 797 North American fish. Minisatellite DNA variation can be successfully applied to problems of stock discrimination in chum salmon.

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Chum salmon, *Oncorhynchus keta*, have the widest natural geographic distribution of all Pacific salmon species, ranging in Asia from Korea to the Arctic coast of Russia, and in North America from California to the Arctic coast of Canada (Salo, 1991). Chum salmon support major fisheries in both Asia and North America, and management of the fisheries in North America usually requires that stock composition of the catches be determined in order to prevent excessive exploitation of particular stocks. A variety of methods have been applied to discriminate among chum salmon populations and to estimate stock composition in fisheries. Early work consisted in applying physical tags to individual fish (Pritchard, 1931; Anderson and Beacham, 1983), but quantitative estimates of stock composition were generally unable to be derived from these studies. Variation in scale characters has also been used for stock identification in chum salmon (Kovtun, 1983; Nikolayeva and Semenets, 1983; Ishida et al., 1989), but the ability to discriminate among stocks in a localized area is limited.

Genetic methods of stock identification for chum salmon have been evaluated by using both protein- and DNA-level variation. Stock identification techniques based upon genetic variation at protein-coding loci have been shown to provide information on stock structure (Okazaki, 1982; Omelchenko et al., 1992; Kondzela et al., 1994; Phelps et al., 1994; Winans et al., 1994) and stock composition in chum salmon fisheries (Beacham et al., 1985, 1987). By screening genetic variation at the DNA level, using mitochondrial DNA variation (Ginatulina and Mashkin, 1990; Ginatulina, 1992; Cronin et al., 1993; Park et al., 1993) and minisatellite DNA variation (Taylor et al., 1994), the population structure of a species can be determined. Variation in minisatellite DNA has been used to provide accurate and precise estimates of stock composition in simulated mixtures in a number of *Oncorhynchus* species (Beacham et al., 1995, 1996; Miller et al., 1996. Minisatellite DNA consists of tandemly repeated arrays of nucleotides where each array contains a core sequence (Jarman and Wells, 1989). Variable numbers of the tandem repeats (VNTR) occur between restriction sites, resulting in allelic variation at the minisatellite locus. Heterozygosity at these loci can be substantially greater than that commonly observed with protein electrophoresis. Average heterozygosity at protein electrophoretic loci is less than 10% in chum salmon (Winans et al., 1994); heterozygosities at minisatellite loci in salmonids are reported to be between 35 and 80% (Taggart and Ferguson, 1990; Bentzen and Wright, 1993; Taylor et al., 1996). The high level

of variation at minisatellite loci offers the potential for increased population differentiation in contrast with other methods of stock identification.

Initial screening of Asian and North American chum salmon populations with a single-locus minisatellite probe suggested that there were three regional groups of populations, namely Japanese, Russian and Yukon River, and southeast Alaska and British Columbia (Taylor et al., 1994). However, detection of population structure or differentiation among populations within the three major regional groups of chum salmon was limited, even though previous surveys of variation at protein-coding loci suggested that there was at least regional structuring within the British Columbia populations (Okazaki, 1982; Beacham et al., 1987). In the current study, variation at two additional minisatellite DNA loci is reported, and the efficacy of using variation at three minisatellite loci to discriminate among chum salmon populations in local areas is evaluated.

Materials and methods

Samples, laboratory procedures, and probes

The stocks surveyed, their geographic locations, and the methods of DNA extraction, restriction enzyme digestion (*Hae*III), Southern blotting, and membrane preparation have been outlined by Taylor et al. (1994). Summarized briefly, 4 µg of *Hae*III-digested DNA were loaded onto agarose gels containing 30 wells. For the 30 lanes on each gel, 4 lanes were used for λDNA restricted with *Hind*III and *Eco*RI as a molecular weight-size marker, and 26 lanes were used for genomic DNA, one of which was a control fish run. DNA was size-fractionated by electrophoresis in 0.8% agarose gels in 0.5× TBE buffer (45 mM Tris-borate, 1 mM EDTA, pH 8.0). After electrophoresis, the agarose gels were depurinated, alkali-denatured, and then the DNA was transferred under vacuum to nylon hybridization membranes and fixed to the membranes by crosslinking under ultraviolet illumination for 3 min.

The probes used in the laboratory analysis were p*Ssa*-A33 and p*Ssa*-A34, hypervariable minisatellite single locus probes in salmonids (Taggart and Ferguson, 1990; Prodöhl et al., 1994). Prior to hybridization with the target probe, the previous probe used was stripped from the membrane by the high temperature method outlined by Noppinger et al. (1992). Following hybridization with each probe, the membranes were washed twice in 2× SSC/0.1% SDS at room temperature for 15 min, once in 2× SSC/0.1% SDS at 65°C for 30 min, once in 1× SSC/0.1% SDS at 65°C for 30 min, and were given a final wash in 1× SSC at room temperature for 15 min. The probes were labelled with ^{32}P, and the membranes exposed to X-ray film. Up to 42 stocks of chum salmon were surveyed in the analysis (the term "stock" was used according to the sense of Ricker (1972), where a stock represents a discrete breeding unit spawning at a given time or place in a river).

Analysis of autoradiographs

The autoradiographs were analyzed with Bioimage software (Millipore Corp. Imaging Systems, Ann Arbor, MI) and scanned with a Kodak high-resolution two-dimensional charge coupled device (CCD) camera at a 1,024 × 1,024 pixel density. The images were translated into digital file images and stored at a workstation for later analysis. Lambda DNA-size markers (21.23, 5.15, 4.97, 4.27, 3.53, and 2.03 kilo base pairs [kbp]) were run on four lanes of each gel and used to create a size standard network that spanned the whole image. Molecular sizes were then assigned by the software to each fragment in each lane on the basis of their relationship to the size standard network. When the p*Ssa*-A33 and p*Ssa*-A34 probes were used, each lane contained either one or two bands; fish with a single band were considered homozygous and two comigrating bands of the same size were scored for those fish. The two probes detect alleles in chum salmon at a single locus where the alleles are inherited in a Mendelian fashion (unpublished data), as was observed for p*Ssa*-A34 in sockeye salmon, *O. nerka* (Taylor et al., 1996), and chinook salmon, *O. tshawytscha* (Stevens et al., 1993), and for both p*Ssa*-A33 and p*Ssa*-A34 in brown trout, *Salmo trutta* (Prodöhl et al., 1994).

Band assignment

Fish from one stock could be analyzed on multiple gels, and thus it was necessary to determine measurement error of band size among gels in order to combine the data. Precision of the estimation of band size was determined by analyzing a standard fish over all gels and by determining the relationship between precision of the estimate and fragment size as outlined by Taylor et al. (1994). As measurement error was present in the estimation of fragment size, a binning procedure (Gill et al., 1990; Galbraith et al., 1991) was used to assign each observed fragment to a particular size class or bin. Distribution of fragment sizes at the *Ssa*-A33 locus ranged from about 4 to 22 kbp, whereas the distribution at the *Ssa*-A34 locus ranged from 2.5 to 8.5 kbp, with very few fragments observed greater than 6.0 kbp (Fig. 1). Bin

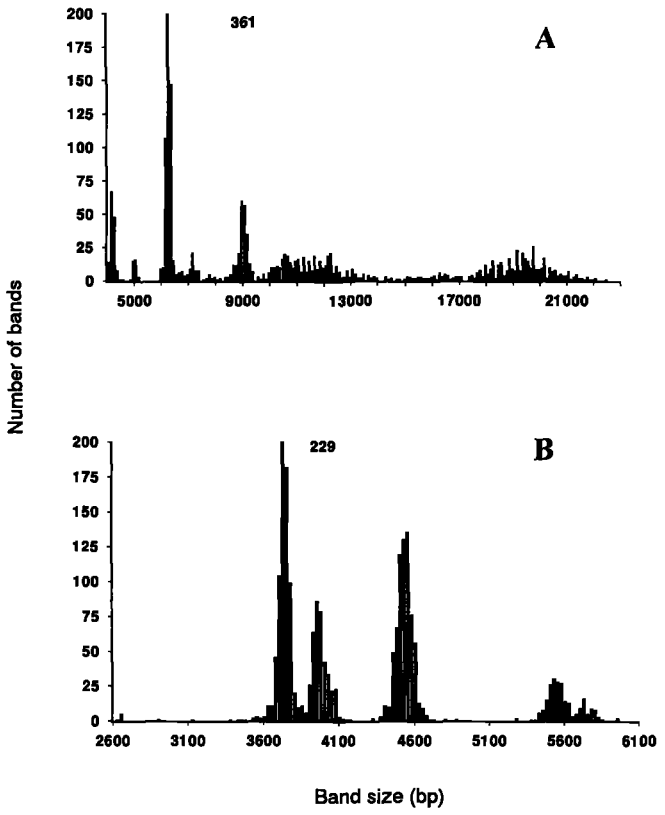

Figure 1

Observed frequency distribution of DNA band size over all chum salmon, *Oncorhynchus keta*, populations surveyed for variation with the probes p*Ssa*-A33 (**A**) and p*Ssa*-A34 (**B**). Frequencies of any band over 200 were truncated and the limits are indicated in the figure (i.e. 361 and 229).

intervals for definition of alleles at the *Ssa*-A33 locus were defined by 15 classes as outlined in Table 1, and bin intervals for definition of alleles at the *Ssa*-A34 locus were defined by 18 classes as outlined in Table 2. The average bin width was 9.8 standard deviations (SD) for bins containing bands <5,000 bp and 8.3 SD's for bins containing bands >5,000 bp. Variation previously observed with the *Ssa*1 probe was reanalyzed from the 44-bin characterization of Taylor et al. (1994) to a 31-bin characterization, with bin limits outlined by Beacham et al. (1996).

Data analysis

Mean allele frequencies were calculated by stock for *Ssa*-A33 and *Ssa*-A34 loci with the bins considered as alleles. Differences in heterozygosity among stocks in different areas were evaluated by the log-likelihood ratio or *G*-test statistic (Sokal and Rohlf, 1981). Annual variation in the allele frequency distributions was evaluated for each probe for three stocks that had been sampled over two years. The chi-square (χ^2) test with 1,000 Monte Carlo simulations of the distribution of the χ^2 statistic (Roff and Bentzen, 1989) was used to evaluate significance of annual variation in allele frequency distributions (McElroy et al., 1992). Genotype frequencies within populations were compared with those expected under Hardy-Weinberg equilibrium by 500 Monte Carlo simulations of the distribution of the χ^2 statistic. As the data set included both allele frequencies (*Ssa*-A33 and *Ssa*-A34) and band counts (*Ssa*1), a generalized or chord distance value (Pimentel, 1979) was calculated between each pair of stocks. A dendrogram was obtained by clustering the distance estimates by means of the neighbor-joining algorithm (Felsenstein, 1990). Classification of individual fish to specific stocks was conducted by using the DISCRIM procedure of SAS (SAS Institute Inc., 1989) with a jackknife sampling procedure, whereby classification

Table 1

Allele frequencies at the *Ssa*-A33 locus for 42 stocks of chum salmon. Genomic DNA was restricted with *Hae*III and hybridized with the p*Ssa*-A33 probe. Bin intervals for definition of alleles were: 4100–4400 bp (1), 4401–4700 bp (2), 4701–5000 bp (3), 5001–5500 bp (4), 5501–6000 bp (5), 6001–6500 bp (6), 6501–7000 bp (7), 7001–7700 bp (8), 7701–8500 bp (9), 8501–9300 bp (10), 9301–10,000 bp (11), 10,001–11,000 bp (12), 11,001–13,000 bp (13), 13,001–16,000 bp (14), >16,001 bp (15). *n* is sample size. North = two stocks from southeast Alaska and two from northern British Columbia; WCVI = west coast of Vancouver Island; ECVI = east coast of Vancouver Island; and Mainland = southern coastal mainland of British Columbia.

Stock	*n*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Chitose	46	0.217	0.011	0.000	0.043	0.000	0.391	0.043	0.152	0.011	0.000	0.000	0.000	0.000	0.076	0.054
Tokachi	47	0.245	0.000	0.000	0.074	0.000	0.223	0.053	0.128	0.021	0.011	0.000	0.000	0.000	0.106	0.138
Miomoto	16	0.281	0.000	0.000	0.031	0.000	0.281	0.000	0.063	0.063	0.000	0.000	0.000	0.063	0.094	0.125
Ohkawa	8	0.188	0.063	0.000	0.125	0.000	0.250	0.000	0.063	0.000	0.063	0.000	0.000	0.063	0.125	0.063
Shibetsu	14	0.214	0.000	0.000	0.000	0.000	0.357	0.036	0.036	0.000	0.107	0.000	0.000	0.071	0.071	0.107
Teshio	8	0.250	0.000	0.000	0.063	0.000	0.313	0.000	0.000	0.188	0.000	0.000	0.000	0.125	0.063	0.000
Tokoro	10	0.350	0.000	0.000	0.000	0.000	0.150	0.050	0.300	0.000	0.000	0.000	0.000	0.000	0.050	0.100
Honoari	48	0.229	0.000	0.010	0.115	0.000	0.354	0.000	0.073	0.052	0.000	0.010	0.000	0.010	0.031	0.115
Abashiri	48	0.281	0.000	0.010	0.052	0.000	0.281	0.010	0.073	0.021	0.010	0.000	0.000	0.042	0.063	0.156
Total for Japan	245	0.247	0.004	0.004	0.063	0.000	0.304	0.024	0.102	0.031	0.012	0.002	0.000	0.024	0.071	0.110
Anadyr	34	0.147	0.000	0.000	0.000	0.000	0.485	0.000	0.000	0.000	0.088	0.029	0.000	0.103	0.029	0.118
Kanchalan	38	0.145	0.013	0.000	0.000	0.000	0.408	0.013	0.000	0.000	0.079	0.013	0.026	0.079	0.066	0.158
Ola	16	0.000	0.000	0.000	0.000	0.000	0.844	0.000	0.000	0.000	0.000	0.000	0.000	0.063	0.000	0.094
Kamchatka	9	0.111	0.000	0.000	0.000	0.000	0.389	0.000	0.000	0.000	0.056	0.056	0.056	0.000	0.167	0.167
Total for Russia	97	0.119	0.005	0.000	0.000	0.000	0.505	0.005	0.000	0.000	0.067	0.021	0.015	0.077	0.052	0.134
Andreafsky	35	0.043	0.000	0.000	0.000	0.000	0.529	0.000	0.043	0.000	0.000	0.014	0.000	0.014	0.000	0.358
Kluane	29	0.017	0.000	0.000	0.000	0.000	0.483	0.000	0.103	0.000	0.086	0.000	0.000	0.000	0.000	0.310
Fishing Branch	29	0.034	0.000	0.000	0.000	0.000	0.552	0.000	0.000	0.000	0.155	0.000	0.000	0.034	0.000	0.224
Sheenjek	28	0.071	0.000	0.000	0.000	0.000	0.589	0.018	0.000	0.000	0.214	0.000	0.000	0.000	0.000	0.107
Tatchun	28	0.000	0.000	0.000	0.000	0.000	0.714	0.018	0.000	0.000	0.125	0.000	0.000	0.000	0.000	0.143
Total for Yukon River	149	0.034	0.000	0.000	0.000	0.000	0.570	0.007	0.030	0.000	0.111	0.003	0.000	0.010	0.000	0.234
Fish Creek	46	0.000	0.000	0.000	0.000	0.000	0.402	0.120	0.000	0.000	0.033	0.000	0.011	0.087	0.000	0.347
Breezy Bay	42	0.000	0.000	0.000	0.000	0.000	0.405	0.012	0.000	0.000	0.048	0.012	0.012	0.036	0.000	0.476
Atnarko	24	0.000	0.000	0.000	0.000	0.000	0.583	0.000	0.000	0.000	0.000	0.000	0.042	0.042	0.000	0.333
Pallant	50	0.000	0.000	0.000	0.000	0.000	0.630	0.000	0.000	0.000	0.000	0.010	0.020	0.040	0.000	0.300
Total for North	162	0.000	0.000	0.000	0.000	0.000	0.500	0.037	0.000	0.000	0.022	0.006	0.019	0.052	0.000	0.364
Conuma	23	0.000	0.000	0.000	0.000	0.043	0.478	0.000	0.000	0.022	0.043	0.000	0.043	0.065	0.043	0.261
Nitinat	48	0.000	0.000	0.000	0.000	0.000	0.615	0.042	0.000	0.000	0.010	0.021	0.052	0.125	0.021	0.115
Demamiel	24	0.000	0.000	0.000	0.000	0.000	0.417	0.000	0.000	0.000	0.063	0.000	0.000	0.125	0.000	0.396
Total for WCVI	95	0.000	0.000	0.000	0.000	0.011	0.532	0.021	0.000	0.005	0.032	0.011	0.037	0.111	0.021	0.222

continued

Table 1 (continued)

Stock	*n*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Alouette	23	0.000	0.000	0.000	0.000	0.000	0.283	0.000	0.000	0.000	0.087	0.000	0.130	0.196	0.022	0.282
Chehalis	24	0.000	0.000	0.000	0.000	0.000	0.354	0.021	0.000	0.000	0.042	0.000	0.063	0.250	0.000	0.271
Chilliwack	48	0.000	0.000	0.000	0.000	0.000	0.302	0.000	0.000	0.000	0.063	0.000	0.052	0.302	0.031	0.250
Inch	21	0.000	0.000	0.000	0.000	0.000	0.381	0.000	0.000	0.000	0.119	0.024	0.119	0.190	0.000	0.167
Stave	23	0.000	0.000	0.000	0.000	0.000	0.391	0.000	0.000	0.022	0.043	0.000	0.109	0.109	0.043	0.282
Wahleach	22	0.000	0.000	0.000	0.000	0.000	0.318	0.000	0.000	0.000	0.114	0.023	0.000	0.364	0.023	0.159
Total for Fraser River	161	0.000	0.000	0.000	0.000	0.000	0.332	0.003	0.000	0.003	0.075	0.006	0.075	0.245	0.022	0.240
Cowichan	22	0.000	0.000	0.000	0.000	0.000	0.159	0.000	0.000	0.000	0.023	0.000	0.045	0.386	0.000	0.387
Big Qualicum	59	0.000	0.000	0.000	0.000	0.000	0.246	0.008	0.000	0.000	0.051	0.000	0.085	0.237	0.042	0.331
Chemainus	24	0.000	0.000	0.000	0.000	0.000	0.229	0.000	0.000	0.000	0.167	0.000	0.125	0.208	0.000	0.271
Goldstream	24	0.000	0.000	0.000	0.000	0.000	0.333	0.000	0.000	0.000	0.104	0.000	0.021	0.333	0.021	0.188
L. Qualicum	36	0.000	0.000	0.000	0.014	0.000	0.194	0.014	0.056	0.000	0.056	0.042	0.028	0.153	0.139	0.306
Nanaimo	24	0.000	0.000	0.000	0.000	0.000	0.250	0.000	0.000	0.021	0.083	0.000	0.063	0.292	0.000	0.292
Puntledge	23	0.000	0.000	0.000	0.000	0.000	0.239	0.000	0.000	0.000	0.174	0.022	0.174	0.130	0.022	0.239
Total for ECVI	212	0.000	0.000	0.000	0.002	0.000	0.236	0.005	0.009	0.002	0.085	0.009	0.075	0.241	0.040	0.295
Tzoonie	23	0.000	0.000	0.000	0.000	0.000	0.239	0.000	0.000	0.000	0.043	0.022	0.043	0.283	0.065	0.304
Mamquam	28	0.000	0.000	0.000	0.018	0.000	0.214	0.000	0.000	0.000	0.125	0.018	0.018	0.304	0.071	0.232
Sliammon	6	0.000	0.000	0.000	0.000	0.000	0.500	0.083	0.000	0.000	0.167	0.000	0.083	0.083	0.000	0.083
Cheakamus	6	0.000	0.000	0.000	0.000	0.000	0.333	0.000	0.000	0.000	0.000	0.000	0.000	0.417	0.000	0.250
Total for Mainland	63	0.000	0.000	0.000	0.008	0.000	0.262	0.008	0.000	0.000	0.087	0.016	0.032	0.286	0.056	0.246

functions were developed with all fish sampled except the one to be classified. The accuracy of classification of individual fish was summarized both on a population and on a regional basis.

Estimation of stock composition

Baseline data

In this study, counts were available from 15 alleles at the *Ssa*-A33 locus, 18 alleles at the *Ssa*-A34 locus, and from 31 band counts at the *Ssa*1 locus for each fish. The maximum-likelihood model (Fournier et al., 1984) used in the estimation of stock composition requires that the characters used in the analysis be independent. When allele counts and band counts were used to characterize the chum salmon stocks, a principal-components analysis on the correlation matrix of the 64 variables in the study was conducted in order to obtain uncorrelated variables or principal components, as was described by Beacham et al. (1996). Summarized briefly, the PRINCOMP procedure in SAS was used in the principal-components analysis. The observed data (number of bands per bin) were standardized by subtracting the overall corresponding mean and by dividing by the corresponding bin standard deviation over all populations for the original variables. The original variables were then represented as factor scores for uncorrelated variables or principal components. The first 57 principal components accounted for 100% of the total observed variation. The input to the maximum-likelihood model required discrete frequency counts for each variable, and as outlined by Beacham et al. (1995), the continuous distributions of the principal component scores were represented as 12-bin histograms. Limits of the bins were as follows: ≤–2.50 (1), –2.49 to –1.50 (2), –1.49 to –1.00 (3), –0.99 to –0.60 (4), –0.59 to –0.30 (5), –0.29 to 0.00 (6), 0.00 to 0.29 (7), 0.30 to 0.59 (8), 0.60 to 0.99 (9), 1.00 to 1.49 (10), 1.50 to 2.49 (11), and ≥2.50 (12). Each stock was then characterized as an input matrix of 57 rows (principal components) and 12 columns (counts of principal component scores in each of the 12 bins).

Table 2

Allele frequencies at the *Ssa*-A34 locus for 42 stocks of chum salmon. Genomic DNA was restricted with *Hae*III and hybridized with the p*Ssa*-A34 probe. Bin intervals for definitions of alleles were as follows: 2600–2700 bp (1), 2701–2800 bp (2), 2801–2900 bp (3), 2901–3100 bp (4), 3101–3300 (5), 3301–3500 bp (6), 3501–3700 bp (7), 3701–3900 bp (8), 3901–4100 bp (9), 4101–4400 bp (10), 4401–4700 bp (11), 4701–5000 bp (12), 5001–5500 bp (13), 5501–6000 bp (14), 6001–6500 bp (15), 6501–7000 bp (16), 7001–7700 bp (17), 7701–8500 bp (18). *n* is sample size. Abbreviations for geographic regions are defined in Table 1.

Stock	*n*	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Chitose	46	0.000	0.000	0.000	0.000	0.000	0.000	0.011	0.054	0.446	0.022	0.152	0.000	0.022	0.250	0.000	0.000	0.000	0.043
Tokachi	48	0.000	0.000	0.000	0.000	0.000	0.000	0.031	0.104	0.302	0.021	0.240	0.010	0.010	0.250	0.000	0.010	0.021	0.000
Miomoto	16	0.000	0.000	0.000	0.000	0.000	0.031	0.000	0.094	0.563	0.000	0.125	0.000	0.031	0.156	0.000	0.000	0.000	0.000
Ohkawa	16	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.656	0.000	0.094	0.000	0.000	0.219	0.000	0.031	0.000	0.000
Shibetsu	14	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.036	0.321	0.000	0.357	0.000	0.071	0.214	0.000	0.000	0.000	0.000
Teshio	8	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.188	0.375	0.000	0.188	0.000	0.063	0.188	0.000	0.000	0.000	0.000
Tokoro	10	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.050	0.350	0.000	0.250	0.000	0.100	0.250	0.000	0.000	0.000	0.000
Honoari	48	0.000	0.000	0.000	0.000	0.000	0.010	0.031	0.115	0.344	0.000	0.240	0.010	0.094	0.156	0.000	0.000	0.000	0.000
Abashiri	48	0.000	0.000	0.000	0.000	0.000	0.000	0.031	0.083	0.375	0.000	0.240	0.000	0.042	0.219	0.010	0.000	0.000	0.000
Total for Japan	254	0.000	0.000	0.000	0.000	0.000	0.004	0.020	0.083	0.394	0.008	0.213	0.004	0.043	0.215	0.002	0.004	0.004	0.008
Anadyr	25	0.000	0.000	0.000	0.000	0.000	0.000	0.040	0.100	0.060	0.040	0.640	0.000	0.000	0.120	0.000	0.000	0.000	0.000
Kanchalan	39	0.000	0.000	0.000	0.000	0.013	0.013	0.013	0.282	0.064	0.000	0.590	0.000	0.000	0.026	0.000	0.000	0.000	0.000
Ola	15	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.200	0.067	0.000	0.600	0.000	0.000	0.100	0.000	0.033	0.000	0.000
Kamchatka	13	0.000	0.000	0.000	0.000	0.000	0.000	0.038	0.269	0.038	0.000	0.538	0.000	0.000	0.115	0.000	0.000	0.000	0.000
Total for Russia	92	0.000	0.000	0.000	0.000	0.005	0.005	0.022	0.217	0.060	0.011	0.598	0.000	0.000	0.076	0.000	0.005	0.000	0.000
Andreafsky	36	0.000	0.000	0.000	0.000	0.000	0.000	0.014	0.236	0.069	0.000	0.611	0.000	0.000	0.069	0.000	0.000	0.000	0.000
Kluane	30	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.217	0.300	0.017	0.467	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Fishing Br	29	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.224	0.241	0.000	0.448	0.000	0.000	0.086	0.000	0.000	0.000	0.000
Sheenjek	28	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.286	0.125	0.000	0.571	0.000	0.000	0.018	0.000	0.000	0.000	0.000
Tatchun	28	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.268	0.286	0.000	0.393	0.000	0.000	0.054	0.000	0.000	0.000	0.000
Total for Yukon River	151	0.000	0.000	0.000	0.000	0.000	0.000	0.003	0.245	0.199	0.003	0.503	0.000	0.000	0.046	0.000	0.000	0.000	0.000
Fish Creek	48	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.563	0.125	0.000	0.271	0.010	0.000	0.031	0.000	0.000	0.000	0.000
Breezy Bay	46	0.000	0.000	0.000	0.000	0.000	0.011	0.054	0.413	0.098	0.000	0.348	0.000	0.011	0.065	0.000	0.000	0.000	0.000
Atnarko	24	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.396	0.083	0.000	0.417	0.000	0.000	0.104	0.000	0.000	0.000	0.000
Pallant	50	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.510	0.110	0.000	0.260	0.010	0.000	0.110	0.000	0.000	0.000	0.000
Total for North	168	0.000	0.000	0.000	0.000	0.000	0.003	0.015	0.482	0.107	0.000	0.310	0.006	0.003	0.074	0.000	0.000	0.000	0.000
Conuma	23	0.000	0.000	0.000	0.000	0.000	0.000	0.022	0.522	0.130	0.000	0.304	0.000	0.000	0.022	0.000	0.000	0.000	0.000
Demamiel	23	0.000	0.000	0.000	0.000	0.000	0.000	0.043	0.391	0.174	0.000	0.370	0.000	0.022	0.043	0.000	0.000	0.000	0.000
Nitinat	48	0.000	0.000	0.000	0.000	0.000	0.000	0.042	0.354	0.115	0.000	0.417	0.000	0.010	0.063	0.000	0.000	0.000	0.000
Total for WCVI	94	0.000	0.000	0.000	0.000	0.000	0.000	0.037	0.404	0.133	0.000	0.378	0.000	0.011	0.048	0.000	0.000	0.000	0.000

continued

Table 2 (continued)

Stock	n	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Alouette	23	0.000	0.000	0.000	0.000	0.000	0.000	0.152	0.348	0.130	0.065	0.130	0.000	0.043	0.130	0.000	0.000	0.000	0.000
Chehalis	24	0.000	0.000	0.000	0.000	0.000	0.000	0.063	0.333	0.208	0.000	0.354	0.000	0.021	0.021	0.000	0.000	0.000	0.000
Chilliwack	48	0.000	0.000	0.000	0.000	0.000	0.000	0.010	0.417	0.208	0.000	0.281	0.000	0.010	0.073	0.000	0.000	0.000	0.000
Inch	21	0.048	0.000	0.000	0.000	0.000	0.000	0.000	0.381	0.095	0.000	0.381	0.000	0.000	0.095	0.000	0.000	0.000	0.000
Stave	23	0.000	0.000	0.000	0.000	0.000	0.000	0.043	0.543	0.174	0.022	0.130	0.022	0.000	0.065	0.000	0.000	0.000	0.000
Wahleach	22	0.000	0.000	0.000	0.000	0.000	0.000	0.068	0.477	0.068	0.000	0.318	0.000	0.000	0.068	0.000	0.000	0.000	0.000
Total for Fraser River	161	0.006	0.000	0.000	0.000	0.000	0.000	0.050	0.416	0.158	0.012	0.267	0.003	0.012	0.075	0.000	0.000	0.000	0.000
Cowichan	22	0.023	0.000	0.000	0.000	0.000	0.000	0.045	0.591	0.045	0.000	0.250	0.000	0.000	0.045	0.000	0.000	0.000	0.000
Big Qualicum	58	0.000	0.000	0.000	0.000	0.000	0.000	0.017	0.612	0.121	0.017	0.181	0.000	0.000	0.043	0.000	0.009	0.000	0.000
Chemainus	24	0.042	0.000	0.000	0.000	0.000	0.000	0.000	0.458	0.229	0.000	0.208	0.000	0.021	0.042	0.000	0.000	0.000	0.000
Goldstream	23	0.000	0.000	0.000	0.000	0.000	0.000	0.065	0.457	0.196	0.022	0.217	0.000	0.000	0.043	0.000	0.000	0.000	0.000
L. Qualicum	36	0.000	0.000	0.000	0.014	0.000	0.000	0.028	0.625	0.069	0.014	0.236	0.000	0.014	0.014	0.000	0.000	0.000	0.000
Nanaimo	24	0.000	0.000	0.000	0.000	0.000	0.000	0.083	0.417	0.146	0.000	0.292	0.000	0.021	0.042	0.000	0.000	0.000	0.000
Puntledge	23	0.000	0.000	0.000	0.000	0.000	0.000	0.152	0.261	0.043	0.000	0.413	0.000	0.065	0.065	0.000	0.000	0.000	0.000
Total for ECVI	210	0.007	0.000	0.000	0.002	0.000	0.000	0.048	0.517	0.119	0.010	0.243	0.000	0.014	0.040	0.000	0.002	0.000	0.000
Tzoonie	24	0.021	0.000	0.000	0.000	0.000	0.000	0.000	0.479	0.167	0.000	0.208	0.000	0.000	0.083	0.000	0.042	0.000	0.000
Mamquam	29	0.000	0.000	0.000	0.000	0.000	0.000	0.017	0.397	0.172	0.017	0.345	0.000	0.000	0.052	0.000	0.000	0.000	0.000
Sliammon	13	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.692	0.077	0.000	0.192	0.000	0.000	0.038	0.000	0.000	0.000	0.000
Cheakamus	13	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.462	0.115	0.000	0.346	0.000	0.000	0.077	0.000	0.000	0.000	0.000
Total for Mainland	79	0.006	0.000	0.000	0.000	0.000	0.000	0.006	0.481	0.146	0.006	0.278	0.000	0.000	0.063	0.000	0.013	0.000	0.000

Mixture data

A series of hypothetical fishery samples that contained fish from a specific region or stock were analyzed in order to evaluate the use of minisatellite DNA for stock composition. Test samples of 100 fish were generated 50 times by randomly resampling with replacement stocks from the appropriate river or region; then the mean and standard deviation of the 50 estimates were computed. Stock compositions of the mixture were determined under the assumption that the baseline data were perfectly representative of the stocks (fixed-frequency distribution) and by simulating random variation involved in the collection of baseline samples (resampled distribution). Each baseline stock was resampled with replacement to obtain new distributions of the principal components with the same sample size as in the original sample (Millar, 1990).

Results

Geographic variation in *Ssa*-A33 allele frequencies

Allele size varied from 4.1 to 21.3 kbp (Fig. 2). Major alleles were observed at the 4.1 to 4.4 kbp (bin 1), 6.0 to 6.5 kbp (bin 6), and 8.5 to 9.3 kbp (bin 10) (Fig. 1; Table 1). Variation in allele frequencies was observed among Japanese, Russian, and Yukon rivers, and other North American stocks. An allele between 4.1 and 4.4 kbp was fairly common in Japanese stocks (mean frequency 0.25), less common in Russian stocks (0.12), and absent in North American stocks south of the Yukon River (Table 1). Similarly, alleles greater than 16.0 kbp were fairly rare in Asian stocks (Japanese stock mean frequency: 0.11; Russian: 0.13) but were more common in North American stocks (regional frequencies: 0.24–0.26). Clear differences in allele frequencies were observed in chum salmon stocks in broadly separated geographic areas.

In North American stocks, regional differences in allelic frequencies were observed. Mean frequency of the 11.0–13.0 kbp allele was 0.01 for Yukon River stocks, 0.05 for southeast Alaska and northern British Columbia stocks, 0.11 for west coast of Vancouver Island (WCVI) stocks, and 0.24

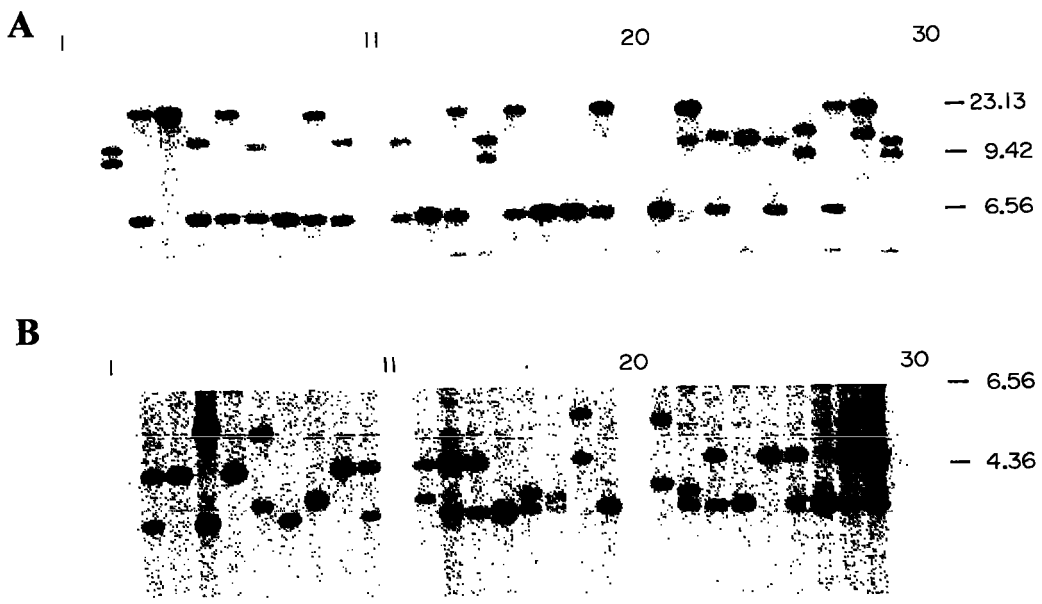

Figure 2

Autoradiographs of chum salmon DNA restricted with *Hae*III and hybridized with the probe p*Ssa*-A33 (**A**) or p*Ssa*-A34 (**B**). In panel A, lanes 1, 11, 20, and 30 represent size-standard fish; lanes 2 and 29 represent standard fish; lanes 3–8, 16–19, and 21–22 represent Atnarko fish; and 9–10, 12–15, and 23–28 represent Chilliwack fish. In panel B, the lanes are similar; Chilliwack chum salmon DNA is seen in lanes 3–8, 16–19, and 21–22, and Nitinat chum salmon DNA in lanes 9–10, 12–15, and 24–29.

or greater for east coast of Vancouver Island (ECVI), mainland British Columbia, or Fraser River stocks (Table 1). However, within a region, marked differences in allelic frequencies could be observed among stocks. For example, frequency of the allele greater than 16.0 kbp ranged between 0.16 and 0.28 for six Fraser River stocks, and frequency of the 11.0–13.0 kbp allele ranged between 0.13 and 0.39 for seven ECVI stocks. This variation in allele frequencies among stocks within regions may allow discrimination among stocks within the region but it increases the complexity of discriminating among stocks between regions.

Genotypic frequencies at the *Ssa*-A33 locus were in Hardy-Weinberg equilibrium in all 42 stocks sampled. On a regional basis, heterozygosity ranged from 54 to 72% for the stocks sampled, with Japanese stocks significantly more heterozygous than the pooled aggregate of North American stocks (G=6.03, df=1, P<0.05)(Table 1).

Geographic variation in *Ssa*-A34 allele frequencies

Allele size varied from 2.6 to 8.5 kbp (Fig. 2), with major alleles at 3.7–3.9 kbp (bin 8), 3.9–4.1 kbp (bin 9), and 4.4–4.7 kbp (bin 11) (Fig. 1; Table 2). As with the *Ssa*-A33 locus, differences in allele frequencies were observed among Japanese, Russian, and North American stocks. Of the Russian stocks surveyed, all had a relatively high frequency (mean 0.60) of the 4.4–4.7 kbp allele, significantly different from Japanese stocks (mean 0.21)(χ^2=89.6, df=1, P<0.01)(Table 2). Mean frequency of the 3.7–3.9 kbp allele was 0.08 in Japanese stocks, 0.22–0.25 in Russian and Yukon River stocks, and 0.40–0.52 in southeast Alaska and British Columbia stocks. Similar patterns of the genetic distinctiveness of the major stock groups were observed at both the *Ssa*-A33 and *Ssa*-A34 loci.

In British Columbia, regional differences in allele frequencies were fairly minor in comparison with the variation among stocks within regions (Table 2). For example, in the six Fraser River stocks, frequencies of the 4.4–4.7 kbp allele ranged from 0.13 to 0.38 (mean 0.27), in the seven ECVI stocks from 0.18 to 0.41 (mean 0.24), and in the four mainland stocks from 0.19 to 0.35 (mean 0.28). The variation in allele frequencies among stocks within regions may be used effectively for localized stock discrimination, but as with the *Ssa*-A33 locus, makes discrimination among regional groups of stocks more difficult.

Table 3

Observed heterozygosities for chum salmon, *Oncorhyncus keta*, from eight regions at the *Ssa*-A33 and *Ssa*-A34 loci. Stocks sampled within each region are listed in Tables 1 and 2. *n* = number of fish sampled in each region. Stocks sampled in each region are outlined in Table 1. Abbreviations for geographic regions are defined in Table 1.

Region	*n*	*Ssa*-A33	*n*	*Ssa*-A34
Japan	245	0.718	254	0.768
Russia	97	0.629	92	0.620
Yukon	149	0.557	151	0.642
North	162	0.568	168	0.655
WCVI	95	0.537	94	0.713
Fraser	161	0.720	161	0.658
ECVI	212	0.703	210	0.579
Mainland	63	0.651	79	0.633

As with the *Ssa*-A33 locus, genotypic frequencies at the *Ssa*-A34 locus were in Hardy-Weinberg equilibrium in all of the 42 stocks sampled. Mean heterozygosity of the Japanese stocks (0.77) was higher than that for any other regional group of stocks (Table 3) and significantly higher than that for North American (G=15.0, df=1, P<0.05) or Russian stocks (G=6.50, df=1, P<0.05). Heterozygosity of Japanese chum salmon was consistently higher than that for other regional groups of chum salmon when both the *Ssa*-A33 and *Ssa*-A34 loci were considered.

Annual variation in allele frequencies

Samples from two Vancouver Island (Big Qualicum, Nitinat) stocks and one Fraser River (Chilliwack) stock were obtained in both 1991 and 1992. No significant annual variation was observed in allele frequencies at either the *Ssa*-A33 or *Ssa*-A34 loci for any stock (P>0.05)(6 tests conducted).

Stock structure

Neighbor-joining analysis of the distances between stocks derived from allele frequencies at the *Ssa*-A33 and *Ssa*-A34 loci and from band counts observed with the *Ssa*1 probe indicated that Japanese chum salmon stocks were distinct from all other groups of stocks (Fig. 3). Regional stock structure was also examined with principal-components analysis, and all nine Japanese stocks sampled were clearly separated from all other stocks (Fig. 4). Russian and Yukon River stocks were more similar to each other than to more distant stocks in Japan and British Columbia (Figs. 3 and 4). There was weak regional structuring among stocks of British Columbia chum salmon, and there was some evidence that southeast Alaska and northern British Columbia stocks were more similar to each other than to stocks in southern British Columbia (Fig. 3) and some evidence that there was separation between ECVI and Fraser River stocks (Fig. 4).

Estimation of stock composition

The potential use of minisatellite DNA variation for estimation of stock composition of stocks from broad geographic areas was evaluated for two main groupings of chum salmon, namely mixtures of Japanese and Russian chum salmon and mixtures of Russian and Yukon River chum salmon. On the basis of stock structure, relatively accurate and precise estimates of stock composition should be derived from samples containing Japanese and Russian chum salmon (Table 4). Similarly, in applications where estimation of Russian and Yukon River chum salmon compositions is of interest, relatively accurate and precise estimates of stock composition of the two target groups should be derived (Table 4). The Andrefsky River stock was in a group with Russian stocks in the neighbor-joining analysis (Fig. 3) but seemed separable from Russian stocks in the principal-components analysis (Fig. 4). The simulations suggested that even if the Andrefsky River comprised all the Yukon River component, separation of Russian and Yukon River stock components should still be possible (Table 4).

The application of minisatellite DNA variation to local stock composition issues was evaluated for three situations; i.e. mixtures of Japanese, Yukon River, and southern British Columbia chum salmon stocks were evaluated separately. The simulations suggested that both discrimination among all of the Japanese stocks sampled and relatively accurate estimates of stock composition observed in both single-stock and multistock simulated mixtures were possible (Table 5). Because less than 20 fish per stock were sampled for five of the nine stocks surveyed (Table 1), increased baseline sampling, however, would be required to confirm these results before application to actual fishery samples. The simulations of Yukon River chum salmon mixtures suggested that all five stocks were distinct from each other and that accurate estimates of stock composition may be possible with minisatellite DNA variation (Table 6). The fall-run Sheenjek River stock was distinguishable from fall-run stocks spawning in the Yukon Territory. The simulations of southern British Columbia chum salmon mixtures suggested that minisatellite DNA variation may be applicable for estimation of stock composition in fishery samples. Estimates of stock composition for

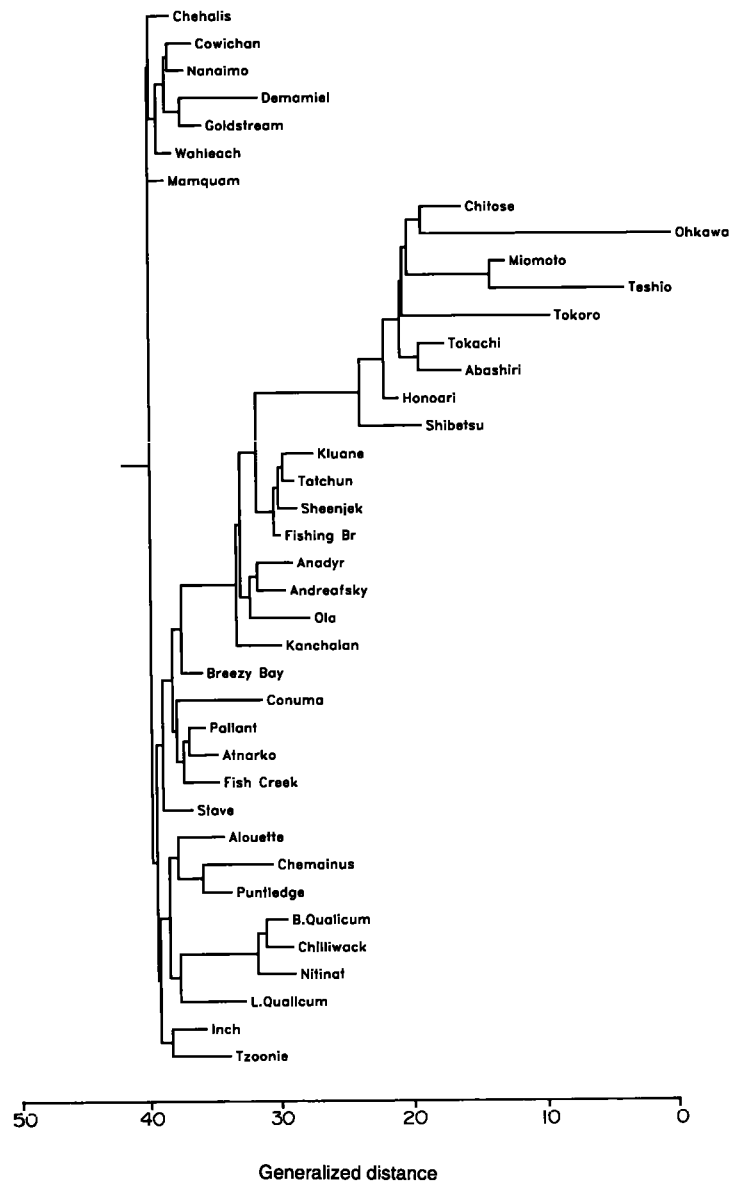

Figure 3

A neighbor-joining dendrogram of relationships among 39 stocks of chum salmon based on allele frequencies at the *Ssa*-A33 and *Ssa*-A34 loci and on band counts of occurrence for the probe *Ssa*1.

the six individual Fraser River stocks, derived from a baseline for Fraser River only, indicate that discrimination among the stocks was possible (Table 7). Similar results were also observed when an ECVI-only or WCVI-only baseline was used and when ECVI and WCVI fish were in the simulated mixtures as appropriate. When an 18-stock regional baseline was used, there was a clear indication of separation among Fraser River, ECVI, and WCVI stocks (Table 7).

Identification of individuals

The accuracy of classifying individuals to specific stocks or regions was dependent upon the specific stock under consideration; the greatest accuracy was observed for the more distinctive stocks or regional groups. With a 39-stock baseline (Sliammon, Cheakamus, and Kamchatka were removed owing to lack of *Ssa*1 band counts), classification accuracy

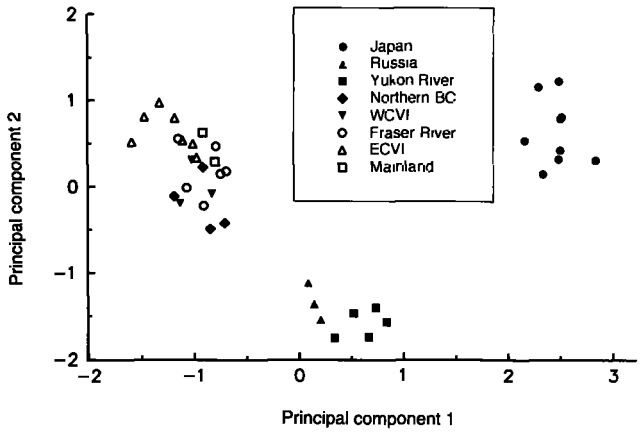

Figure 4

Plot of first two principal components (PC) incorporating variation at the *Ssa*-A33 and *Ssa*-A34 loci and including *Ssa*-1 band counts for 39 stocks indicated in Figure 2. North = two stocks from southeast Alaska and two stocks from northern British Columbia. WCVI = west coast of Vancouver Island; ECVI = east coast of Vancouver Island; Mainland = southern coastal mainland of British Columbia.

for Japanese chum salmon to specific stocks averaged 15%, but 82% were correctly identified as Japanese in origin (Table 8). Similarly, classification accuracy for Russian chum salmon to stock of origin was 30%, and to region of origin, 47%. Yukon River chum salmon were fairly distinctive and the origin of about 75% of the fish was correctly identified. Accurate classification for individual southern British Columbia chum salmon to region of origin ranged from about 9 to 44% (Table 8), presumably reflecting less separation among these groups compared with that among Japanese, Russian, and Yukon River chum salmon. With Asian and North American stocks pooled into two groups, accuracate classification to continent of origin for 323 Asian fish was 78%, and that for 797 North American fish was 94%. The minisatellite DNA variation provided a reasonable measure of accuracy in classifying individuals to continent of origin.

Discussion

Allele frequencies at the *Ssa*-A33 and *Ssa*-A34 loci indicated that there were three regional groups of chum salmon stocks: the Japanese, Russian and Yukon River, and southeast Alaska and British Columbia stocks. The greatest differences were observed between stocks from Japan and British Columbia. Similar results were also observed in a survey of minisatellite DNA variation with the *Ssa*1 probe (Taylor et al., 1994). The differentiation between stocks from Japan and British Columbia has also been demonstrated in studies of variation at protein-coding loci (Okazaki, 1982) and more recently in mitochondrial DNA in the region coding for NADH dehydrogenase subunits 5 and 6 (Park et al., 1993). These results are consistent with the conclusion that stocks that are more distant geographically also show more distinct genetic differentiation (Taylor et al., 1994). These patterns presumably reflect the dispersal of salmon from different refuges after the retreat of glaciers at the end of the Wisconsinian glacial period (Lindsey and McPhail, 1986). The separation between Japanese and Russian stocks reported by Winans et al. (1994) in a survey of variation at protein-coding loci was also observed in the current study with variation at minisatellite loci. A high degree of genetic differentiation has been consistently observed between Japanese and North American chum salmon, regardless of

Table 4

Estimated percentage composition of a variety of mixtures of chum salmon. Each mixture of 100 fish was generated 50 times with replacement, and a stock composition of the mixtures estimated by using either a fixed distribution of the allele frequencies or band counts in the baseline stocks, or by randomly resampling each baseline stock with replacement to obtain a resampled distribution of the frequencies or counts for each baseline stocks, with the same sample size in the new distribution as in the original one. Band frequencies used included those derived from genomic DNA restricted with *Hae*III and hybridized with *Ssa*-1, p*Ssa*-A33, and p*Ssa*-A34. Twelve (9 Japanese, 3 Russian) baseline stocks were used to resolve the Japanese and Russian mixtures, and 8 (3 Russian, 5 Yukon) baseline stocks for Russian and Yukon River chum salmon mixtures. Standard deviations are given in parentheses.

	Distribution (%)		
Origin	Actual	Fixed	Resampled
Japan vs. Russia			
Japan	0	0.0 (0.0)	5.2 (4.2)
Japan	25	24.8 (0.4)	28.3 (4.3)
Japan	50	49.5 (0.6)	51.3 (5.4)
Japan	75	74.7 (0.05)	74.5 (4.8)
Japan	100	99.6 (0.6)	99.6 (0.9)
Russia vs. Yukon			
Russia	0	0.1 (0.4)	3.6 (3.5)
Russia	25	24.1 (1.4)	28.2 (3.6)
Russia	50	48.3 (1.5)	49.9 (4.7)
Russia	75	72.4 (1.9)	72.5 (3.9)
Russia	100	97.5 (1.8)	96.0 (3.7)
Andreafsky	100	100.0 (0.0)	94.5 (5.0)

Table 5

Estimated percentage composition of 100-fish mixtures of Japanese chum salmon stocks resolved with a 9-stock baseline in which distributions of the allele frequencies or band counts in each baseline stock were fixed or resampled as outlined in Table 4. Standard deviations are given in parentheses.

	Distribution (%)		
Stock	Actual	Fixed	Resampled
Single-stock mixtures			
Chitose	100	100.0 (0.0)	94.1 (4.5)
Tokachi	100	100.0 (0.0)	94.4 (5.2)
Miomoto	100	100.0 (0.0)	91.0 (9.6)
Ohkawa	100	100.0 (0.0)	91.8 (10.4)
Shibetsu	100	100.0 (0.0)	92.3 (7.8)
Teshio	100	100.0 (0.0)	87.6 (13.5)
Tokoro	100	100.0 (0.0)	97.2 (5.8)
Honoari	100	100.0 (0.0)	94.2 (4.8)
Abashiri	100	100.0 (0.0)	93.2 (5.2)
Multistock mixture			
Chitose	10	9.7 (0.5)	11.0 (4.1)
Okachi	20	20.3 (0.6)	19.4 (3.0)
Honoari	30	30.2 (0.3)	29.7 (4.4)
Abashiri	40	39.8 (0.6)	39.8 (4.5)

Table 6

Estimated percentage composition of 100-fish mixtures of Yukon River chum salmon stocks resolved with a 5-stock baseline in which distributions of the allele frequencies or band counts in the baseline stock were fixed or resampled as outlined in Table 4. Standard deviations are given in parentheses.

	Distribution (%)		
Stock	Actual	Fixed	Resampled
Single-stock mixtures			
Andreafsky	100	100.0 (0.0)	97.0 (3.3)
Sheenjek	100	98.2 (1.7)	97.5 (3.1)
Fishing Branch	100	96.5 (2.0)	95.1 (4.1)
Tatchun	100	100.0 (0.0)	98.7 (3.4)
Kluane	100	100.0 (0.0)	95.9 (4.6)
Multistock mixture			
Kluane	10	9.3 (0.8)	10.0 (2.4)
Tatchun	20	20.3 (0.7)	19.8 (3.7)
Sheenjek	30	30.3 (0.4)	30.8 (4.0)
Fishing Branch	40	39.1 (1.1)	38.8 (4.5)

whether the survey has used protein electrophoretic, mitochondrial DNA, or minisatellite DNA variation.

In the current study, DNA bands were grouped in bins or "alleles" on the basis of the estimated size of the DNA fragment. The precision of estimated fragment size was based on analyzing a single standard fish on all gels, on obtaining repeated estimates of fragment size, and on determining a relationship between estimated fragment size and precision or standard deviation of the estimate (Galbraith et al., 1991; Taylor et al., 1994). The bin width was set at 8 to 10 SD, less than the 16 SD suggested by Galbraith et al. (1991) as necessary before the chances of assigning a band to the wrong bin falls below 0.05. However, because most of the source of variation in the Galbraith et al. (1991) study was due to digitizing bands that were manually marked on an acetate overlay, the computerized estimation system employed in the present study should result in greater precision of estimation of fragment size. Taylor et al. (1994) used a bin width of 6 SD, based upon the measurement precision of the fragment size of a standard fish, but a more conservative bin width of 8 to 10 SD was used in the current study.

The variation observed at the minisatellite loci examined in the current study was probably less than that actually present at the loci. Given the level of precision of the measurements of fragment size, closely spaced true alleles could not be distinguished reliably and were therefore combined in the binning process. It was assumed that there was no consistent bias in the assignment of fragments to specific bins. Additionally, differences in DNA sequence variation of two alleles of the same size were not determined. It is possible, for example, that an allele occurring in both Japanese and North American populations will show the same length for both populations but will reveal a considerably different DNA sequence.

The simulations conducted for mixtures containing localized stocks (Japan, Yukon River, and Fraser River) suggested that the minisatellite DNA variation surveyed may provide relatively accurate and precise estimates of individual stocks in the mixtures. Although the simulations were encouraging, the performance of the minisatellite DNA variation for estimation of stock composition needs to be verified by actual applications in field situations, where fish in the mixture can originate from stocks not found in the baseline, and where novel genotypes can be observed. In the present study, sample sizes of the baseline stocks were usually less than 50 fish; therefore, increased sampling of individuals in the stocks would be required in order to obtain representative distributions of allele frequencies or band counts.

The simulations suggested that accurate estimates of stock composition of individual stocks may be possible for mixtures of either Fraser River or Yukon River chum salmon. A previous survey of variation at seven protein-coding loci indicated that there was

Table 7

Estimated percentage composition of 100-fish mixtures of southern British Columbia chum salmon resolved with either an area-specific baseline (Fraser: 6 stocks; ECVI: 7 stocks; WCVI: 3 stocks) or an 18-stock baseline of southern stocks in which distributions of the allele frequencies or band counts in the baseline stocks were fixed or resampled as outlined in Table 4. The area sum is the total percentage allocated to all area stocks when the 18-stock regional baseline was used to resolve the mixtures. Standard deviation are given in parentheses. Abbreviations for geographic regions are defined in Table 1.

		Fixed			Resampled		
	Actual	Area baseline	Regional baseline	Area sum	Area baseline	Regional baseline	Area sum
Fraser River							
Single-stock mixtures							
Wahleach	100	95.5 (2.4)	95.5 (2.0)	100.0 (0.0)	93.9 (6.3)	87.1 (9.3)	93.1 (7.3)
Alouette	100	95.5 (2.4)	95.5 (2.4)	100.0 (0.0)	96.6 (3.6)	87.7 (7.9)	91.2 (7.9)
Chehalis	100	95.0 (2.9)	95.6 (2.0)	100.0 (0.0)	91.3 (6.7)	82.3 (8.6)	87.9 (8.6)
Chilliwack	100	100.0 (0.0)	100.0 (0.0)	100.0 (0.0)	98.4 (3.1)	85.4 (7.6)	87.4 (6.4)
Inch	100	100.0 (0.0)	100.0 (0.0)	100.0 (0.0)	95.1 (6.2)	93.0 (9.3)	93.8 (8.3)
Stave	100	92.0 (2.3)	92.0 (2.6)	100.0 (0.0)	88.6 (6.2)	82.2 (9.9)	91.8 (8.4)
Multi-stock mixture							
Wahleach	10	9.5 (0.7)	9.7 (0.5)	100.0 (0.0)	10.0 (2.6)	9.0 (2.8)	88.8 (5.1)
Alouette	20	19.1 (0.9)	18.9 (0.8)		17.5 (3.4)	16.0 (2.8)	
Chehalis	30	27.7 (1.4)	27.6 (1.3)		26.9 (4.7)	23.7 (3.9)	
Chilliwack	40	43.7 (1.8)	43.7 (1.6)		45.3 (4.8)	39.3 (5.3)	
ECVI							
Multi-stock mixture							
Cowichan	10	10.0 (0.0)	9.5 (0.6)	94.0 (2.8)	9.1 (2.1)	8.7 (2.1)	92.8 (3.8)
Nanaimo	20	20.0 (0.0)	18.8 (1.1)		18.2 (3.4)	16.4 (3.8)	
Little Qualicum	30	29.3 (0.7)	28.9 (0.8)		26.2 (3.6)	26.6 (4.2)	
Big Qualicum	40	40.7 (0.7)	36.8 (2.1)		46.3 (4.8)	42.0 (5.5)	
WCVI							
Multi-stock mixture							
Demamiel	20	20.0 (0.0)	19.3 (0.9)	98.2 (1.2)	18.4 (3.2)	17.0 (3.6)	89.0 (5.0)
Conuma	30	30.0 (0.0)	30.0 (0.0)		27.5 (4.3)	24.5 (3.2)	
Nitinat	50	50.0 (0.0)	48.9 (0.9)		54.1 (5.1)	47.6 (5.4)	

no marked distinction among Fraser River stocks (Beacham et al., 1987). Minisatellite DNA variation may provide the means to discriminate among Fraser River stocks if necessary in management applications. In the Yukon River drainage, summer-run stocks were well differentiated from fall-run stocks by analysis of variation at protein-coding loci (Wilmot et al., 1992, 1994). However, in the fall-run stocks, which spawn in rivers in both Alaska and the Yukon Territory, some stocks spawning in Alaskan rivers (Sheenjek and Chandalar rivers) were more similar to stocks spawning in the Yukon Territory rivers in Canada than they were to other Alaskan fall-run stocks. The addition of minisatellite DNA variation to techniques of stock discrimination may provide more accurate estimates of stock composition in mixed stocks (e.g. Canadian and American stocks).

Compared with some other methods of stock identification that are based upon biological tags, genetic-based methods of stock identication generally have the advantage of temporal stability of the characters used. For example, variation at protein-coding loci has usually been found to be temporally stable (Beacham et al., 1985, 1987; Kondzela et al., 1994; Wilmot et al., 1994), and similar results have been reported for minisatellite loci (Taylor et al., 1994; Beacham et al., 1996). The two-year temporal stability of allelic frequencies at the *Ssa*-A33 and *Ssa*-A34 loci observed in the current study suggests that annual sampling of contributing baseline stocks would not be required in order to estimate stock composition of appropriate mixtures. Because the populations sampled in this study tended to be major ones (escapement of British Columbia populations is usually >10,000 fish), the ratio of sample size to effective population size was less than 0.1, and the probability of a significant test to detect temporal variation is similar to the presumed level of significance (Waples, 1989).

Table 8

Percentage of correct classification of individual fish with discriminant analyses for 39 stocks of chum salmon. The percentage of fish that were correctly classified to stock is indicated, as is the percentage of fish classified to other stocks in the same and other regions. Results listed are for jackknife samples, in which the fish tested were not included in the sample used to derive the discriminant functions. The regional percentage correct is the sum of the percentage of fish correctly classified to stock and the percentage classified to other stocks within the same region. *n* = the number of fish classified in each stock. Abbreviations for geographic regions are defined in Table 1.

Stock	*n*	Correct	Japan	Russia	Yukon	North	ECVI	WCVI	Fraser	Mainland	Regional
Chitose	46	19.6	58.7	2.2	6.5	6.5	0.0	0.0	4.3	2.2	78.3
Tokachi	47	10.6	76.7	2.1	2.1	2.1	2.1	0.0	2.1	2.1	87.3
Miomoto	16	0.0	87.5	6.3	6.3	0.0	0.0	0.0	0.0	0.0	87.5
Ohkawa	8	0.0	62.5	0.0	25.0	0.0	0.0	0.0	0.0	12.5	62.5
Shibetsu	14	14.3	50.0	0.0	21.4	7.1	7.1	0.0	0.0	0.0	64.3
Teshio	8	37.5	50.0	0.0	12.5	0.0	0.0	0.0	0.0	0.0	87.5
Tokoro	10	30.0	60.0	0.0	0.0	0.0	0.0	0.0	0.0	10.0	90.0
Honoari	48	14.6	66.7	0.0	4.2	4.2	4.2	0.0	6.2	0.0	81.3
Abashiri	47	17.0	66.0	4.2	6.4	2.1	2.1	0.0	2.1	0.0	83.0
Japan	244	15.2	66.4	2.0	6.6	3.3	2.0	0.0	2.8	1.6	81.6
Anadyr	25	40.0	0.0	12.0	20.0	12.0	0.0	0.0	16.0	0.0	52.0
Kanchalan	39	25.6	5.1	18.0	25.6	7.7	10.2	0.0	7.7	0.0	43.6
Ola	15	26.7	20.0	20.0	20.0	0.0	6.7	0.0	6.7	0.0	46.7
Russia	79	30.4	6.3	16.5	22.8	7.6	6.3	0.0	10.1	0.0	46.9
Andreafsky	28	39.3	7.1	21.4	21.4	3.6	3.6	0.0	0.0	3.6	60.7
Kluane	27	44.4	7.4	7.4	37.0	0.0	0.0	0.0	3.7	0.0	81.4
Fishing Branch	28	10.7	3.6	14.3	64.3	7.1	0.0	0.0	0.0	0.0	75.0
Sheenjek	28	17.9	7.1	21.4	50.0	0.0	0.0	0.0	3.6	0.0	67.9
Tatchun	28	14.3	0.0	7.1	75.0	0.0	0.0	0.0	3.6	0.0	89.3
Yukon	139	25.2	5.0	14.4	49.6	2.1	0.7	0.0	2.2	0.7	74.8
Pallant	50	18.0	0.0	4.0	4.0	32.0	8.0	12.0	20.0	2.0	50.0
Fish Creek	46	10.9	4.4	0.0	10.9	37.0	8.7	10.9	10.9	6.1	47.9
Breezy Bay	40	27.5	2.5	5.0	12.5	10.0	10.0	12.5	10.0	10.0	37.5
Atnarko	24	29.2	0.0	4.2	8.3	41.7	0.0	4.2	12.5	0.0	70.9
North	160	20.0	1.9	3.1	8.9	29.4	7.5	10.6	13.8	4.9	49.4
Big Qualicum	58	8.5	0.0	1.7	1.7	16.9	37.3	8.5	23.7	1.7	45.8
Chemainus	24	16.7	0.0	0.0	0.0	4.2	37.5	4.2	37.5	0.0	54.2
Cowichan	22	4.6	4.6	4.6	4.6	13.7	31.8	4.6	22.7	9.1	36.4
Goldstream	23	13.0	4.4	0.0	8.7	13.1	30.5	13.1	13.1	4.4	43.5
Little Qualicum	24	37.5	0.0	0.0	0.0	12.5	16.7	0.0	33.3	0.0	54.2
Nanaimo	24	0.0	4.2	4.2	4.2	20.8	29.2	0.0	20.8	16.7	29.2
Puntledge	25	16.0	4.0	0.0	0.0	12.0	24.0	16.0	20.0	8.0	40.0
ECVI	200	13.0	2.0	1.5	2.5	13.9	30.8	7.0	24.4	5.0	43.8
Demamiel	23	17.4	0.0	0.0	0.0	4.4	26.1	17.4	34.8	0.0	34.8
Nitinat	47	23.4	0.0	4.3	6.4	23.4	19.2	2.1	14.9	6.4	25.5
Conuma	22	0.0	4.6	0.0	9.1	31.8	9.1	13.6	27.3	4.6	13.6
WCVI	92	16.3	1.1	2.2	5.4	20.7	18.5	8.7	22.8	4.4	25.0
Alouette	23	21.7	0.0	0.0	8.7	8.7	21.7	4.4	21.7	13.0	43.4
Chehalis	24	8.3	4.2	4.2	8.3	16.7	20.9	8.3	20.8	8.3	29.1
Chilliwack	48	16.7	0.0	2.1	18.8	12.5	18.8	6.3	16.7	8.3	33.4
Inch	21	0.0	0.0	4.8	14.3	4.8	47.6	4.8	19.1	4.8	19.1
Stave	21	4.8	4.8	0.0	0.0	28.6	28.6	0.0	33.1	0.0	37.9
Wahleach	22	4.6	0.0	13.7	0.0	7.6	27.3	18.2	18.2	13.6	22.8
Fraser	159	10.7	1.3	3.8	10.1	12.6	25.8	6.9	20.7	8.2	31.4
Mamquam	24	0.0	4.2	0.0	8.3	25.0	16.7	4.2	33.3	8.3	8.3
Tzoonie	22	9.1	9.1	0.0	0.0	18.2	9.1	9.1	45.5	0.0	9.1
Mainland	46	4.5	6.7	0.0	4.1	21.6	12.9	6.6	39.4	4.2	8.7

The simulations suggest that relatively accurate estimates of stock composition may be possible should minisatellite DNA variation be applied to practical fisheries management issues but that identification of individual fish to specific regions, particularly in North American stocks surveyed, is less accurate. For example, estimated Fraser River stock composition of pure samples of Fraser River chum salmon ranged from 87 to 93% when resolved with an 18-stock resampled southern British Columbia baseline, but only about 31% of individual Fraser River fish were correctly identified as of Fraser River origin when a 39-stock North Pacific baseline was used. About 26% of the Fraser River individuals were classified as originating from the east coast of Vancouver Island, a result which may seem in conflict with the greater separation observed between Fraser River and ECVI stocks in the estimation of mixture composition. However, estimation of stock composition of a mixture and classification of individual fish in the mixture are separate problems, with classification of individual fish the more difficult problem. Data from only a single fish that is to be identified are considered in classification problems, but data from all fish in the mixture as a whole are considered when estimates of stock composition are determined. Higher levels of accuracy (99%) have been observed previously in estimation of chum salmon composition by using the entire mixture sample rather than by classifying individual fish in the same mixture to region of origin (<60%) (Fournier et al., 1984).

Although analysis of minisatellite DNA variation may be an effective method for estimation of stock composition of chum salmon, a number of improvements would be required before it could be applied (either by itself or as an enhancement) to existing stock identification techniques for chum salmon. Determination of the allelic frequency distributions or band counts at the minisatellite loci for all stocks contributing significantly to fisheries, as well as ensurance that sampling of the contributing populations is adequate to represent samples of the stock that have been collected, would be required.

Genetic variation provides a powerful means to estimate stock composition of chum salmon catches. The particular method used to screen variation will depend on the issue to be resolved. Estimation of stock composition to large regional groups could be conducted with analysis of variation at protein-coding loci, in mitochondrial DNA, in minisatellite DNA, or in the major histocompatability complex (MHC) genes (Miller and Withler, in press). Estimation of local stock composition to a fine scale, such as to tributaries of a major river system, will likely require direct measurement of DNA variation. Surveys of variation at minisatellite loci provide one possibility of achieving fine-scale estimation of stock composition, but analysis of variation at other minisatellite loci, in addition to those utilized in the current manuscript, will be required. No surveys of population variation at microsatellite loci for chum salmon have been conducted yet, although there may be great potential in their application (e.g. Brooker et al., 1994). Given the relative ease of laboratory analysis of variation at microsatellite loci, compared with that at minisatellite loci, microsatellite loci may be more practical than minisatellite loci, on a routine basis, for stock-identification analysis.

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The reproductive condition of white sturgeon, *Acipenser transmontanus*, in San Francisco Bay, California

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Abstract.—White sturgeon, *Acipenser transmontanus*, adults (n=855) were collected on their feeding grounds in San Francisco Bay, California, and their sex and stage of sexual maturity were evaluated histologically. They did not exhibit external sexual dimorphism, and the overall sex ratio did not differ from 1:1. Average fork length was 139 cm ±1.1 cm (mean ± standard error of the mean); females were longer (145 cm ±1.2 cm, n=443) than males (133 cm ±1.0 cm, n=412). In smaller size classes (≤115 cm), males were significantly (P<0.05) more numerous than females. The proportion of females, however, was significantly higher among larger fish (>155 cm). The sample of females consisted of 70% fish with "immature" (previtellogenic) ovaries, 12% with "maturing" (vitellogenic) ovaries, and 18% with "ripe" (large, pigmented eggs) ovaries. In contrast, most males were either "maturing" (meiosis, 56%) or "ripe" (spermatozoa, 39%). Ripe females represented only 9% of all fish sampled. Egg production by females, estimated by hatchery spawning, averaged 5,648 eggs/kg of body weight. The length at which white sturgeon in San Francisco Bay attain sexual maturity was estimated to be 95–135 cm in females and 75–105 cm in males. The duration of one ovarian cycle in iteroparous females was estimated to be longer than one year, with an apparent 2- to 4-year interval between spawning periods; the reproductive cycle of males was estimated to be 1–2 years. The low reproductive potential of white sturgeon in San Francisco Bay should be considered in fishery management of the species.

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White sturgeon, *Acipenser transmontanus*, have long been valued for their caviar and flesh for human consumption. Recently white sturgeon have become popular as a recreational fish (Galbreath, 1985; Kohlhorst et al., 1991) and are being raised by commercial aquaculturists (Logan et al., 1995). During the last four decades, researchers have gathered sufficient information on the biology of wild populations to improve management of the fishery. Information now exists on white sturgeon migratory patterns (Miller, 1972; Kohlhorst et al., 1991), feeding habits (Schreiber, 1962; Semakula and Larkin, 1968; McKechnie and Fenner, 1971; McCabe et al., 1993), age, growth, and population structure (Semakula and Larkin, 1968; Kohlhorst et al., 1980; Brennan and Cailliet, 1991; Kohlhorst et al., 1991; DeVore et al.[1]). Significant knowledge exists on their reproduction, including gonadal development (North et al.[2]; Welch and Beamesderfer[3]), natural spawning (Stevens and Miller, 1970; Kohlhorst, 1976; Parsley et al., 1993; McCabe and Tracy, 1994), gamete and fertilization biology (Cherr and Clark, 1985), and early development (Beer, 1981; Wang et al., 1987; Bolker, 1993).

White sturgeon are anadromous and endemic to Pacific estuaries and coastal rivers of North America. They are found from the Aleutian Islands of Alaska to Monterey Bay, California (Scott and Crossman, 1973). In the Pacific Northwest, they are most abundant in the Fraser, Columbia, and Sacramento–San Joaquin rivers. The San Fran-

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[2] North, J. A., A. L. Ashenfelter, and R. C. Beamesderfer. 1993. Gonadal development of female white sturgeon in the lower Columbia River. *In* R. C. Beamesderfer and A. A. Nigro (eds.), Status and habitat requirements of the white sturgeon populations in the Columbia River downstream from McNary Dam, vol. 2, report G, p. 109–121. Final Report (Project No. 86-50) to Bonneville Power Admin., Portland, Oregon.

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cisco Bay estuary has the largest population of white sturgeon in California. Adults spend most of their life in the bay and migrate into the Sacramento River in the late winter or early spring to spawn (Pycha, 1956; Stevens and Miller, 1970; Kohlhorst, 1976). White sturgeon are believed to reach sexual maturity at age 10 to 30 years, and iteroparous females spawn at intervals of two or more years (Pycha, 1956; Semakula and Larkin, 1968).

We focused our initial studies on the collection of wild broodstock for captive breeding in order to develop artificially induced spawning techniques and hatchery technology (Conte et al., 1988). Concomitantly, we sampled white sturgeon in San Francisco Bay in order to characterize the composition of the population in relation to sex and gonadal maturity.

Materials and methods

White sturgeon were collected in the San Francisco Bay estuary, California, from late October to February 1983–86. The fishing grounds included the area between Golden Gate Bridge, Angel Island, and San Francisco Bay Bridge. Miller (1972) observed that sturgeon congregate in this area to feed and that fish that were ripe migrated into the Sacramento River later in the season to spawn. Sturgeon aggregated while feeding on herring eggs and were seen frequently jumping out of the water. These aggregations of sturgeon were located with sonar. Fishing gear consisted of a short (167–214 cm) stiff pole (rated for 28 kg) equipped with reel (4/0), heavy monofilament line (18–28 kg strength), leader (45–55 kg strength), treble hook (4/0 or 5/0), and heavy sinker (142–227 g). The line was weighted with a sinker at the end of the leader, and the treble hook was attached approximately 30 cm above the sinker.

Sturgeon were usually encountered at water depths of 6 to 9 m and were snagged as they rubbed the line or hooked when they took a bait of herring fillet or eggs. Water temperatures and salinities during collection periods were 9–15°C and 24–32 ppt, respectively. Further details on fish-collection techniques are described and illustrated by Cuanang (1984). White sturgeon broodstock handling, sampling, and care followed procedures of Conte et al. (1988).

Sturgeon were examined for external structure and size, including morphometric and meristic characters. Measurements included fork and total length (±0.1 cm), head length (±0.1 cm), mouth width (including the lips, ±0.1 cm), and body weight (±0.1 kg). Meristic characters of the scutes in the dorsal, lateral, and ventral rows were recorded according to the methods of Vladykov and Greeley (1963). Proportional measurements (snout and head) were expressed as percentages of the head and fork length, respectively. Sturgeon were alive when sampled, and all fish, except for ripe broodstock, were released after capture. Samples of gonadal tissue and blood plasma were collected for histological analysis, but sections of fin rays were not collected for age determinations in order to avoid excessive trauma.

Sex and stages of sexual maturity in white sturgeon were examined by using histological slides of gonadal tissue and light microscopy (Chapman, 1989; Doroshov et al., 1991). Gonadal samples were collected from 300 females and 325 males. Ovarian stages in females were assigned a numerical score according to differentiation in the shape and size of the ovarian follicle (according to oocyte cytoplasm staining properties, nuclear and cytoplasmic inclusions, presence or absence of yolk platelets, differentiation of the vitelline envelope, and differentiation in the granulosa cells and thecal follicular layers). A numerical score was assigned to each male testis according to the proportion of cysts with different types of germ cells that were counted in several random fields on the slide (spermatogonia, spermatocytes, spermatids, and spermatozoa). Based on histological scores, the following classification was assigned for individual fish: (1) "immature," (2) "maturing," or (3) "ripe." Group-1 fish included females in the previtellogenic stage of ovarian development (in chromatin nucleolar stage and primary oocyte growth) and males in the gonial proliferation stage of testicular development. Group-2 fish included females with ovaries in early or intermediate phases of vitellogenesis (oocyte cytoplasm containing yolk bodies) and males with testes in the meiotic phase (spermatocytes and spermatids). Group-3 fish included females with ovaries containing large and darkly pigmented oocytes exhibiting yolk polarization and germinal vesicle migration and males in the postmeiotic testicular phase (spermiogenesis and differentiated spermatozoa).

Data on egg production (approximate individual relative fecundity) were collected from gravid females that had been captured in the Sacramento River from February to March 1991–94 in order that they might spawn in the hatchery. Estimation of egg production was based on the number of eggs collected surgically (a procedure routinely performed during artificial spawning of sturgeon [see Conte et al., 1988]) and represents 60–80% of actual individual fecundity.[4] The number of eggs removed from each female was

[4] The percentage of eggs collected was determined by comparing egg production at spawning of domestically raised sturgeon with a total fecundity estimate of domestic sturgeon (of equivalent size) processed for caviar production.

estimated volumetrically by using three 5-mL volume subsamples. Egg diameters were measured (±0.01 mm) along the animal-vegetal axis with a dissecting microscope and ocular micrometer.

Procedures described in Steel and Torrie (1986) were followed for statistical analyses. The Statistical Analyses System software (SAS, 1985) was used for data processing. The measure of variability is reported as standard error of the mean (±SEM), and the accepted level of statistical significance is $P<0.05$. All length measurements are given in fork length (FL).

Results

Body size, sex ratio, and sexual dimorphism

We sampled a total of 855 white sturgeon, ranging in fork length from 79 to 202 cm (mean=139 ±1.1 cm). Mean length of females (145 ±1.2 cm) was significantly greater than that of males (133 ±1.0 cm). The sex ratio was 1:1 (Table 1). The proportion of males, however, was significantly higher among fish ≤115 cm, whereas the proportion of females was higher among fish >155 cm (Table 1).

In most cases we could not determine by external examination the sex of white sturgeon, except for spermiating males and some ripe females (recognized by an enlarged abdomen). We found no significant differences between the sexes in numbers of dorsal and lateral scutes, relative lengths of the head and snout, and width of the mouth. Among all fish examined histologically, we found only one case of hermaphroditism, a maturing testis containing a few ovarian follicles with previtellogenic oocytes.

Table 1

Size classes and sex ratios of white sturgeon, *Acipenser transmontanus*, sampled in San Francisco Bay, California, from October to February, 1983–86. Significant deviations (chi-square) from the expected 1:1 sex ratio are marked by asterisks.

	Sample size			
Fork length (cm)	Total	No. of males	No. of females	Sex ratio
<95	14	9	5	0.64:0.36*
95.1–105	84	53	31	0.63:0.37*
105.1–115	119	79	40	0.66:0.34*
115.1–125	120	59	61	0.49:0.51
125.1–135	109	57	52	0.52:0.48
135.1–145	135	58	77	0.43:0.57
145.1–155	93	46	47	0.50:0.50
155.1–165	87	33	54	0.38:0.62*
165.1–175	56	12	44	0.21:0.79*
>175	38	6	32	0.16:0.84*
Total	855	412	443	0.48:0.52

Distribution of maturity stages in the population

The smallest ripe female and male were 104 cm and 100 cm, respectively. The female sample population comprised 70% group-1, 12% group-2, and 18% group-3 individuals (Table 2). Except for one large size class (175.1–185 cm), the proportion of immature females remained high (>62%) in each length class. Although females with vitellogenic or ripe ovaries (groups 2 and 3) appeared in length classes 95.1 to 125.1 cm, their proportions were small (average 3% for group 2 and 6% for group 3). In 135.1–195 cm sturgeon, the proportions of females with maturing and ripe

Table 2

Proportions of gonadal maturity stages in different size classes of white sturgeon females (n=300) and males (n=325) in San Francisco Bay, California.

Female size class (cm FL)	Number in sample	Female gonadal maturity stage (%)		
		Group-1	Group-2	Group-3
75.1–85	1	1.00	0.00	0.00
85.1–95	1	1.00	0.00	0.00
95.1–105	9	0.89	0.00	0.11
105.1–115	28	0.96	0.00	0.04
115.1–125	31	0.90	0.03	0.07
125.1–135	33	0.88	0.06	0.06
135.1–145	34	0.65	0.15	0.20
145.1–155	47	0.66	0.13	0.21
155.1–165	45	0.56	0.13	0.31
165.1–175	39	0.62	0.15	0.23
175.1–185	22	0.27	0.32	0.41
185.1–195	10	0.70	0.20	0.10
Male size class (cm FL)	**Number in sample**	**Male gonadal maturity stage (%)**		
		Group-1	Group-2	Group-3
75.1–85	2	0.50	0.50	0.00
85.1–95	1	0.00	1.00	0.00
95.1–105	18	0.33	0.50	0.17
105.1–115	52	0.10	0.59	0.31
115.1–125	59	0.04	0.64	0.32
125.1–135	54	0.04	0.54	0.42
135.1–145	51	0.02	0.63	0.35
145.1–155	37	0.00	0.49	0.51
155.1–165	33	0.00	0.45	0.55
165.1–175	12	0.00	0.42	0.58
175.1–185	3	0.00	0.67	0.33
185.1–195	3	0.00	0.67	0.33

ovaries (groups 2 and 3) increased and stabilized at an overall average of 16% (= 32/197) in group 2 and at a overall average of 25% (= 50/197) in group 3; the remaining 59% consisted of group-1 females. The average proportion of ripe females (group 3) in size groups less than 135.1 cm was statistically less than that observed in the combined size class of 135.1 to 195 cm (chi-square, $P<0.05$). A similar result holds for maturing (group-2) females (chi-square, $P<0.05$). Together, these data indicated that proportions of reproductively active females in the sturgeon population may be determined by a combination of two factors: 1) the recruitment of females into puberty (first vitellogenic cycle) occurs over a range of body sizes beginning at 95.1 cm; and 2) female white sturgeon require more than a one-year interval between consecutive spawnings. If one conjectures a predominant 4-year spawning period in iteroparous females (because of the percentage [25%] of ripe females), we could expect to see a ratio of immature to mature to ripe around 2:1:1 in size classes above 135 cm. Our data reject this ratio (chi-square, $P<0.005$). Unfortunately, we were not able to clearly distinguish between the first and second spawning cycles by histological examination of vitellogenic and ripe ovaries.

Male samples, in contrast to female samples, had overall low proportions of immature (premeiotic phase) individuals (5% in group 1), and recruitment into the meiotic phase of spermatogenesis (group 2) occurred at a smaller size, beginning at 75.1 cm (Table 2). Sampled fish from 105.1 to 195 cm were practically all (294 of 304) in group 2 (57%) or group 3 (40%). If one conjectures a predominant biennial spawning interval, we would expect the data to show a 1:1 ratio of meiotic and postmeiotic testicular stages. Our data reject this ratio (chi-square, $P<0.001$).

Relative fecundity (egg production)

Egg production from artificially spawned wild white sturgeon females ranged from 3,192 to 8,582 eggs/kg of body weight. The average size of ova was 3.7 mm ±0.02 mm. The average weight of these females was 36 ±2 kg and fork length was 153 ±4 cm (n=40). The estimated hatchery production was 203,328 ova for a female of average size; individual fish produced between 63,840 and 469,432 eggs. The relationship between the egg diameter and fork length was not statistically significant.

Discussion

We found that white sturgeon do not have external sexual dimorphism and, except for ripe fish on spawning grounds, there are no apparent morphological differences between the sexes. The 1:1 sex ratio (overall) of white sturgeon in San Francisco Bay is in agreement with data for the Columbia River system (Beamesderfer and Rien[5]) and Eurasian acipenserid species (Chugunov and Chugunova, 1964; Zubova, 1971; Persov, 1975). A greater proportion of males in smaller size classes and a predominance of females in larger size classes have also been observed in other species of sturgeon (e.g. *A. sinensis,* Xin et al., 1991). One possible explanation for this difference in sizes is that growth rates diverge between the sexes during the reproductive phase of life. Kohlhorst et al. (1980) found no difference in growth rates between sexes in white sturgeon of the San Francisco Bay; however, their study was limited to a narrow size and age range. An alternative explanation may be a higher rate of mortality in males and a resultant shorter life span in comparison with females. High rates of mortality for males may be associated with earlier puberty, more frequent breeding, and longer residence on the spawning grounds. Assuming that the population was sampled randomly, both differences in growth and mortality may have contributed to the substantial divergence in modal size classes between the males (105.1–115 cm FL) and females (135.1–145 cm FL). Although the predominance of females among larger fish may be explained by these factors, the predominance of males among smaller fish appears to contradict a chromosomally determined (gonochoristic) sex ratio and should be investigated further.

Although subject to high individual variation, the relative fecundity among sturgeon species appears to be generally similar. For example, for the large anadromous species *Huso huso*, Raspopov (1987) reported a relative fecundity of 2,750 to 10,500 eggs/kg of body weight. Smaller species such as shortnose sturgeon, *A. brevirostrum*, had an average relative fecundity of 11,568 eggs/kg of body weight (Dadswell, 1979). Although we could not directly estimate relative fecundity for white sturgeon females in San Francisco Bay, egg production from artificially spawned females averaged 5,648 eggs/kg of body weight and 203,328 eggs for an average length (153 cm) female. Relative fecundity for white sturgeon females in the Columbia River was not reported; however, the number of eggs produced was from

[5] Beamesderfer, R. C., and T. A. Rien. 1993. Dynamics and potential of white sturgeon populations in three Columbia River reservoirs. *In* R. C. Beamesderfer and A. A. Nigro (eds.), Status and habitat requirements of the white sturgeon populations in the Columbia River downstream from McNary Dam, vol.1, report H, p. 175–204. Final Report (Project 86-50) to Bonneville Power Admin., Portland, Oregon.

98,200 to 699,000 eggs for fish 115 to 215 cm FL (DeVore et al.[1]). Comparisons of egg diameters in ripe females from the Sacramento and Columbia rivers revealed that female sturgeon from the Sacramento River had larger eggs (3.4–4.0 mm) than those found in females from the Columbia River (2.6–3.6 mm) (North et al.[2]). This difference may account for the apparent higher fecundity of white sturgeon females in the Columbia River. We found no relation between size of the female sturgeon and mature egg diameters. Lutes et al. (1987) also did not detect a relation between female body size and diameters of postvitellogenic oocytes in white sturgeon.

The size at which white sturgeon attain sexual maturity appears to vary between populations. Our observations indicate that female white sturgeon in San Francisco Bay mature at larger sizes (>95 cm) than males (>75 cm). Because the proportions of ripening individuals (groups 2 and 3) increased and stabilized above 135 cm in females and 105 cm in males, recruitment into puberty most likely occurs from 95 to 135 cm for females and from 75 to 105 cm for males. In the Columbia River, female white sturgeon did not mature until they were even larger (160–193 cm FL), revealing significant size variations in the river downstream from all dams and between different river reservoirs (DeVore et al.[1]; Welch and Beamesderfer[3]; Beamesderfer and Rien[5]). These differences in size at first sexual maturity were largely attributed to food availability and hydrologic conditions. Working with wild and domestic stocks, Chapman (1989) postulated that size and age at sexual maturity in white sturgeon were dependant on body size and nutrient composition. Size or age at sexual maturity, however, could be modified by growth, nutrition, and environmental factors.

Examination of the stage of gonadal development in different length classes of white sturgeon females in San Francisco Bay indicated a high fraction of group-1 (immature) individuals. The proportions of group-2 (maturing) and group-3 (ripe) females in the sampled population were low (12% and 18%, respectively); ripe females represented only 9% of all sturgeon sampled. Similar observations in the Columbia River system revealed even lower proportions, 6% maturing and 2% ripe (DeVore et al.[1]; North et al.[2]; Welch and Beamesderfer[3]). From histological analysis of oogenesis (Chapman, 1989) and from the proportions of different ovarian stages in the white sturgeon population of San Francisco Bay, we assume that iteroparous sturgeon females require longer than one year to complete an egg development cycle, including vitellogenic growth and prematurational polarization of the oocyte. Because the proportion of females with ripe ovaries (group 3, >135 cm) was on average 25% of all sampled individuals, the interval between two consecutive spawnings is most likely between 2 and 4 years. Our recent observations of domestically raised and continuously fed white sturgeon suggest predominantly biennial ovarian cycles. Because wild female sturgeon, compared with other fish including domestic sturgeon, lose a substantial percentage of weight and energy at spawning (Krivobok and Tarkovskaya, 1970), it is possible that they defer a new wave of ovarian vitellogenesis for some time after spawning, allowing recovery from spawning depletions (the high percentage [59%] of fish in group 1 strongly suggests this event). A final conclusion regarding spawning periodicity of white sturgeon cannot, however, be reached until fish that have been tagged are recaptured and sampled repeatedly or until the size and age interval of female recruitment to puberty is known. These are important considerations, because pubertal age of white sturgeon females may extend from 15 to 32 years (White Sturgeon Planning Committee[6]).

Considering the season of our sampling (late fall–early winter) and the potential overlap between meiotic and maturational phases of testicular development, the adult male white sturgeon may spawn annually (as in commercial hatcheries) or biennially. Existence of a biennial cycle in sturgeon males could be verified by continued sampling throughout spring and summer. Most spawning males accommodate the protracted spawning season (February–June) of females. This shorter reproductive cycle, which is associated with annual spawning migrations, may also result in a higher mortality for older and larger males.

A 2–4.5 year spawning period has been suggested for female white sturgeon in the Columbia River (Welch and Beamesderfer[3]). According to Trusov (1975), the refractory ovarian stages in iteroparous sevryuga, *A. stellatus*, last 2 to 5 years, whereas the ovarian vitellogenesis occurs within 1 to 2 years. Examining the sexual maturation of Russian sturgeon, *A. guldenstadti*, in the Sea of Azov, Kornienko et al. (1988) found that 72% of the sampled adult-size fish had either immature or refractory ovaries and that the remaining fish were approximately equally distributed between "maturing" and "ripe." In males, spermatogenesis was a continuous process.

We conclude that sexual maturation in white sturgeon is prolonged. Females mature slowly, and first maturation takes place over a wide range of body sizes. The average interval between spawnings by iteroparous females appears to range from 2 to 4

[6] White Sturgeon Planning Committee. 1992. White sturgeon management framework plan. 2501 S.W. First Avenue, Pacific States Marine Fisheries Commission, Gladstone, Oregon.

years. Males mature at a smaller body size and have shorter intervals between spawnings than do females. Sex differences in maturation rates of sturgeon create incredible combinations of individual matings from different generations that favor genetic diversity even with a small number of spawning females. Annual recruitment and genetic structure of a sturgeon population may be influenced by its sex ratio, the proportion of females spawning each year, and the number of eggs they produce. Monastyrski (1949) noted that the complex age-size structure of spawning populations and the iteroparity of sturgeons require a special approach for their management. Our data on the reproductive conditions of white sturgeon in the San Francisco Bay provide additional evidence for potential sensitivity of sturgeon populations to exploitation by either commercial or sport fisheries. The effect of prolonged sexual maturation may be compromised further by loss of spawning habitat, altered seasonal changes of temperature in rivers with controlled flow, and environmental pollutants that may affect sexual development and the reproductive cycle.

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Abstract.—The vermilion snapper, *Rhomboplites aurorubens*, is an important species in headboat and commercial reef fisheries in the southeastern United States, especially in the Carolinas. The reproductive biology of vermilion snapper was determined from samples collected on biweekly research cruises (April to August 1992 and May 1993) and from samples collected from commercial vessels (September to April 1992–93). Vermilion snapper did not exhibit a 1:1 sex ratio; 63% of the specimens were female. The reproductive season of vermilion snapper is April through late September in the southeastern United States. All vermilion snapper examined were mature, with the smallest female at 165 mm FL, the smallest male at 179 mm FL. The smallest fish aged (165 mm FL) was two years old. Length was the best predictor of batch fecundity (BF=0.0438$FL^{2.508}$). Vermilion snapper spawn approximately every five days or about 35 times a year. Atresia did not significantly affect fecundity estimates. Vermilion snapper is an indeterminate spawner; its oocytes mature continuously during the spawning season and there is no hiatus between the size distribution of the oocyte classes. Total fecundity did not decline over the spawning season. Rather, it gradually increased through August and then declined in September. Mean oocyte diameter stayed constant over the reproductive season. The order of spawning batches was not consistent with the determinate fecundity prediction.

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Reproductive seasonality, maturation, fecundity, and spawning frequency of the vermilion snapper, *Rhomboplites aurorubens*, off the southeastern United States*

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The vermilion snapper, *Rhomboplites aurorubens*, is a small lutjanid distributed from North Carolina and Bermuda, through the West Indies and the Gulf of Mexico, and south to southeastern Brazil (Böhlke and Chaplin, 1968). It is associated with two distinct habitats on the outer continental shelf near the Carolinas: shelf-edge habitat (64–183 m) and inshore "live-bottom" habitat (26–56 m) (Grimes, 1976). This lutjanid attains a maximum total length of approximately 600 mm (24 in) and a maximum weight of 2.8 kg (6 lb) (Grimes, 1978).

Vermilion snapper is an important species in the headboat and commercial reef fish fisheries of the Carolinas. Despite an increase in landings in North Carolina, South Carolina, and Georgia from 6.8 metric tons (t) (15,000 lbs) in 1988 to 499 t (1.1 million lbs) in 1991, catch per unit of effort (CPUE) exhibited a marked decline (Zhao and McGovern[1]); there was also a significant decrease in mean length of vermilion snapper taken by fishery independent sampling and by headboat and commercial fisheries (Collins and Sedberry, 1991; Zhao and McGovern[1]) over the same period.

Declines in CPUE and mean size in fishery-independent samples indicate that vermilion snapper is overfished (Collins and Sedberry, 1991). Owing to the importance of vermilion snapper in the southeastern U.S. fisheries, current information on all aspects of its reproduction is needed to manage the vermilion snapper fishery effectively. Fecundity and sexual maturity information is essential for management of any fishery of economic consequence to a region (Hunter et al., 1992). Fecundity data are needed to calculate a spawning stock ratio (SSR) in annual stock assessments for use in evaluating management regulations. To quantify fecundity

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[1] Zhao, B., and J. C. McGovern. 1996. Population characteristics of the vermilion snapper, *Rhomboplites aurorubens*, from the southeastern United States. In preparation.

and spawning frequency more accurately, new techniques, such as the hydrated oocyte method for fecundity estimates (Hunter et al., 1985) and the postovulatory follicle method (Hunter and Goldberg, 1980; Hunter and Macewicz, 1985) for determining spawning frequency, need to be used. There is considerable information on the reproductive biology of over 40 lutjanids (Grimes, 1987); however, there is only one recent study (Davis and West, 1993) that uses the new assessment methods on a lutjanid.

Recent studies of the reproductive biology of vermilion snapper in the southeastern U.S. are quite limited. Current management of the vermilion snapper fishery is based on age, growth, and reproductive data collected in the early to mid-1970's, prior to the rapid expansion of the fishery (Grimes, 1978; Grimes and Huntsman, 1980). Grimes (1976) and Grimes and Huntsman (1980) examined aspects of the reproductive biology of vermilion snapper in this area in the early 1970's, but neither used a histological technique to assess reproductive season, spawning frequency, or maturity. Collins and Pinckney (1988) reported on the maturity of vermilion snapper in the southeastern United States from 1978 to 1980 but used only scales to age fish. The reproductive biology of vermilion snapper has also been studied in the Gulf of Mexico. Nelson (1988) examined the sex ratio, size at maturity, spawning frequency, and fecundity of vermilion snapper off Flower Garden Banks, Gulf of Mexico, from 1980 to 1982 but did not use a histological technique. These data need to be supplemented with more recent information, including histological criteria and more accurate assessment methods.

Although vermilion snapper is considered a multiple spawner on the basis of its prolonged spawning season, variation in the gonadosomatic index for similarly sized fish, and variation in the number of maturing ova types found in the ovary (Grimes and Huntsman, 1980), a reassessment of the reproductive biology of vermilion snapper, using recently developed techniques, is necessary 1) to quantify the annual reproductive cycle; 2) to determine age and size at maturity and to detect changes that may have occurred because of the fishery; 3) to estimate spawning frequency; 4) to describe vermilion snapper as either a determinate or indeterminate spawner; and 5) to calculate fecundity (corrected for atresia) of the vermilion snapper in the southeastern United States.

Materials and methods

Specimens were obtained between April 1992 and May 1993 on research cruises conducted as part of a fishery-independent survey of reef fishes. Scientists of the MARMAP (Marine Resources Monitoring, Assessment, and Prediction) program (see Collins and Sedberry [1991] and Zhao and McGovern[1]) conducted biweekly cruises to randomly selected reef sites, from Cape Lookout, North Carolina, to Jacksonville, Florida (Fig. 1). Sampling in 1992 was conducted from April through August, and in 1993 from May through August by using baited chevron-shaped (arrowhead) fish traps (Collins, 1990) soaked for 90 min during daylight only. The time of trap deployment was recorded as time of catch. Some (n=24) fish were collected with hook-and-line gear fished at dawn or dusk (Collins and Sedberry, 1991). Measurements taken from the vermilion snapper catches were lengths in mm (total length [TL] and fork length [FL])

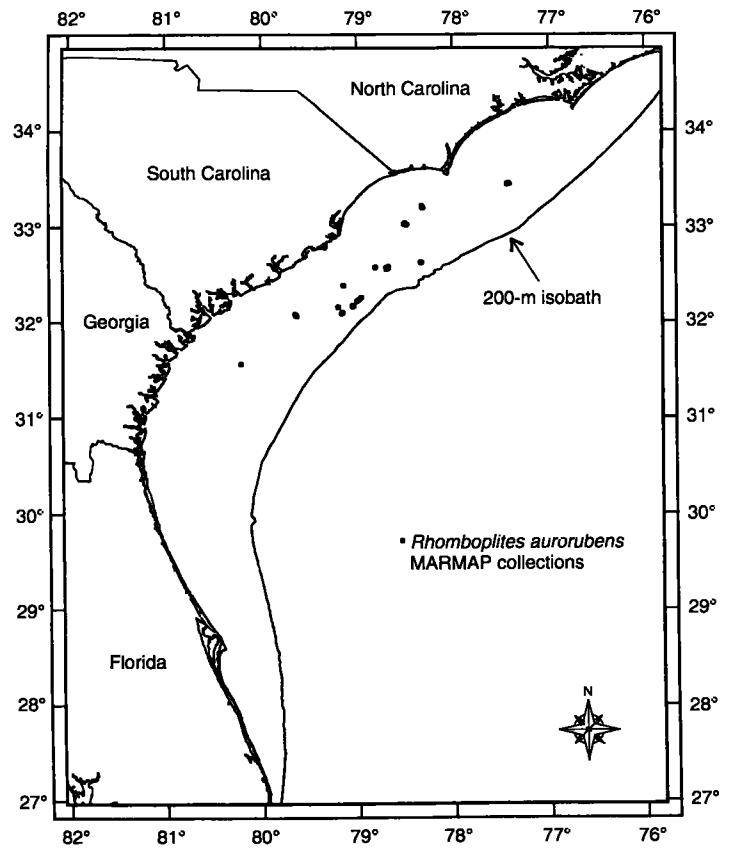

Figure 1

MARMAP station locations of vermilion snapper, *Rhomboplites aurorubens*, captured from April to August 1992 and in May 1993. (n=110)

and weights (g/total body weight and g/ovary-free body weight [OFWT] ±1 g). Ovaries were removed, blotted dry, and weighed and fixed in 10% buffered seawater formalin. After fixation, samples of ovarian tissue were weighed with an Ohaus digital balance (±0.001 g) for fecundity determination. Conversion factors were developed for samples taken during the first three months of the study because fresh gonad weight and OFWT were not measured. When sampling was not untertaken (September to April), additional samples were purchased from the commercial hook-and-line catch landed in Georgetown, South Carolina. Commercial samples were used for histological examination (see below), both to define the spawning season and to gather atresia measurements.

A modified gonadosomatic index (GSI) was used to quantify the reproductive cycle. The GSI was calculated as $GSI = (gonad\ weight/OFWT) \times 100$ (Nieland and Wilson, 1993; Nikolsky, 1963). In order to make comparisons with the findings of Grimes (1976), the following gonad index (GI) equation was used:

$$K_G = (WT_G / TL^3) \times 10^6,$$

where WT = preserved weight of the gonad (g), and
TL = total length (mm).

GI values from Grimes (1976) were compared with GI values from the present study to evaluate possible differences between the two studies in reproductive timing and size and age at maturity.

A chi-square test was used to evaluate the sex ratio of vermilion snapper. A 2 × 2 contingency table was used to compare the sex ratios in Grimes (1976) with those in the present study and to compare MARMAP samples with commercial samples (Zar, 1984). Sex-ratio data were also analyzed by 50-mm length classes by using a 2 × 4 contingency table (Zar, 1984)

Histological analysis was used to assess maturity and spawning activity and to verify whole-oocyte staging. Gonad sections were prepared according to the methods of Wenner et al. (1986). The developmental stage of each ovary was identified by using the criteria of Hunter et al. (1992) (Table 1). Each ovary was also examined for the presence or absence of the two stages of postovulatory follicles (POF's). Testes were classified by means of the modified criteria of Wyanski and Pashuk[2] (Table 2).

Maturity definitions I–V from Hunter et al. (1992) were used to classify females. Mature females included the following: all active females; all inactive mature females; inactive females with early yolked oocytes and with alpha, beta, or no atresia; and inactive females with unyolked oocytes and with alpha or beta atresia (Table 1). If testes were developing, ripe, spent, or resting, they were considered mature (Table 2).

Transverse sections of otoliths were made with a Buehler Isomet low-speed saw. Sections were mounted on slides, immersed in cedarwood oil, and viewed under a dissecting microscope. The dissecting microscope was linked by a video camera to a MATROX frame grabber and personal computer with OPTIMAS image analysis software.

The following fecundity definitions from Hunter et al. (1992) were used in the present study:

Determinate fecundity	Annual fecundity is fixed prior to the onset of the spawning season.
Indeterminate fecundity	Annual fecundity is not fixed prior to the onset of the spawning season, and unyolked oocytes continue to mature and are spawned during the spawning season.
Annual fecundity (AF)	Total number of eggs spawned per year.
Total fecundity (TF)	Standing stock of advance-stage yolked oocytes (AYO's).
Potential fecundity (PF)	Total AYO's that mature per year. Potential fecundity was considered to be equivalent to the standing stock of AYO's in fully developed prespawning females.
Batch fecundity (BF)	Total number of hydrated oocytes (HO's) released in one spawning.

If vermilion snapper is a determinate spawner, then the following are expected: a hiatus will develop in the frequency distribution of oocyte diameter between the oocytes that mature for the season and the reservoir of less advanced oocytes present year round; TF declines over the spawning season; mean oocyte diameter (MOD) increases over the spawning season; and the spawning order of batches is consistent with the determinate fecundity definition (see Hunter et al., 1992).

To determine whether AYO's were randomly distributed throughout the ovary, the densities of AYO's at six locations within the ovaries of nine fish were

[2] Wyanski, D. M., and O. Pashuk. 1996. Processing and interpretation of fish reproductive tissue at the Marine Resources Research Institute of the South Carolina Department of Natural Resources. In preparation.

compared. The locations were anterior, center, and posterior in both the left and right lobes of the ovary. A wedge from the exterior of the ovary to the interior of the ovary was taken for each location sampled. A two-way ANOVA was run to test for effects of location and individual fish on oocyte density.

Whole oocytes were staged by using the criteria of Hunter et al. (1992). Yolk density was used to discriminate between the different developmental stages of oocytes, with counts of stage-3 AYO's (Fig. 2A) being the basis of TF estimates. The definitions of each stage were as follows:

Stage 1 Initial layer of yolk along the periphery of the oocyte appearing as a narrow band but not extending over 20% of the distance

Table 1

Histological stages of female vermilion snapper, *Rhomboplites aurorubens*, modified from Hunter et al. (1992).

Inactive	Active
Not capable of spawning now or in the near future.	Capable of spawning now or in the near future. Ovary contained enough advanced yolked-oocytes (AYO's) for one spawning.
Mature Ovaries show clear evidence of past spawning or past maturation of AYO's.	**Mature** AYO's present with no or minor (<49%) alpha atresia of AYO's.
Postspawning. Contains either postovulatory follicles (POF's) and no AYO's, or contains POF's with mostly atretic AYO's.	Spawning. Evidence of past spawning (POF's) or imminent spawning (hydrated oocytes [HO's]) or migratory nucleus-stage oocytes (MNO's).
Major atresia. AYO's present, alpha atresia of AYO's ≥50%.	Nonspawning. No evidence of recent or imminent spawning, but fish are capable of spawning in the near future.
Uncertain maturity No AYO's present.	
Early yolked. Early yolked oocytes present. May have alpha, beta, or no atresia of early yolked oocytes.	
Unyolked. Unyolked oocytes present. Alpha or beta atresia of unyolked oocytes evident.	
Immature Unyolked oocytes present with no atresia.	

Table 2

Histological staging of male vermilion snapper following modified criteria developed by Wyanski and Pashuk (1990).

Inactive	Active
Not capable of spawning now or in the near future.	Capable of spawning now or in the near future.
Mature Spent. No spermatogenesis; some residual sperm in tubules and lumina.	**Mature** Developing. A few primary and secondary spermatocytes through tubules and lumina (no spaces) with spermatozoa.
Resting. Large cross section compared to immature male; little or no spermatocyte development; empty tubules and lumina evident.	Ripe. Predominance of spermatozoa; areas of spermatogenesis toward outer surface of testes in some specimens.
Immature Small cross section compared to resting male; little or no spermatocyte development; empty tubules and lumina not evident.	

between the nucleus and the zona pellucida (egg diameter ~0.15–0.25 mm)

Stage 2 Lightly packed yolk possibly extending from the periphery to the nucleus with the nuclear area still evident (~0.25–0.35 mm)

Stage 3 Yolk dense enough to occlude the nucleus (~0.35–0.45 mm)

Stage 4 Parts of the dense yolk become translucent usually beginning at the periphery (~0.45–0.60 mm)

Stage 5 Oocyte is translucent except for the oil droplet (~0.60–1.25 mm).

Alpha-atretic AYO's were not included in TF estimates.

To estimate total fecundity, whole oocytes were examined by using a modified version of the hydrated oocyte method of Hunter et al. (1985). Each sample weighed approximately 50 mg and consisted of about 100 to 150 oocytes. Three diameter measurements per oocyte were taken and then averaged to obtain a mean oocyte diameter (MOD). A mean of the MOD's of all AYO's in the two samples taken from each female was calculated for 138 females and then analyzed for TF. Oocytes on each gridded slide were counted, measured, and staged with GLOBAL LAB image analysis software linked by a video camera system to a compound microscope. The following fecundity equation was used to assess TF:

$$TF = Z \times C,$$

where Z = ovary weight in grams, and
C = oocyte density (number of AYO's per gram of ovarian tissue).

To see if time had an impact on TF, TF was regressed on OFWT and on days elapsed since 15 April. Also, an ANCOVA was performed on monthly TF regression equations to see if there was a temporal effect on TF.

To see if atresia had any effect on fecundity estimates, the proportion of atretic oocytes was calculated for each whole oocyte sample that was counted. The number of alpha atretic AYO's in a sample was divided by the total number of AYO's in that sample (Hunter et al., 1992). Atresia subclasses were defined by Bretschneider and Duyvene de Wit (1947) and Hunter and Macewicz (1985). Alpha atresia involves the reabsorption of the entire oocyte, and beta atresia involves the major degeneration and reabsorption of the follicle (Hunter and Macewicz, 1985). Three subclasses of alpha atretic AYO's were noted: no atresia, minor atresia (1–49%), and major atresia (50–100%).

To estimate PF, only females from the beginning of the spawning season that showed no recent signs of spawning (presence of HO's or POF's) were used in analyses. Because PF is estimated at the beginning of the season, some oocytes may not have yet been recruited into the stock of advanced yolked oocytes. To find the size at which oocytes are fully recruited, a series of stepwise multiple regressions was run on 59 females (Table 3). Data were removed by 0.005 mm increments beginning with the lowest diameter class of 0.360 mm. Analysis indicated that the threshold for a significant effect of diameter on PF occurred between 0.445 mm and 0.450 mm. The regression coefficient for oocyte diameter was significant for females with a MOD equal to or less than 0.445 mm but insignificant for females with a MOD

Figure 2

Photographs of whole oocytes of vermilion snapper at 40×: (**A**) stage-3 advanced yolked oocyte (AYO), in which the oocyte is completely opaque except the perivitelline border; (**B**) late migratory nucleus-stage oocyte (MNO), in which some droplets of the peripheral yolk have coalesced and become translucent; and (**C**) hydrated oocyte (HO), in which the whole oocyte is translucent.

Table 3

Results of a stepwise multiple regression of the total fecundity of vermilion snapper on ovary-free weight and mean oocyte diameter for a succession of oocyte diameter classes. Dashed line separates oocyte diameter classes, where diameter is a significant variable, from those where it is not.

Oocyte diameter class (mm)	Multiple regression coefficient and t-ratio						
	Constants		Fish weight		Oocyte diameter		
	n	a	b_1	t	b_2	t	r^2
0.360–0.470	59	–271,217	83.5	2.73	720,838	5.86	0.405
0.365–0.470	58	–273,751	84.0	2.71	726,434	5.57	0.384
0.370–0.470	57	–274,239	84.1	2.66	727,502	5.24	0.357
0.375–0.470	55	–267,604	84.1	2.56	712,304	4.56	0.306
0.380–0.470	52	–228,103	87.9	2.54	620,040	3.34	0.230
0.385–0.470	50	–242,944	106	2.95	645,696	3.31	0.260
0.400–0.470	48	–239,170	112	3.04	634,478	2.98	0.248
0.405–0.470	47	–229,442	189.3	4.15	578,788	2.87	0.347
0.410–0.470	41	–247,829	210.5	4.47	611,076	2.55	0.385
0.415–0.470	40	–233,730	214.7	4.48	577,705	2.33	0.389
0.420–0.470	34	–295,305	222.9	5.24	711,614	2.86	0.506
0.425–0.470	27	–312,154	355.1	6.66	694,250	2.52	0.684
0.430–0.470	24	–300,087	364.1	6.45	663,948	2.09	0.680
0.435–0.470	18	–501,504	389.7	6.64	1,093,714	2.63	0.750
0.440–0.470	16	–510,147	398.6	6.74	1,108,996	2.40	0.782
0.445–0.470	13	–700,475	551.9	5.41	1,462,344	2.85	0.770
0.450–0.470	7	–652,740	536.4	2.37	1,365,795	.855	0.749

greater than 0.445 mm. Thus, only females with a MOD greater then 0.445 mm were used to estimate PF. Fecundity was regressed on OFWT to evaluate the predictability of the relationship.

Batch fecundity was determined by calculating the number of migratory nucleus-stage oocytes (MNO's; Fig 2B) or hydrated oocytes (HO's; Fig. 2C) in two weighed subsamples from each female (Hunter et al., 1992). Ovaries that contained hydrated oocytes loose in the lumen were eliminated from BF analyses. A modified version of the hydrated oocyte procedure of Hunter et al. (1985) was also used in BF estimates. Definitions from Hunter et al. (1992) were used to separate each spawning batch (Table 4). To see if batch size varied with the order of spawning, a one-way ANOVA was run on 49 females. To evaluate the temporal effects on BF, ANCOVA was run on monthly equations of BF.

Exact ages of POF's were not known because sampling on MARMAP cruises occurred only from dawn through dusk and because trap deployment time was assigned to the catch, regardless of when the fish entered the trap. Therefore, we defined POF's in terms of "new" and "old," on the basis of data from reports in the literature and from our observations. There is limited work on other lutjanids (Davis and West, 1993); thus, descriptions from Hunter and Macewicz (1985) were also used to define POF's. New POF's were generally large and had an orderly arrangement of distinct columnar granulosa cells with prominent nuclei intact (Fig. 3A). New POF's resembled the early stage POF of *Lutjanus vittus* (Davis and West, 1993). Old POF's were small, coiled, eosin-

Table 4

Batch number classification for vermilion snapper following Hunter et al. (1992).

Batch number	Definition
1	Nonhydrated advanced yolked oocytes (AYO's) present and post-ovulatory follicles (POF's) absent.
2	One class of POF's and nonhydrated AYO's present.
3	Two classes of POF's and nonhydrated AYO's present.
4	Only one batch of migratory nucleus-stage oocytes (MNO's) and one batch of hydrated oocytes (HO's) present, no other AYO's present.
5	Only one batch of HO's present, no other AYO's present.

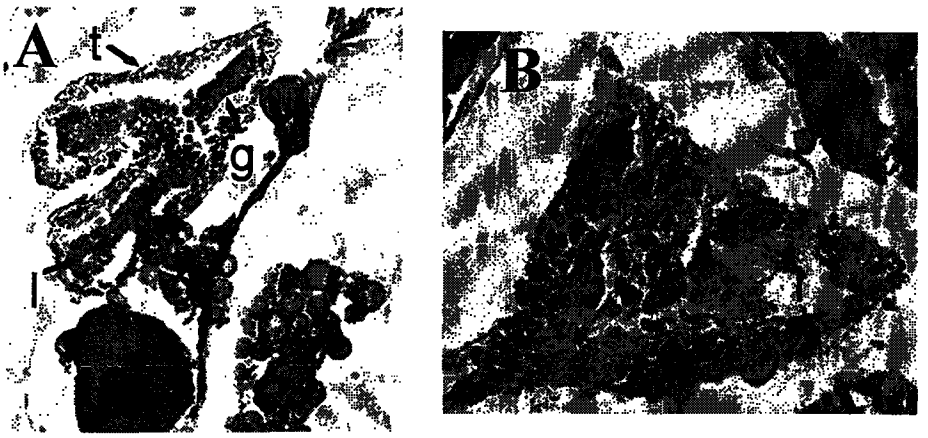

Figure 3

Photographs of histological section of the ovary of vermilion snapper, showing (**A**) new postovulatory follicle (POF) at 100×, in which the columnar granulosa cells with prominent nuclei are distinct and the lumen is visible, and (**B**) old POF at 400× with a typical triangular shape, in which most of the granulosa cells without nuclei are disintegrating. (g=granulosa layer, t=thecal layer, l=lumen)

y–stained structures with approximately half to very few of the granulosa cells intact (Fig. 3B). Old POF's resembled 1-day-old POF's of *Engraulis mordax* (Hunter and Macewicz, 1985). To confirm temporal trends in the occurrence of hydrated females, the samples collected for this study were supplemented with additional histological slides (from spawning females collected on MARMAP research cruises in 1991 and June to August 1993) for examination of POF age.

To calculate spawning frequency, the method of Fitzhugh et al. (1993) was used to calculate overall percentages of HO's, new POF's, and old POF's. A proportion was computed for each category by dividing the total number observed in each category by the total number of mature females. An overall average was computed by summing the three category proportions and by dividing by three. The overall average was then multiplied by number of days in the spawning season to determine spawning frequency. We defined the spawning season as the date (15 April 1992) when spawning condition was histologically evident until the date (24 September 1992) when major atresia of AYO's first occurred. If the proportions for each criterion were independent of those of other criteria and similarly distributed, then they could be combined to increase the sample size (Alheit et al., 1984). If spawning frequencies are to be combined, they must not be statistically different; therefore, we used the Mann-Whitney test to examine differences between frequencies of the HO's versus new POF's and between new POF's versus old POF's.

Results

Sex ratio, ovarian development, maturity, and spawning season

Vermilion snapper did not exhibit a 1:1 sex ratio; females were 63% of the samples (Table 5). Comparisons of sex ratio by 5-cm length classes revealed significant differences from a 1:1 ratio for every length class. Trap and hook-and-line samples collected during MARMAP cruises and samples collected by the commercial hook-and-line fishery yielded similar sex ratios. The sex ratio from Grimes (1976) was comparable to the sex ratio for all samples of vermilion snapper in this study.

Oocyte size-frequency (percent) distributions for five oocyte stages (Fig. 4) revealed the developmental sequence of ovary maturation. Oocyte size was correlated with stage of development; however, there was considerable overlap in size between stages. This asynchronous pattern of development means that the number of batches cannot be inferred from the size-frequency distribution of oocytes.

The mean oocyte diameter (MOD) appeared constant over the spawning season (Fig. 5). This is evidence that oocytes matured and were developing throughout the spawning season.

Table 5

A comparison of sex ratios among different groups of vermilion snapper.

Comparison group (and ratios)	χ^2	P	Result
Females vs. Males: (62.6% vs. 37.4%; 1.67:1)	6.35	$0.025<P<0.01$	Significant difference from 1:1 ratio.
MARMAP catches (67% female) vs. commercial catches (57% female)	1.72	$0.10<P<0.25$	No significant difference between the sex ratios of MARMAP catches and commercial catches.
Length-class comparison 20–24 cm TL: 62.7% female 25–29 cm TL: 66.5% female 30–34 cm TL: 64.3% female 35–39 cm TL: 68.1% female	9.92	0.0193	Significant difference from 1:1 ratio within each 5 cm length classes.
Grimes (1976) vs. present study (62.5% vs. 62.6% females, respectively)	0.01728	$0.75<P<0.90$	No significant difference between overall sex ratios of Grimes (1976) and the present study.

All vermilion snapper in this study were mature. Of the 750 females (Table 6) and 254 males (Table 7) examined histologically, the smallest female was 165 mm FL (186 mm TL) and smallest male 179 mm FL (197 mm TL). Ages of 176 females ranged from 2 to 10 yr; 87 males ranged from 3 to 11 yr (Tables 6 and 7).

Owing to gear selectivity, fish under two years old were not found in the present study; however, three- and four-year old fish were about the size of those found by Grimes (1976) (Fig. 6). After age four, fish in the present study were dramatically smaller than fish in the study by Grimes (1976).

The spawning season of vermilion snapper was from April to September (Fig. 7). The mean gonadosomatic index (GSI) for females increased in April and was high through August, decreasing in September. Mean GSI values remained constant from October through March. Spawning was first evident histologically on 15 April 1992 and no longer evident in sections taken at the end of September 1992. Gonad index (GI) values of Grimes (1976) for 1973–74 showed trends similar to those for GI values from this study (Fig. 8).

Reproductive activities of males began earlier in the year and lasted longer in the season than did the reproductive activity of females (Fig. 9). Percentages of active males and females were similar for July, August, and September. There were reproductively active portions of the population present from April through October (during which period there were correspondingly higher GSI values for females).

Table 6

Number of mature specimens by size class for 750 female vermilion snapper. Specimens with evidence of histological criteria I–V (see Hunter et al., 1992) were considered mature. All females were examined histologically.

	Age (yr)										
FL (mm)	2	3	4	5	6	7	8	9	10	11	No age
151–175											1
176–200	1	6	3	3	1	1					142
201–225	2	3	6	6	4	2	2				227
226–250	1	2	4	22	12	4	2				92
251–275		2	9	14	6	5	1	2			60
276–300	1		5	17	4	1					31
301–325			3	2	4	1	1	1			13
326–350			2	1	1	1					3
351–375				1		1	2		1		5
Total	5	13	32	66	32	16	8	3	1		574

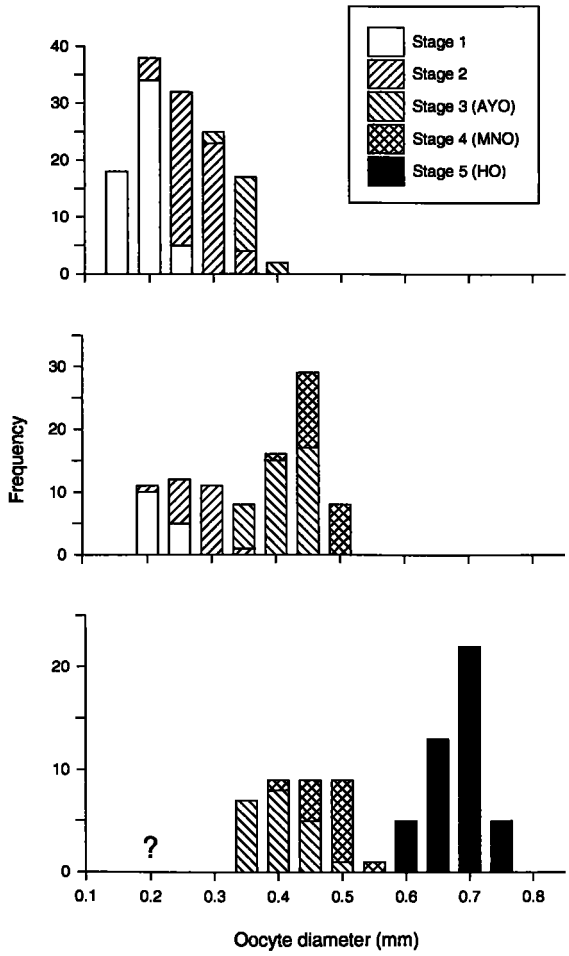

Figure 4

Oocyte size-frequency (percent) distributions and oocyte stage of three mature vermilion snapper representing the developmental sequence of maturation. Females were collected in May and length range was 192 mm to 213 mm FL. (? = stages that were not counted.)

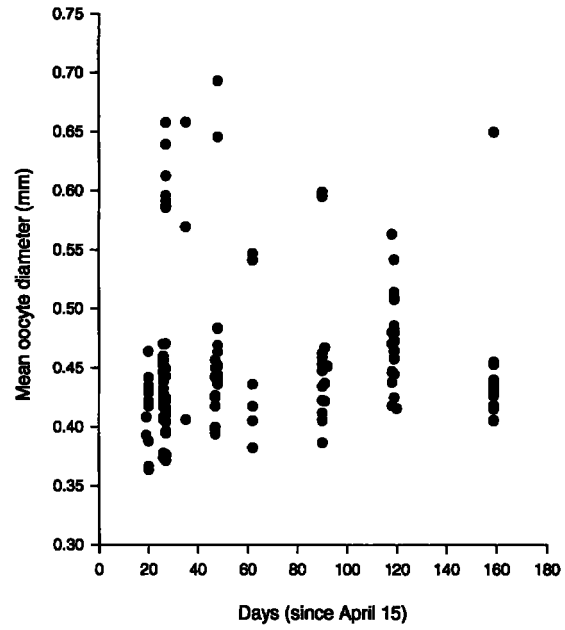

Figure 5

Mean oocyte diameter of vermilion snapper versus number of days since April 15.

Fecundity

Location of oocytes within the ovary revealed no significant effect on oocyte density (Table 8). Advanced yolked oocytes (AYO's) were randomly distributed within the ovary; samples could be taken from any location within the ovary without bias.

The relationship between ovary-free body weight (OFWT) and potential fecundity (PF) was expressed by the following equation:

$$PF = -25{,}992 + (508 \times OFWT).$$

The coefficient of determination (r^2) was 0.583 for the 13 fish used in the analysis (Fig. 10). The PF ranged from 17,374 to 122,130 oocytes for an OFWT range of 109 g to 265 g.

Monthly mean TF estimates of vermilion snapper increased from 54,100 oocytes in May (n=16, OFWT range 109–194 g) to 118,500 in August (n=25, OFWT range 108–442 g); then decreased to 58,200 in September (n=15, OFWT range 106–238 g). Analysis of covariance of monthly equations of TF on OFWT indicated that equations were similar over the spawning season (Fig. 11). The slopes of the equations were similar (F=0.02984, df=4,85, P>0.25) and, assuming a common slope, there was no significant difference in intercepts between months (F=0.02936, df=4,89, P>0.25). Regression of TF on OFWT for days elapsed since 15 April indicated that the coefficient for elapsed days was not significant (t=1.338, df=94, P=0.1842). Thus, TF did not decline continually over the spawning season.

In whole oocyte samples used to estimate fecundity, the average fraction of AYO's that were atretic was 0.011 (SD=± 0.023, n=138). Minor alpha atresia of AYO's was observed in 29% of the fish used in fecundity estimates. A stepwise multiple regression of OFWT, days, and atretic fraction of AYO's on TF, indicated that the coefficient for the atretic fraction of AYO's was not significant and thus atresia does not result in a significant loss of oocytes (Table 9).

Table 7

Number of mature specimens by size class for 254 male vermilion snapper. Males were classified as mature based on criteria in Table 2. All males were examined histologically.

	Age (yr)										
FL (mm)	2	3	4	5	6	7	8	9	10	11	No age
151–175											0
176–200			2	2							40
201–225				5	2	2	1				50
226–250		1	2		1	1					28
251–275		1	13	14	3	6	1	1	1		22
276–300			7	6	3	1					19
301–325			1	1	1						5
326–350			1	3	1					1	2
351–375				1	1						0
376–400											1
Total		2	26	32	12	10	2	1	1	1	167

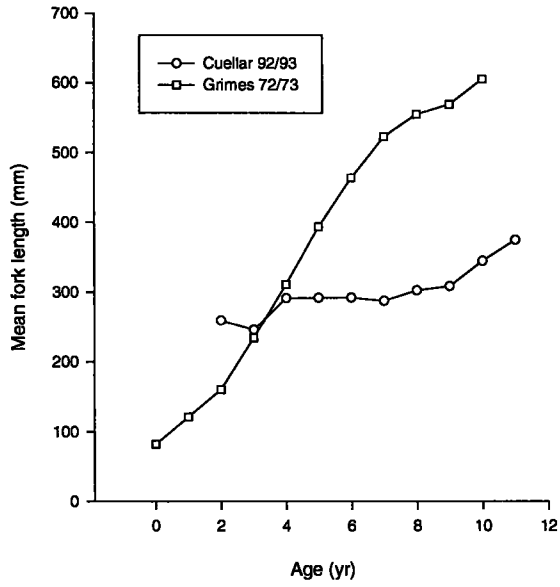

Figure 6

A comparison of mean fork length (at capture [in mm]) at age for vermilion snapper from 1972–73 (Grimes's study) with fork length at age from 1992 to 1993 (present study).

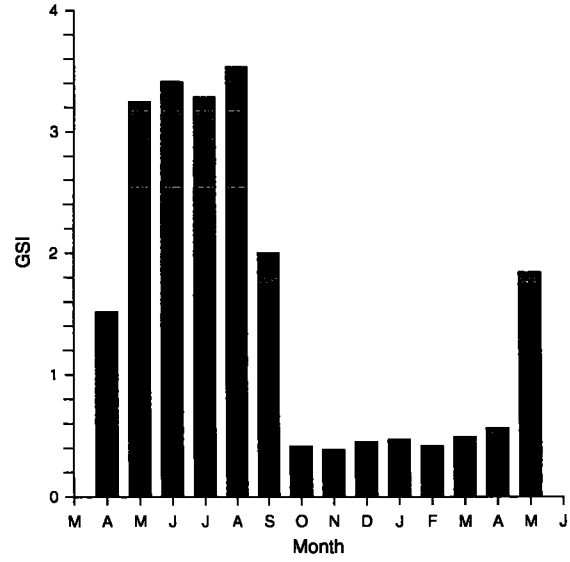

Figure 7

Gonadosomatic index (GSI) values by month for female vermilion snapper that were collected from April 1992 through May 1993. GSI = gonad weight (g)/ovary-free body weight (g).

Histological examination for alpha atresia of samples with AYO's (n=410) revealed that only 2% of all females had major alpha atresia of AYO's and that 27.5% had minor alpha atresia of AYO's (Table 10). Percentages of minor and major alpha atresia of AYO's were similar between whole oocyte samples and histological samples.

A one-way ANOVA on 49 females detected no significant difference among batch sizes (Table 11). All spawning batches were found throughout the spawning season, with batch 1 and batch 2 having the highest percentages in each month (Fig. 12). The relationship between fish length and batch fecundity was best described by the following equation, with r^2= 0.444 (Fig. 13):

Table 8

Effect of location of tissue samples within the ovary on oocyte density (number of advanced oocytes per unit sample weight) vermilion snapper for mean, standard deviation (SD), and two-way analysis of variance of results are given.

	Location of sample			Oocyte density	
Position no.	Lobe	Long. plane	*n*	Mean	SD
1	Left	Anterior	9	4470.7	3311.8
2	Left	Center	9	5730.9	4721.0
3	Left	Posterior	9	4660.6	3266.1
4	Right	Anterior	9	3619.7	2112.3
5	Right	Center	9	5746.9	2629.3
6	Right	Posterior	9	4633.3	2501.3

Analysis of variance on six locations within the ovary of vermilion snapper

Source	df	Sum of squares	Mean square	*F*	*P*
Fish	8	150,536,374.2	18,817,046.8	2.007	0.0704
Location	5	29,043,522.9	5,808,704.6	0.620	0.6855
Error	40	374,972,921.2	9,374,323.0		
Total	53	554,552,818.3	10,463,260.7		

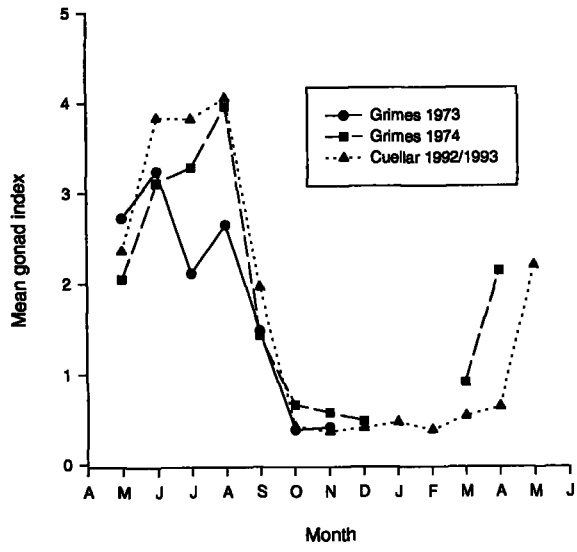

Figure 8

A comparison of mean gonad index [K_G=(WT_G/TL^3) × 10^6] by month for vermilion snapper from 1973 and 1974 (Grimes, 1976) with mean gonad index by month in the present study (1992–93).

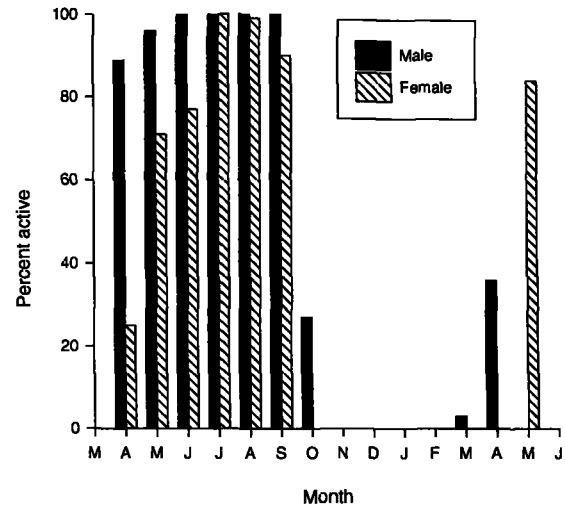

Figure 9

Percentages of reproductively active male and female vermilion snapper in each month from April 1992 through May 1993.

$$BF = 0.0438FL^{2.508} \quad (F=37.6, \text{df}=1,47, P<0.0001);$$

and the relation between OFWT and batch fecundity by the following equation, with r^2 = 0.332 (Fig. 14):

$$BF = 14{,}037 + (112 \times OFWT) \quad (F=23.3, \text{df}=1,47, P<0.0001).$$

Batch fecundity varied remarkably among fish of the same size (Table 12; Fig. 13). ANCOVA was run on monthly linear regression equations of FL on BF.

This analysis indicated that the slopes were similar between months (F=0.06548, df=4,44, P>0.25). Assuming a common slope, we concluded that there were no differences among intercepts of each month (F=1.90, df=4,44, 0.10<P<0.25). The variation of BF estimates was high (4,000–90,000 oocytes), and there was not a significant difference in BF between months.

Spawning frequency

Although no significant temporal trends in the frequencies of POF's were evident, the following observations provide a preliminary age to new POF's of vermilion snapper. MARMAP sampling occurred

Table 9

Analysis of the relation between total fecundity on ovary-free body weight (OFWT), on elapsed days since April 15, and on fraction of atretic oocytes of vermilion snapper with stepwise regression. Boldface refers to the coefficient of the atretic fraction of oocytes.

	Step		
	1	2	3
Constant	26,848.2	-6,968.8	-9,117.2
OFWT	258.8	291.7	293.7
t	6.398	7.620	7.597
P			<0.0001
Days		403.1	415.9
t		4.703	4.589
P			<0.0001
Atretic oocytes			81177.8
t			**0.445**
P			0.6574
r^2	0.2313	0.3395	0.3405
Adjusted r^2	0.2257	0.3298	0.3258

Table 10

Histological determination of number of vermilion snapper with no atresia, minor atresia (<49%), and major atresia (>50%) of advanced yolked oocytes (AYO's) expressed as a percentage of all females with AYO's during the spawning season (April–October).

State	Atresia	Percentage	Number
Nonspawning	none	41.4	172
Nonspawning	minor	22.4	93
Spawning	none	28.2	117
Spawning	minor	5.1	21
Inactive	major	2.2	9
Total			415
Total samples without AYO's			335
Total: minor		27.5	114
Total: major		2.2	9

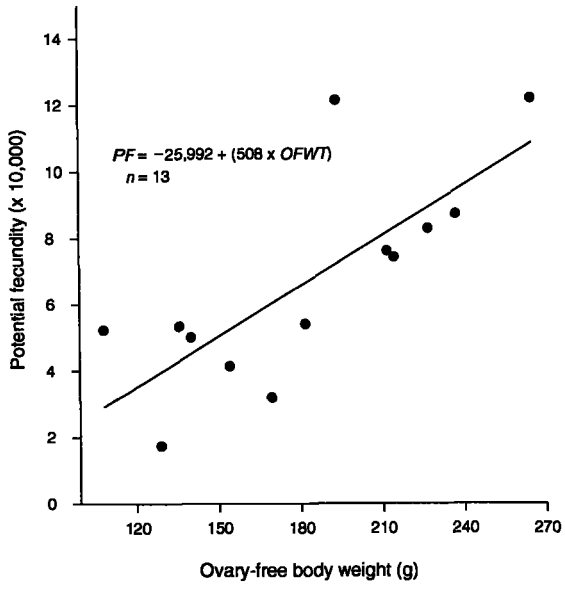

Figure 10

Linear regression of potential fecundity (PF) of vermilion snapper on ovary-free body weight (OFWT).

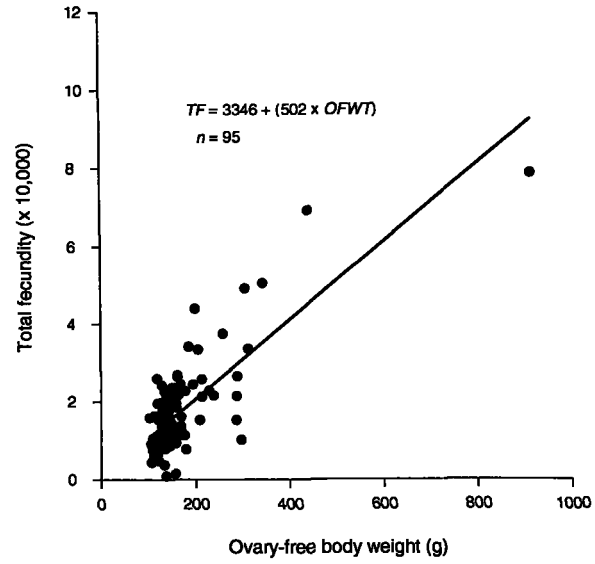

Figure 11

Linear regression of total fecundity (TF) of vermilion snapper on ovary-free weight (OFWT) in g.

from approximately 0800 to 1900 h local (Eastern) time and in all fish examined from samples collected during MARMAP cruises from 1991 to 1993, 70–100% of spawning females (i.e. those with hydrated oocytes (HO's); n=54) were captured between 1300–1900 h. During the April 1992–May 1993 sampling,

Table 11

Mean relative batch fecundity for five batch order numbers. Relative batch fecundity = number of oocytes/ovary-free body weight.

Batch number	No. of females	Relative batch fecundity Mean	SD
1	14	202	125
2	14	174	73
3	2	271	34
4	16	193	59
5	3	186	111

ANOVA on five batch orders

Source	df	Sum of squares	Mean square	F	P
Batch order	4	34,753.7	8,688.4	1.331	0.282
Error	44	189,321.1	6,528.3		
Total	48	367,605.5	7,658.4		

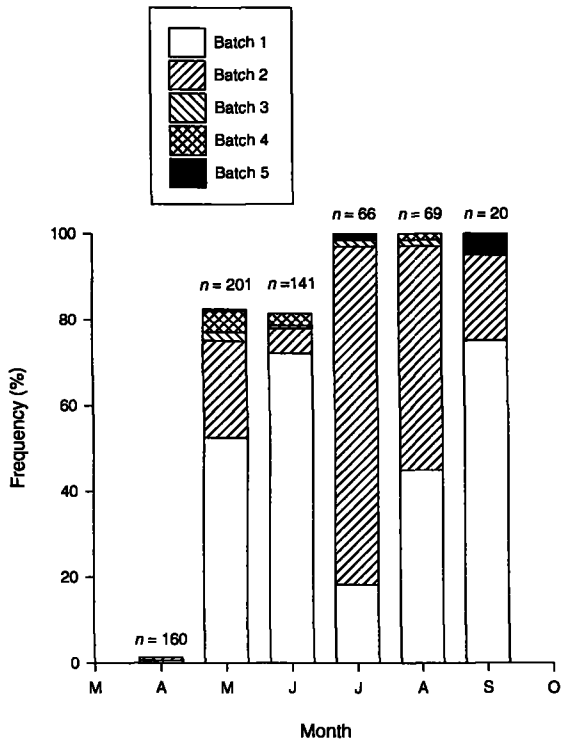

Figure 12

Percent frequencies of batch numbers by month for vermilion snapper. Definitions for batch numbers are listed in Table 4. n = total number of females collected each month.

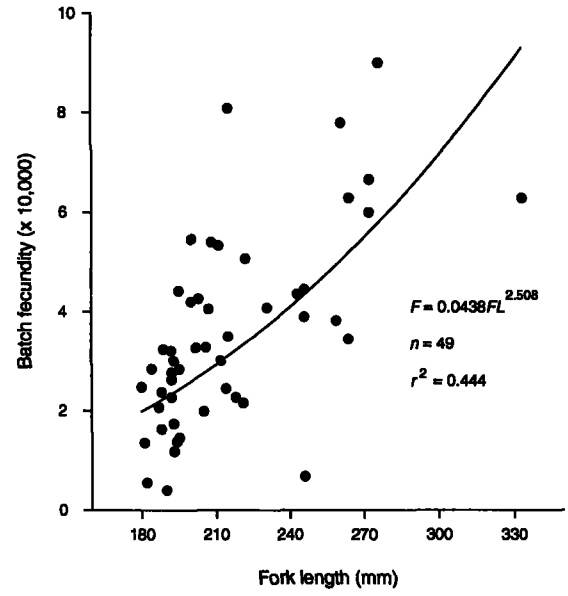

Figure 13

Nonlinear regression of batch fecundity (BF) of vermilion snapper on fork length (FL) in mm.

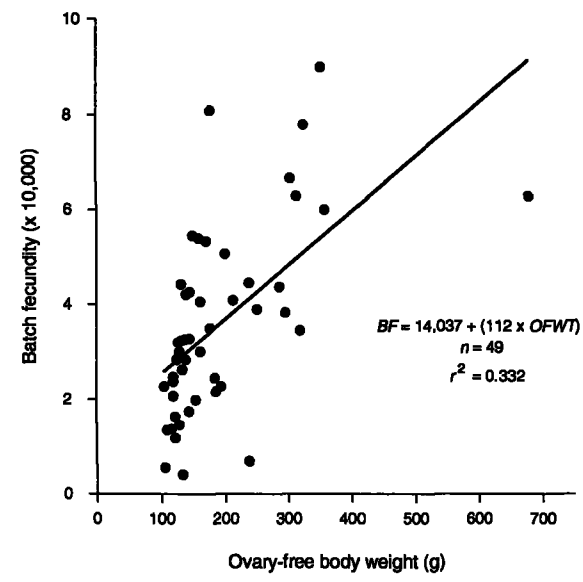

Figure 14

Linear regression of batch fecundity (BF) of vermilion snapper on ovary-free weight (OFWT) in g.

80% of hydrated females (n=10) were found between 1300–1800 h. In 1992, 70% of fish with new POF's (n=25) were collected between 0800–1200 h. Histological examination of 128 females (from April 1992 to May 1993 [MARMAP sampling]) revealed that only two fish had hydrated oocytes (HO's) as well as old POF's and that only seven fish had two classes of POF's (new and old). Because new POF's in lutjanids are ~12–24 hours old (Davis and West, 1993), these new POF's in vermilion snapper indicate that spawning took place during the previous afternoon or evening.

In 23 collections, 3.5% of spawning females had HO's, 8.9% had new POF's, and 30.5% had old POF's (Table 13). This finding corresponded to a spawning periodicity of about every seven days or 23 times per

Table 12

Fork length (FL), ovary-free body weight (OFWT), batch fecundity (BF), and annual fecundity (AF) ranges by month for vermilion snapper from the southeastern United States. Annual fecundity is the batch fecundity multiplied by the spawning frequency (35 times). n = number of specimens.

Month	n	FL range (mm)	OFWT range (g)	BF range (no. of oocytes)	AF range (no. of oocytes)
May	17	180-333	109–678	4,005–90,000	140,175–3,150,000
Jun	11	187–259	119–296	16,312–54,519	570,920–1,908,165
Jul	9	182–211	105–170	5,520–53,972	193,200–1,889,020
Aug	9	195–264	124–313	28,289–80,848	990,115–2,829,680
Sep	3	188–246	119–238	6,846–23,685	239,610–828,975

Table 13

Numbers of female vermilion snapper with histological evidence of spawning used to determine spawning frequency. Hydrated oocytes (HO's), new postovulatory follicles (POF's), and old POF's were classified according to descriptions from Hunter and Macewicz (1985) and Davis and West (1993) (See Fig. 3, A and B). Sampling period in 1992 was 162 days. Total % was calculated by dividing the total of each category by the total number of mature females (282) and by multiplying by 100.

Date	Collection	No. of HO's	No. of new POF's	No. of old POF's	Total mature
15 Apr	1077			1	1
4 May	1129–1133			1	8
20 May	1169–1173	2	4		8
1 Jun	1175–1180			4	37
2 Jun	1183–1188	1	1	3	33
2 Jun	1203	1			7
16 Jun	1241			1	25
16 Jun	1246–1248	2			8
14 Jul	1312–1317		6	1	13
14 Jul	1319–1323			5	6
14 Jul	1331–1333	2		1	4
15 Jul	1336–1340		4		5
15 Jul	1342–1347		4		4
15 Jul	1351–1352			3	5
16 Jul	1355–1358		1	10	12
16 Jul	1362–1364		1	18	19
11 Aug	1371			1	1
11 Aug	1373			1	1
11 Aug	1378–1384	1		7	13
12 Aug	1388–1390			11	22
12 Aug	1395			12	24
13 Aug	1408–1410			6	6
21 Sep		1	4		20
Total		10	25	86	282
Total %		3.50	8.90	30.50	

year. From visual observations of histological slides, it appeared that the duration of HO's and new POF's might be more similar than the duration of new POF's and old POF's. Thus, we decided to test the populations statistically to see if this might be true. There was no difference in the frequencies of HO's and new POF's (Mann-Whitney, n=23, P=0.675), but there was a significant difference in the frequencies of new POF's and old POF's (Mann-Whitney, n=23, P= 0.00598). Thus, HO's and new POF's probably have similar durations that allow us to combine the categories statistically to increase the sample size. An overall average was recalculated by summing only two categories ((*HO+new POF*)/2, and *old POF*) and by dividing by two. This overall average was then multiplied by days in the spawning season to determine a new spawning frequency. Combining categories results in a spawning frequency of approximately every five days or 35 times per year. The duration between new POF's and old POF's was long enough that the combination of categories was not statistically possible.

Discussion

Hunter et al. (1992) listed four lines of evidence that indicate determinate fecundity (see Materials and Methods section). Vermilion snapper, however, is an indeterminate spawner because it does not demonstrate any of the four characteristics given for determinate fecundity. Each line of evidence is addressed in detail in the following section.

The oocyte size-frequency distribution is continuous in vermilion snapper (without a hiatus between any oocyte stages) except for the hydrated batch. Traditional evidence for determinate fecundity is 1) the obvious gap in oocyte maturity stages or size classes among the oocytes that are maturing during the season and 2) the reservoir of less mature oocytes present year-round in the ovary (Yamamoto, 1956). Although the absence of such a hiatus is evidence for indeterminate fecundity, in some cases fish with a continuous oocyte distribution are still considered to have determinate fecundity (Hunter and Macewicz, 1985). In such cases, the product of batch fecundity multiplied by spawning frequency needs to be compared with the standing stock of mature oocytes at the beginning of the season. For example, a 300-g vermilion snapper in this study produces approximately 126,408 oocytes on the basis of the potential fecundity equation, whereas a 300-g female produces approximately 1.7 million oocytes according to the product of BF multiplied by spawning frequency. It is quite obvious from this study that the product of BF multiplied by spawning frequency must be used to estimate annual fecundity.

The mean oocyte diameter of vermilion snapper stayed constant over the spawning season. Species with determinate fecundity would produce larger oocytes as the season progressed because, as maturation continued during the spawning season, no new oocytes would be recruited into the advanced stock, and eggs that were present would be developing and increasing in size. In contrast, indeterminate spawners are continually producing oocytes during the spawning season, with smaller immature oocytes replacing those that mature and are spawned, resulting in a constant MOD.

Total fecundity and BF in vermilion snapper did not consistently decline over the spawning season as would be expected if the vermilion snapper was a determinate spawner. Total fecundity and BF actually increased through August and declined in September in this study. No trends in TF existed over the months of the spawning season. Atresia also had no significant effect on fecundity estimates to account for a decrease in the number of oocytes. Similarly, Davis and West (1993) found that the BF of *Lutjanus vittus* did not decline over the spawning season. Vermilion snapper in the northern central Gulf of Mexico appear to have a similar trend of peak spawning in late summer according to larval abundances found in that area (Comyns and Lyczkowski-Shultz[3]). Grimes (1976) found peak spawning activity (according to gonsomatic index [GSI] values) in August off the Carolinas, and Nelson (1988) found peak activity in the Gulf during the summer. This trend toward peak spawning during middle to late summer would be expected for an indeterminate spawner with continuous development of oocytes over the reproductive season.

The order of spawning batches was not consistent with the determinate fecundity prediction. Of 750 females examined histologically, three had hydrated oocytes (HO's) in the ovary in the absence of any other advanced-stage yolked oocyte (AYO) batch, and only 16 had a batch of early migratory nucleus-stage oocytes (MNO's) and a late HO batch. Many of the females sampled from September contained all mature oocyte stages, except in the HO batch.

According to Hunter and Macewicz (1985), determinate fecundity is generally found in species in cooler climates and with shorter spawning seasons. Many fishes (snappers, grunts, jacks, dolphin, some

[3] Comyns, B. H., and J. Lyczkowski-Schultz. 1993. Spawning and early life history of snappers in the northcentral Gulf of Mexico. Proceedings of the sixth annual MARFIN conference; Atlanta, Georgia, 12–13 October 1993, p. 1–3.

porgies, and sea basses) in the Carolinas have a protracted spawning season extending from early spring to early fall (Hardy, 1978; Johnson, 1978; Grimes, 1987). The southeastern United States has temperate and tropical characteristics, with surface water temperatures from about 22°C to 29°C (Mathews and Pashuk, 1986) and bottom temperatures of 15°C to 25°C on the middle continental shelf (18–60 m) during summer (present study). Vermilion snapper fit the expectation of being indeterminate spawners on the basis of the temperate and tropical characteristics of this area and on the basis of their long spawning season.

Length was the best predictor of batch fecundity, but great variability was seen in BF estimates for same-size fish, perhaps because some oocytes may have been spawned. This is not likely, however, because fish with hydrated oocytes free in the lumen and fish with postovulatory follicles (POF's) were not used in BF estimates. The monthly average BF appeared to peak in August and decline in September. However, time (months) did not have a significant effect on BF estimates, and it is unlikely that differences in station locations within the sampling area could account for the variation in BF. Davis and West (1993) suggested that the variation seen in BF estimates of *Lutjanus vittus* might be due to the collection of samples during various phases of the lunar cycle. *Lutjanus vittus* seemed to follow a lunar rhythm in spawning, as do many lutjanids (Grimes, 1987; Carter and Perrine, 1994). Thresher (1984) suggested that lunar periodicities are probably universal in lutjanids. Environmental cues of spawning events were not examined in this study; however, Grimes (1976) found that vermilion snapper spawning correlated with temperature and photoperiod, but not with the lunar cycle.

Because of differences in fecundity estimation methods, comparisons between the present study and that of Grimes (1976), or with most other studies on lutjanids, are not particularly useful (Grimes, 1987). For example, Grimes (1976) estimated fecundity on vermilion snapper taken off the Carolinas early in the season. He counted all developing oocytes in each female (the total count is approximately equivalent to a PF estimate in this study). His fecundity equation for a 300-g fish results in a fecundity estimate of 49,152 oocytes, compared with a PF of 126,408 oocytes for the same size fish in the present study.

Collins and Johnson[4] used the hydrated oocyte method (Hunter et al., 1985; Hunter and Macewicz, 1985) for spawning frequency and annual fecundity measurements of vermilion snapper in the northeastern Gulf of Mexico. The spawning frequency (44 times per year) of vermilion snapper in the Gulf exceeded spawning frequency in this study (35 times per year). Also, the annual fecundity of the vermilion snapper in the Gulf (1.32 to 21.9 million eggs) was much higher than the annual fecundity determined in the present study for vermilion snapper in Atlantic waters off the southeastern United States (140,175 to 3.2 million eggs). The spawning season of vermilion snapper in the Gulf is slightly longer than the spawning season of vermilion snapper in the southeastern United States (April to late September), and this additional time in the warmer waters of the Gulf may result in the differences in annual fecundity estimates between the two regions. The use of the hydrated oocyte method instead of the postovulatory method to estimate spawning frequency may also account for the difference between the two studies.

Larger fish in the Gulf study may also account for some of the differences in annual fecundity estimates between the two studies; however, the sizes of fish studied by Collins and Johnson[4] were not available. The largest female in the present study was 440 mm TL, but the majority of the vermilion snapper were between 200 mm TL and 300 mm TL. It is generally accepted that larger females produce more oocytes. Grimes and Huntsman (1980) found that fecundity increased dramatically in larger (older) vermilion snapper.

Davis and West (1993), using new assessment techniques, found that the annual fecundity of a 300-mm *Lutjanus vittus* was about 4.5 million oocytes (if it spawned 90 times a season) or 7.6 million oocytes (if it spawned 150 times a season) on the northwest shelf of Australia. This annual fecundity estimate for *Lutjanus vittus* is closer to the annual fecundity estimate for vermilion snapper (140,175 to 3.2 million eggs) in this study than to the estimate for vermilion snapper calculated by Collins and Johnson.[4] Examination of the annual fecundity estimates reveals that the major difference between vermilion snapper and *Lutjanus vittus* is spawning frequency. Batch sizes were relatively similar: a batch size for a 300-mm *L. vittus* was about 71,000 oocytes and a batch size for a similarly sized vermilion snapper was about 50,000 oocytes. The spawning season for *Lutjanus vittus* is year round, and most spawning occurs from September to April. The longer spawning season of *L. vittus* accounts for a major portion of the large difference in spawning frequency between the two species.

In the vermilion snapper of our study, POF's could not be given an exact age because of a lack of 24-h sampling and because of small sample sizes; therefore time of day for spawning could not be deter-

[4] Collins, L. A., and A. G. Johnson. 1994. Spawning and annual fecundity of gag, red snapper and vermilion snapper in the northeastern Gulf of Mexico. Southeastern U.S. and Caribbean reef fish workshop: Charleston, South Carolina, 15–16 September 1994 [abstract].

mined. Because of these limitations the spawning-frequency estimate calculated in this study should be considered preliminary. More detailed work needs to be done to calculate a more representative spawning-frequency estimate for the population in this region. Additional work should include sampling over a 24-h period for a series of days during the spawning season to define POF age from a larger number of fish.

In spite of limitations, a preliminary estimate of spawning time and POF duration can be derived from the literature and our observations. Postovulatory follicles in *Lutjanus vittus* persist for only about 24 h (Davis and West, 1993), and POF's in vermilion snapper may be similar in duration owing to the higher temperature of shelf waters during the spawning season, which may accelerate reabsorption of POF's (Hunter and Macewicz, 1985). Most lutjanids appeared to spawn at dusk (Wicklund, 1969; Starck and Schroeder, 1971; Thresher, 1984) but recently some lutjanids were found to spawn in the mid-afternoon (Davis and West, 1993; Carter and Perrine, 1994). In addition, vermilion snapper are nocturnally active (Grimes, 1979; Sedberry and Cuellar, 1993); thus spawning activity may continue into the night. In the present study, some vermilion snapper appeared to spawn from mid-afternoon to early dusk, as do other lutjanids; when the majority spawn was not determined.

A comparison of the sex ratio, based on present data and Grimes (1976), indicated that the sex ratio of vermilion snapper had not changed in 20 years (62.6 and 62.5% females, respectively). Sex ratios for western Atlantic snappers often deviate from 1:1, with males outnumbering females in more cases than the reverse (Grimes, 1987). MARMAP data collected with standardized methods over a 15-yr period revealed an increase in the percentage of females in the vermilion snapper population in the region from about 60% in 1978–79 to about 72% in 1991–93 (Zhao and McGovern[1]). This change in sex ratio has occurred in spite of no significant difference in fishing mortality (F) between males and females (Zhao and McGovern[1]). Temperature changes have been known to induce change in sex ratio in fish (Lagomarsino and Conover, 1993) but summer water temperatures on the middle and outer continental shelf off the southeastern United States have been remarkably uniform for the 17 years preceding this study (National Environmental Satellite, Data, and Information Service[5]). Decreases in mean size of vermilion snapper in recent years are well documented (Collins and Sedberry, 1991; Zhao and McGovern[1]). This change in size may be caused by intense fishing, which is believed to have resulted in fewer individuals and smaller fish size (Collins and Pinckney, 1988; Bas and Calderon-Aguilera, 1989; Sutherland, 1990) and, hence, reduced fecundity (PDT, 1990). Unknown compensatory mechanisms may be at work under the intense selection pressure exerted by fishing on vermilion snapper; these mechanisms may result in altered sex ratios to compensate for reduced individual fecundity.

All vermilion snapper in this study were mature, with the smallest fish measuring 186 mm total length (TL). The smallest aged fish was two years old at 186 mm TL. Grimes (1976) found most mature fish at age three were 186–256 mm TL and at age four were 256–324 mm TL; only a few individuals matured in their second year at approximately 150 mm TL. After age four, vermilion snapper in our study were much smaller than those in the study by Grimes (1976). The size difference could, again, be explained by increased fishing pressure or by the fact that Grimes (1976) used scales and whole otoliths, not sectioned otoliths, to determine age. Collins and Pinckney (1988), like Grimes (1976), used scales rather then sectioned otoliths and found that 60% of females and 90% of males mature at 160 mm TL. Recently, Zhao and McGovern[1] found mature vermilion snapper at an even a smaller size, with 100% of males and females mature at 140 mm TL. This change in size at maturity may be a result of fishing pressure.

Vermilion snapper has a protracted spawning season throughout the summer months in the southeastern United States. The gonad index used by Grimes (1976) indicated that vermilion snapper in this area spawn from late April to September. In the Carolinas and Georgia, Powles (1977) and Fahay (1975) found high abundances of larvae during July–September, although they did not sample beyond that period of time. Nelson (1988) and Collins and Johnson[4] found that the spawning season of vermilion snapper occurred during spring and summer in the Gulf of Mexico. Also in the Gulf of Mexico, Comyns and Lyczkowski-Shultz[3] indicated that spawning occurred from May through September on the basis of abundance of larvae. However, in Puerto Rico, Boardman and Weiler (1979) found that vermilion snapper spawned year round, and Munro et al. (1973) found a ripe female vermilion snapper in November in Jamaica. Restricted spawning and year-round spawning in the same species may reflect a difference between temperate and tropical locations, or as Grimes (1987) suggested, a difference between con-

[5] National Environmental Satellite, Data, and Information Service. 1992. Oceanographic monthly summary, July 1978–July 1992. U.S. Dep. Commer., National Ocean Service, National Weather Service. Ocean Products Division, Camp Springs, MD.

tinental versus insular populations of snappers. Vermilion snapper in this study had a spawning season similar to many other continental populations of snappers as reviewed by Grimes (1987).

Grimes (1987) suggested that restricted spawning in continental species may be linked to the production cycle of the environment. Off the southeastern United States, upwelling occurs year-round, but it increases dramatically in spring and summer as the Gulf Stream moves farther offshore, allowing deep waters to upwell near the shelf break (Atkinson et al., 1985; Mathews and Pashuk, 1986). Topographic features in this area (i.e. the Charleston Bump) also cause upwelling events that bring nutrient-rich bottom water to the shelf areas (Mathews and Pashuk, 1986). Periodic meanders and eddies from the Gulf Stream add to the mechanism in which productivity of the shelf increases over the summer months. Phytoplankton blooms develop rapidly within the surface nutrient-rich water (Atkinson et al., 1984), thereby providing a large food source for larval and juvenile fishes. Spawning during this time of high productivity maximizes the survival of the larvae and juveniles of many of the reef fishes of the southeastern United States.

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Post-smolt growth, maturation, and survival of two stocks of Atlantic salmon

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Abstract.—Marine survival and sea-age at maturity of two hatchery-dependent stocks of Atlantic salmon were compared in respect to differences in post-smolt growth as evidenced by the circuli spacing patterns of their scales. The two stocks, the Penobscot and Connecticut, are located at the southern extent of the range of Atlantic salmon in North America. Return rates for 1SW (one seawinter) and 2SW salmon and the fraction of the smolt year class or cohort that matured as 1SW fish were found to be significantly higher for the Penobscot stock. Using image processing techniques, we extracted intercirculi distances from scales of 2,302 2SW fish. Circuli spacing data were expressed as growth indices for spring (when post-smolts first enter the ocean), summer (when growth appears maximal), and winter (when growth appears to be at a minimum). Circuli spacings of the Penobscot fish were wider during the summer season than were those for conspecifics from the Connecticut River of the same smolt year class. The results suggest that post-smolt growth may play a significant role in deciding age at maturity and survival patterns for Atlantic salmon stocks.

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Variation in the marine survival and sea-age of maturation of individual Atlantic salmon stocks, *Salmo salar* L., has ramifications for the management of these stocks in both freshwater and marine environments. Mixed-stock fisheries for salmon indiscriminately harvest stocks of varying productivity, often leading to the over harvesting of weaker stocks even when exploitation is at a level considered safe for the stock complex (Ricker, 1958). Homewater or terminal fisheries can also over harvest weak stocks when shifts in age at maturity and survival occur (Minard and Meacham, 1987). Understanding these periods of changing stock dynamics will help to ensure that management measures are taken to protect the stocks and enhance the fishery.

Events during the post-smolt year are critical to the survival and maturation of Atlantic salmon (Mills, 1989; Salminen et al., 1995); however, the factors shaping salmon population abundances during this period are poorly known (Friedland et al., 1993). Many sources of mortality, such as predation, disease, and parasitism, affect young salmon during their first year at sea. The effect of these sources of mortality is to some extent influenced by the size and condition of the post-smolts; thus, their effect would be expected to vary between years and among stocks (Mathews and Ishida, 1989; Holtby et al. 1990; Salminen et al., 1995). For example, predation during the post-smolt year may determine overall survivorship in salmon, but it is not known how much of the predation on young salmon is controlled by predator abundance versus the size and growth of the post-smolts themselves (Hislop and Shelton, 1993; Hargreaves, 1994). Predation theory suggests that the probability of survival for an individual increases considerably as its body size exceeds sizes vulnerable to potential predators (Werner and Hall, 1974; Mikheev, 1984; L'Abee-Lund et al., 1993). If juveniles remain in a developmental stage that makes them vulnerable to mortality, cumulative mortality will increase (Cushing, 1975). If a stock experiences depressed post-smolt growth, it may be susceptible to high mortality for a longer time compared with other stocks exploiting the same feeding area. Likewise, similar growth-mediated mechanisms can be envisioned for other sources of mortality such as diseases and parasitism.

The onset of sexual maturation in fishes is an inherited trait that operates within a range of phenotypic

plasticity (Via and Lande, 1985; Saunders, 1986; Stearns, 1992; Scheiner 1993; Trippel, 1995). Growth and environment during the post-smolt period play an important role in influencing the sea-age at maturation of salmon (Scarnecchia, 1983; Martin and Mitchell, 1985; Neilson and Geen, 1986; L'Abee-Lund, 1989; Scarnecchia et al., 1989; Skilbrei, 1989). Friedland and Haas (1996) found that summer post-smolt growth was positively correlated with maturation, suggesting that physical readiness to mature may be achieved during the summer period. Examining post-smolt growth in stocks with differing maturation rates should provide new insights into the mechanisms controlling salmon maturation.

In this study, we compare the marine survival and age at maturity of two hatchery dependent stocks of Atlantic salmon. We also describe and analyze circuli spacing and other length measurements from the scales of two seawinter returns to characterize growth during the post-smolt phase and to examine the role of post-smolt growth in affecting survival and maturation.

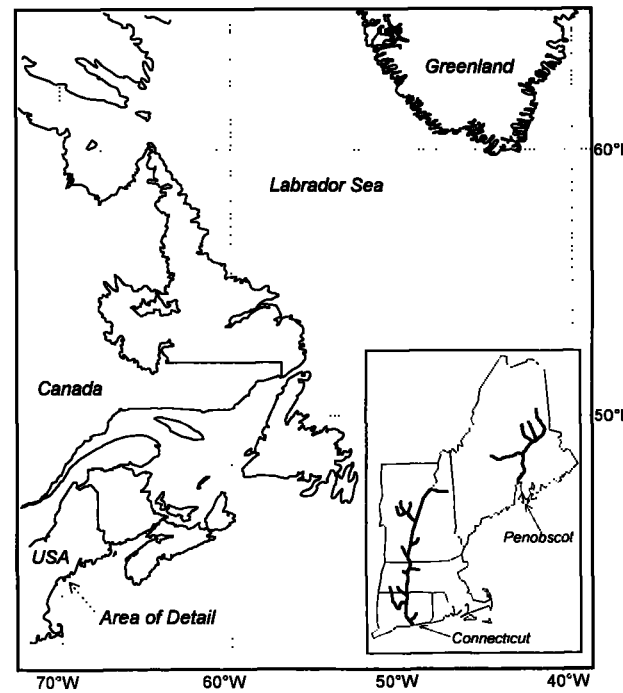

Figure 1

Map of the northwest Atlantic Ocean with detail showing location of the Penobscot and Connecticut rivers.

Materials and methods

Return rate and cohort age at maturity

Return rate by individual sea-age and cohort sea-age at maturity were calculated for two Atlantic salmon stocks, the hatchery components of the salmon runs in the Penobscot and Connecticut rivers in the United States. These rivers are situated at the southern end of the range of Atlantic salmon in North America (Fig. 1). Salmon from these rivers migrate to feeding areas as distant as the Labrador Sea. We analyzed data from 1977 to 1990, a period during which smolt releases in the Penobscot River ranged from 200,000 to 687,000 fish per year and in the Connecticut River from 32,000 to 476,000 fish per year (Table 1). Early in the time series, releases in both rivers were mostly two-year-old smolts, whereas in recent years, most of the releases have been yearlings. Freshwater returns of both 1SW (one seawinter) and 2SW salmon were ascertained from fishway trap counts and from recreational catches in the Penobscot River, as well as from trap counts in the Connecticut River (no legal Atlantic salmon fishery exists for this river). Return rates were calculated as simple ratios, expressed as returns per 1,000 smolts released.

The fraction of a cohort or smolt year class that matured after only a single winter at sea was derived by using both counts of adult returns by sea-age and fishing mortality that impacted the cohort. Fish from the Penobscot and Connecticut rivers were exploited in marine fisheries in Canada and Greenland during the study period. To account for this, we applied annual instantaneous fishing mortality rates (F in Table 1) for North American fish that were maturing as 2SW salmon (Friedland and Haas, 1996).

The observed return of 1SW salmon to freshwater (R_1) is the product of the maturation fraction (Ψ) and the size of the cohort immediately before the 1SW fish return to homewaters and the 1SW fisheries have commenced (N_0). Because we were modeling the cohort split immediately before the 1SW runs occur, natural mortality for this fraction of the cohort (M_1) was zero.

$$R_1 = N_0 * \Psi * \exp^{-M_1}. \quad (1)$$

The observed return of 2SW salmon (R_2) is assumed to be the remainder of the cohort that did not mature as 1SW fish and that survived for an additional 10 months at sea, plus the mortality associated with fishing (M_2=0.1 is from Friedland and Haas, 1996, and F is given in Table 1). The additional time 2SW salmon stay at sea is assumed to be 10 months, as opposed to one year, because 2SW salmon usually return to the river earlier in the year than 1SW fish.

Table 1

Smolt releases (number), returns (number), return rates by sea-age (‰), and 1SW fraction (Ψ) for the Penobscot (Pen) and Connecticut (Conn) Atlantic salmon stocks.

Smolt year	Smolt release		Yearling smolts %		1SW returns				2SW returns				Fishing mortality	1SW fraction	
					Pen		Conn		Pen		Conn				
	Pen	Conn	Pen	Conn	Return	Rate	Return	Rate	Return	Rate	Return	Rate		Pen	Conn
1977	388,500	96,400	34	0	123	0.36	3	0.03	671	1.98	50	0.52	0.511	0.091	0.032
1978	202,500	32,100	30	0	203	1.00	4	0.12	2,570	12.69	164	5.11	0.356	0.048	0.015
1979	296,300	124,900	17	0	652	2.20	4	0.03	2,454	8.28	513	4.11	0.433	0.135	0.005
1980	584,600	51,800	63	0	888	1.52	6	0.12	3,886	6.65	57	1.10	0.576	0.104	0.051
1981	199,500	78,600	12	7	155	0.78	3	0.04	705	3.53	39	0.50	0.592	0.099	0.037
1982	329,700	209,900	33	13	179	0.54	0	0.00	1,387	4.21	65	0.31	0.239	0.084	0.000
1983	436,700	98,000	63	91	239	0.55	7	0.07	2,868	6.57	293	2.99	0.218	0.057	0.017
1984	617,100	312,300	78	100	244	0.40	0	0.00	3,620	5.87	275	0.88	0.413	0.039	0.000
1985	580,900	255,000	82	100	534	0.92	0	0.00	1,477	2.54	343	1.35	0.490	0.167	0.000
1986	589,200	276,100	88	100	749	1.27	0	0.00	1,993	3.38	93	0.34	0.605	0.157	0.000
1987	539,200	205,800	85	100	716	1.33	1	0.00	2,005	3.72	58	0.28	0.480	0.167	0.010
1988	687,000	395,300	87	100	867	1.26	1	0.00	2,520	3.67	226	0.57	0.336	0.182	0.003
1989	416,600	217,700	84	100	430	1.03	1	0.00	1,085	2.60	168	0.77	0.428	0.189	0.003
1990	429,100	475,900	96	100	176	0.41	0	0.00	1,174	2.74	353	0.74	0.585	0.070	0.000
Mean			61	58		0.97		0.03		4.89		1.40		0.113	0.012

$$R_2 = N_0 * (1-\Psi) * \exp^{-(M_2+F)} \quad (2)$$

Both equations contain N_0 and thus can be simplified to the expression

$$\Psi = \frac{\Phi}{(\Phi+1)}, \quad (3)$$

where

$$\Phi = \frac{R_1 \exp^{-(M_2+F)}}{R_2 \exp^{-M_1}}. \quad (4)$$

This formulation assumes that all individuals mature as either 1SW or 2SW fish. This is reasonable because returns of 3SW and older fish have been insignificant during the study period (typically less than 1% of the total runs).

The 1SW:2SW ratio has frequently been used as an index of 1SW maturation rate. However, sea-age classes are often affected by different patterns of marine mortality, particularly fishing mortality. Thus, the 1SW:2SW ratio is a satisfactory measure of maturation rate in only those instances where fishing mortality is constant over time and in fact is linearly related to 1SW maturation rate under these conditions. We know of considerable contrast in the fishing mortality time series for North American 2SW stocks, thus Ψ must be calculated.

Smolt size and age

The size of smolts as a factor affecting return rate and sea-age of maturation could not be directly evaluated in this study because smolt sizes were not available. However, comparability of the smolt releases in the two river systems and the transition from smolt releases of predominantly two-year-old fish to releases of yearling smolts raised concerns about the role smolt size may have had on the observed pattern of return rate and maturation. To address this concern, for each scale the length (mm) of the freshwater zone (taken as the distance from the focus to the end of the freshwater zone along the 360° axis of the scale) was measured (Fig. 2). Back-calculated lengths were not computed because of incomplete data on length at recapture; therefore, freshwater zone lengths were interpreted as an indication of smolt size. The analysis of freshwater zone lengths and other scale measurements were restricted to 2SW salmon owing to the extremely low returns of 1SW salmon to the Connecticut River (Table 1). Cleaned and mounted scales were measured with an Optimas image processing system. Sample sizes are provided in Table 2.

Statistical analysis of freshwater zone lengths was complicated by the lack of a consistent pattern for which stock had the greater zone-length mean. Freshwater zone lengths were compared among years and between stocks with a two-way analysis of variance

(ANOVA). However, the results of this ANOVA are not reported because the interaction term was significant. Instead, a one-way analysis of variance, with stock as the factor, was conducted for each smolt year.

Circuli spacing patterns and post-smolt growth

The spacing of scale circuli deposited during the first year at sea was measured from scales of 2SW salmon returning to the Penobscot and Connecticut rivers. The first spacing was measured between the first circulus of the post-smolt growth zone and the next circulus, and all successive pairs were measured until the end of the post-smolt growth zone. The end of the zone was recognized when circuli spacings began to widen a second time, indicating the beginning of the second sea summer (Fig. 2). All measurements were made along the 360° axis of the scale.

Growth during the post-smolt period was evaluated from the circuli spacings in three regions of the scale. We used the spacing patterns as growth indices because, in salmonids and other fish, scale intercirculi spacing is directly related to growth (Doyle et al., 1987; Barber and Walker, 1988; Fisher and Pearcy, 1990). Three regions of the scale were selected to correspond with seasons of the calendar year. The circuli pair spacings used to represent the "spring" period, or first entry of salmon into the marine environment, was fixed to pairs "two" through "six" (Fig. 3). The "summer" period, or the period of maximum growth, was represented by the five widest and contiguous mean spacings. The first sea "winter" period was represented by the five narrowest and contiguous mean spacings. The general assumption that regions of the scale are associated with seasons of the year is supported by the analysis of post-smolt scales from tagged fish and ocean recaptures (Friedland et al., 1993). The three growth zones were identified from the patterns of mean spacings of circuli pairs from all the data for a smolt year cohort and sea-age. This approach was used because it was not possible to identify seasonal growth zones in the spacing patterns for all individuals because of the variability of these patterns.

Cumulative growth during the post-smolt period was represented by the number of circuli in the post-smolt growth zone and the length of the zone itself. A circuli count was determined for each cohort and sea-age group. The count was based on the mean circuli spacing patterns also used to identify growth zones. The count consisted of the number of circuli from the end of the freshwater zone to the first circulus of the third winter circuli pair. The post-smolt

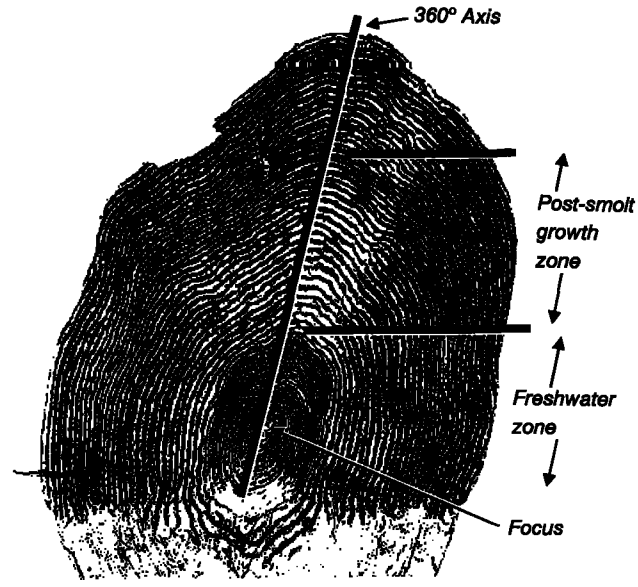

Figure 2

A scale from an Atlantic salmon, *Salmo salar*, with measurement axis and growth zones marked.

Table 2

Sample sizes and post-smolt growth-zone circuli counts for 2SW Atlantic salmon returns to the Penobscot (Pen) and Connecticut (Conn) Rivers.

Smolt year	Sample size		Circuli count	
	Pen	Conn	Pen	Conn
1977	75	25	26	22
1978	65	77	20	24
1979	75	168	24	21
1980	65	24	24	24
1981	75	9	26	17
1982	75	52	26	20
1983	75	81	27	20
1984	40	45	25	21
1985	108	186	28	22
1986	74	70	27	22
1987	51	75	23	24
1988	64	170	26	23
1989	83	121	26	23
1990	95	179	26	22
Mean			25	22

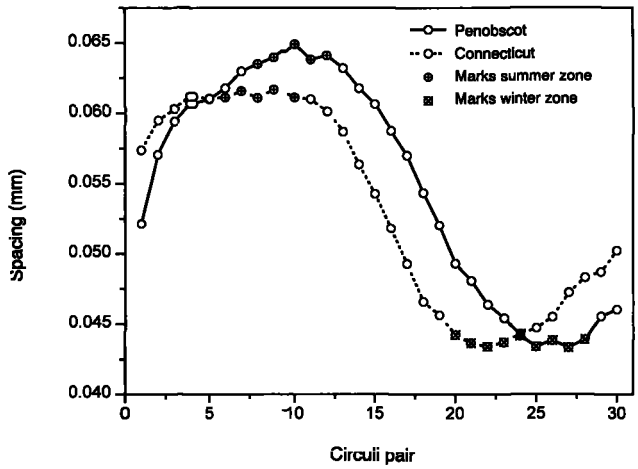

Figure 3

Grand means of circuli spacing versus circuli pair for 2SW returns to the Penobscot and Connecticut rivers. Circuli pairs of summer and winter growth zones are marked as examples.

growth zone length was taken as the distance from the last circulus in the freshwater zone to the outer circulus of the third circuli pair of the winter zone measured along the 360° axis of the scale (Fig. 2). This distance reflects the average spacing of circuli and the number of circuli deposited during the post-smolt period.

Comparison of post-smolt growth

Circuli spacing patterns and lengths of the post-smolt growth zone for both the Penobscot and Connecticut stocks were compared by analysis of variance. Circuli spacings for the spring, summer, and winter zones were compared by means of two-way analysis of variance with year and stock as factors. The growth zone of an individual fish was represented by the mean circuli spacing of the growth-zone circuli pairs identified in the pattern of mean spacings for all fish of that smolt year and stock. In all cases, the interaction terms for these ANOVA's were significant and thus the two-way ANOVA results are not reported. Instead, circuli spacings of both stocks were compared with one-way analysis of variance for each smolt year. The length of the post-smolt growth zone for both stocks was also compared for each year with a series of one-way ANOVA's.

The annual variation in circuli spacing growth-zone indices was compared by using Pearson product-moment correlation. The correlation coefficients were computed by using the seasonal growth-index means for the two stocks.

Results

Return rate and cohort age at maturity

Return rates for both 1SW and 2SW salmon were higher in the Penobscot River than in the Connecticut River. The return rate for 1SW salmon averaged 0.97‰ and ranged from 0.36 to 2.20‰ for the Penobscot stock, whereas for the Connecticut stock the return rate averaged 0.03‰ and ranged from 0.0 to 0.12‰ (Table 1). For 2SW salmon, the return rate for the Penobscot stock averaged 4.89‰ and ranged from 1.98 to 12.69‰, whereas in the Connecticut the return rate averaged 1.40‰ and ranged from 0.28 to 5.11‰. Return rates were significantly different between stocks in a paired t-test ($P<0.01$ for both 1SW and 2SW rates). Despite the differences in the level of 2SW return rates between the two stocks, the pattern of annual variation in 2SW return rates of the two stocks was highly correlated ($r=0.88$, $P<0.01$). Peaks in return rate that occurred with the 1978 and 1983 smolt classes are seen in both time series (Fig. 4A). The relation between the two time series is seen clearly in the normalized or Z-transformed data (Fig. 4B). The transform is simply the observation minus the time-series mean divided by the time-series standard deviation.

The 1SW fraction for the Penobscot, which averaged 11% during the study period, was an order of magnitude higher than the fraction observed for the Connecticut River (Table 1). The difference between stocks was highly significant (paired t-test, $P<0.01$).

Smolt size and age

Smolt sizes of 2SW returns, as indicated by the lengths of the freshwater zone, showed no systematic differences between stocks. Mean freshwater zone lengths ranged from 1.000 to 1.243 mm for both stocks (Fig. 5A). Significant differences between freshwater zone lengths were found for 6 of the 14 smolt classes, but of those 6 years, there were equal numbers of years with greater means in the Penobscot and Connecticut stocks (Table 3).

Circuli spacing patterns and post-smolt growth

Considerable variation in circuli spacing was evident between stocks and among years. Annual mean circuli spacing indices had an approximate range of 0.04 to 0.070 mm (Fig. 5, B–D). Spring and summer spacing indices averaged greater than 0.060 mm for both

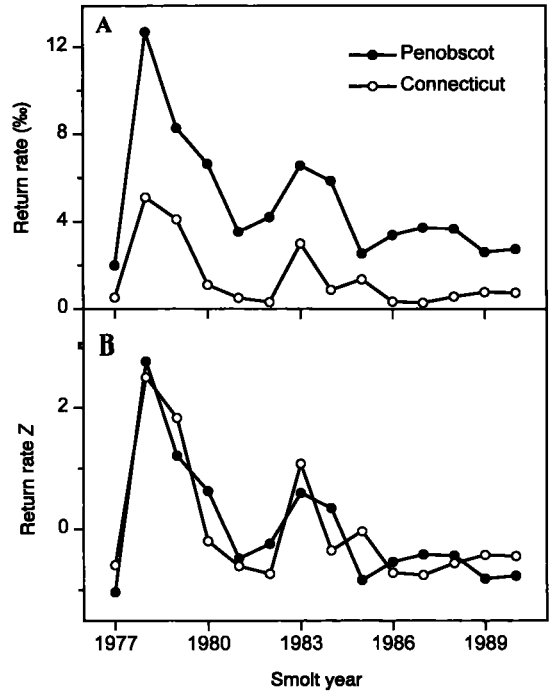

Figure 4

Return rates for 2SW salmon to the Penobscot and Connecticut rivers (**A**). Normalized or *Z*-transformed return rates for 2SW salmon to the Penobscot and Connecticut rivers (**B**).

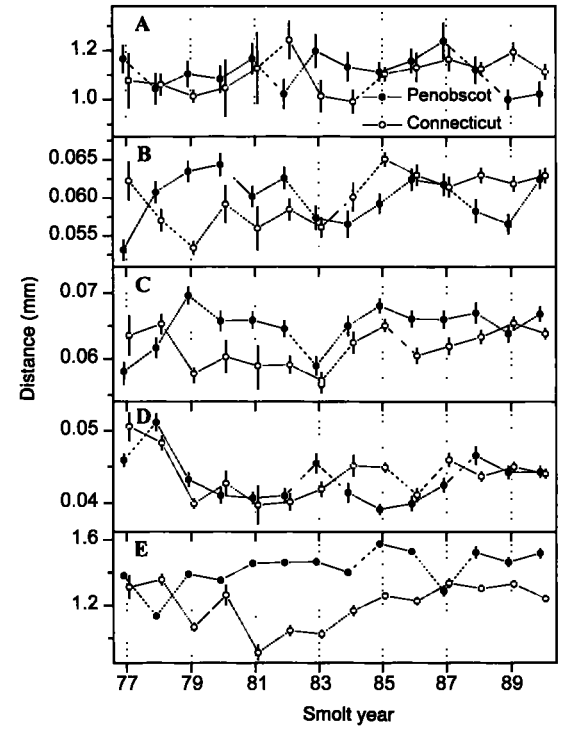

Figure 5

Mean and 95% confidence interval of the following parameters by smolt year: (**A**) freshwater zone length; (**B**) spring growth-zone circuli spacing; (**C**) summer growth-zone circuli spacing; (**D**) winter growth-zone circuli spacing; and (**E**) post-smolt growth-zone length. All measurements are in mm.

the Penobscot and Connecticut stocks, whereas the winter indices averaged less than 0.044 mm. The spring and winter index means were nearly identical for the two stocks, whereas the summer index mean was greater in the Penobscot. The mean number of circuli deposited in the post-smolt growth zone averaged 25 for the Penobscot stock and 22 for the Connecticut stock (Table 2). Post-smolt growth-zone length indices ranged from 0.913 to 1.577 mm and averaged 1.425 mm for the Penobscot stock and 1.204 for the Connecticut stock (Fig. 5E). Differences in the annual seasonal spacing indices and circuli counts were also reflected in the pattern of mean circuli spacings for all years: the Penobscot stock had wider circuli spacing in the summer zone and a greater number of circuli deposited prior to the winter zone (Fig. 3).

Comparison of post-smolt growth

The analyses of variance suggest that post-smolt growth was greater in the Penobscot stock, especially during the summer season. Spring growth indices ranged from 0.053 to 0.065 mm for both Penobscot and Connecticut origin fish (Fig. 5B). Significant differences between Penobscot and Connecticut spring growth-zone means were found for 10 of the 14 smolt classes, and of those 10 years there were equal numbers of years with greater means for the Penobscot and Connecticut stocks (Table 3). Summer growth indices ranged from 0.057 to 0.069 mm for both Penobscot and Connecticut origin fish (Fig. 5C). Significant differences between Penobscot and Connecticut summer-growth-zone means were found for 11 smolt classes, and of those 11 years, 9 were years in which the Penobscot stock had the greater mean (Table 3). Winter growth indices ranged from 0.039 to 0.051 mm for fish of both Penobscot and Connecticut origin (Fig. 5D). Significant differences between Penobscot and Connecticut winter growth-zone means were found for only for 8 of the 14 smolt classes, and of those 8 years, there were equal numbers of years with greater means for Penobscot and Connecticut stocks (Table 3).

Table 3

Probability of one-way ANOVA for stock effect on freshwater zone length (FW zone), seasonal circuli spacing growth indices, and post-smolt growth zone (PS zone). Bolding indicates significance at $P<0.05$. Pen = Penobscot stock; Conn = Connecticut stock.

Smolt year	FW zone	Circuli spacing: Spring	Summer	Winter	PS zone
1977	0.131	**0.000**	**0.005**	**0.000**	**0.003**
1978	0.659	**0.009**	**0.011**	**0.049**	**0.000**
1979	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
1980	0.529	**0.002**	**0.000**	0.152	**0.000**
1981	0.703	**0.039**	**0.000**	0.487	**0.000**
1982	**0.000**	**0.001**	**0.000**	0.366	**0.000**
1983	**0.000**	0.339	0.066	**0.002**	**0.000**
1984	**0.001**	**0.033**	0.068	**0.004**	**0.000**
1985	0.689	**0.000**	**0.001**	**0.000**	**0.000**
1986	0.473	0.594	**0.000**	0.097	**0.000**
1987	0.081	0.805	**0.002**	**0.000**	**0.010**
1988	0.851	**0.000**	**0.005**	**0.008**	**0.000**
1989	**0.000**	**0.000**	0.149	0.329	**0.000**
1990	**0.001**	0.657	**0.002**	0.758	**0.000**
Years with significant differences					
Pen>Conn	3	5	9	4	12
Conn>Pen	3	5	2	4	2

Table 4

Correlation coefficients (r) between Penobscot and Connecticut river circuli spacing seasonal growth indices. Bolding indicates significance at $P<0.05$, $n=14$.

Seasonal growth index	r	P-level
Spring	–0.263	0.364
Summer	–0.018	0.950
Winter	**0.535**	**0.049**

Cumulative growth during the post-smolt year appeared greater in the Penobscot stock. The post-smolt growth zone circuli counts were significantly higher in the Penobscot stock ($P<0.01$). Post-smolt growth zone lengths ranged from 0.913 to 1.577 mm for both Penobscot and Connecticut origin fish (Fig. 5E). Significant differences between Penobscot and Connecticut spring growth-zone means were found for all 14 smolt years, and of these, 12 were years in which the Penobscot stock had a greater mean than the Connecticut stock (Table 3).

Annual variation in circuli spacing was similar for two stocks for one of the three post-smolt growth zones. The correlation coefficient for winter spacing indices was significant, whereas the correlation coefficient for spring and summer indices was not significant (Table 4).

Discussion

The Penobscot and Connecticut stocks exhibited similar interannual patterns of 2SW survivorship despite significant differences between the two stocks in magnitude of survival rate and maturation fraction. Therefore, the sets of conditions affecting the two stocks during the post-smolt year must to some degree intersect to account for the similarity in the survival-rate time series. At the same time, however, there must also be significant differences in these condition sets to account for the significantly lower survival and maturation fraction found for the Connecticut stock. We have found it instructive to consider those factors that appear to be similar and those that appear to be different for the two stocks.

The scales from Penobscot and Connecticut fish returns had similar freshwater zone lengths, circuli spacing indices in the spring and winter, and a correlated pattern of annual variability between winter growth indices. These similarities should be interpreted in respect to the correlation in annual 2SW survivorship. The survivorship of North American multiseawinter stocks has been related to ocean conditions in the Labrador Sea during winter (Friedland et al., 1993). It has been hypothesized that stocks emanating from various rivers in North America intermix and are acted upon by a common set of survival conditions during the winter season. The coherence of the survival time series for the Penobscot and Connecticut stocks, as well as for other North American stocks, is considered evidence that stocks converge on the same overwintering ground. Scale analysis shows that annual variation in growth indices during winter were correlated, which would be consistent with the assertion that these fish were in the same location during that season. The lack of correlation between spring and summer indices suggests that the fish from the respective stocks were acted upon by differing conditions, possibly while they resided in different areas. These data suggest that fish from the Penobscot River are not fully mixed with fish from the Connecticut River until the winter season, thus supporting the survival hypothesis for all North American stocks in general.

Though smolt sizes, as inferred by the freshwater zone lengths of the scales, were similar for the two stocks, we can not conclusively eliminate freshwater effects from contributing to observed differences in survival. There is a large body of evidence that

illustrates the influence of smolt-size and condition and stocking circumstances on the return rates and yields of salmon stocks (Ward et al., 1989; Hvidsten and Johnsen, 1993; Farmer, 1994; Lundqvist et al., 1994). We lack smolt size information on the fish that did not survive; they may have had a different freshwater zone length-size frequency than that observed for the survivors. Smolt age composition was similar each year and appears unrelated to the differences between stocks. However, the trend in smolt age composition is not similar to the time-series trends in survival and maturity for the two stocks and should be considered along with other factors when evaluating long-term changes in stock performance (Friedland et al., 1993).

Summer circuli spacing and post-smolt growth-zone length data suggest that the Penobscot fish grew faster than the Connecticut fish as post-smolts. These differences may have influenced survivorship and maturation. These data suggest that fish from the Connecticut stock grew more slowly during the post-smolt year than did Penobscot fish, matured as 1SW less frequently, and were more vulnerable to mortality. It is generally accepted that larger individuals are less vulnerable to predation (Peterson and Wroblewski, 1984; McGurk, 1986; Anderson, 1988; Miller et al., 1988; Pepin, 1991; L'Abee-Lund et al., 1993). Therefore, smaller, slower-growing Connecticut salmon may be vulnerable to a wider range of potential sources of mortality. For example, under these conditions, we would predict that Connecticut post-smolts would be vulnerable to predators for a longer period of the post-smolt year than would Penobscot post-smolts. Likewise, smaller post-smolts may not effectively compete with other predators for prey or may experience ontogenetic mismatches with prey resources that are also growing or that may be transient in post-smolt habitats (Brodeur, 1991; Healey, 1991; Levings, 1994).

Sea-age at maturation is partly a growth-related phenomenon associated with the seasonal accumulation of lipid stores (Rowe et al., 1991; Thorpe, 1994). In general, maturation at a certain age has been associated with individual growth rate and other causal effects (Alm, 1959; Svedäng, 1991; Thorpe, 1994); however, the effect of sea growth on maturation in salmon has not always been obvious (Power, 1986; Randall et al., 1986; Myers and Hutchings, 1987). Using sea ranching and cage culture experiments with the same genetic stock of salmon, Saunders et al. (1983) reported evidence supporting a hypothesis that first seawinter temperature minima are critical determinants of maturation in salmon. This work was further supported by Herbinger and Newkirk (1987) who described a relationship between 1SW maturation and favorable (or perhaps minimum) winter growth. However, the specificity of seasonal growth effects can be challenged by other experimental evidence that shows that spring growth can influence 1SW maturation (Thorpe et al., 1990). In an analysis of the Penobscot stock, Friedland and Haas (1996) showed that maturation fraction varies with summer growth rate of the cohort as indicated by circuli spacing indices for 2SW returns. This finding is further supported by our comparison of Penobscot and Connecticut fish which shows that the stock with the greater summer growth had produced a higher percentage of mature 1SW fish.

How an environmentally driven maturation mechanism would optimize age at maturation is not clear. For salmon stocks with complex maturation age structures, early maturing fish (1SW) are predominantly males; egg-producing females more frequently mature at a later age when their egg production is maximized. Therefore, a shift in age at maturity allows a brood class to receive genes from more than one spawning cohort without significant loss of egg production. This plasticity in spawning age ensures that genes move within the population while remaining robust to environmental effects on the deposition of female gametes, which are limiting (Stearns and Crandall, 1984; Stearns, 1992). However, Atlantic salmon exhibit a wide range of maturation age structures (Power, 1981; Saunders, 1981; Saunders and Schom, 1985) suggesting within-population heterozygosity may also be maintained by protracted freshwater residency that allows many brood years to contribute to a smolt run in a given year.

Genetic influences have also been shown to affect stock-specific patterns of age at maturity (Saunders et al., 1983; Thorpe et al., 1983). However, genetic factors are unlikely to explain the differences between the Penobscot and Connecticut stocks because the Connecticut stock is derived predominantly from the Penobscot gene pool (Rideout and Stolte, 1988). When the Connecticut River broodstock was developed, gametes from Canadian and U.S. origin (Penobscot River broodstock) donor stocks were used. However, the crosses with Canadian genetic sources, as demonstrated with tagging, produced virtually no progeny; therefore it can be concluded that the Connecticut broodstock is principally derived from the Penobscot River broodstock.

The systematic differences in growth, survival, and maturation between these two stocks may be related to their post-smolt migrations. When salmon first enter the marine environment, they move by active and passive mechanisms (Jonsson et al., 1993). Because of the differences in the timing of the smolt migration, the starting point of the post-smolt feed-

ing migration, and changes in the ecology of the ocean habitat of salmon, Penobscot and Connecticut smolts are probably exposed to different predator and prey communities during the course of their migrations. These differences would be expected to manifest themselves in growth differences, and as a consequence, in differences in survival and maturation of the two stocks.

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Abstract.—The Atlantic sharpnose shark, *Rhizoprionodon terraenovae,* is a small coastal shark that is harvested in both directed and nondirected fisheries throughout its range. Because pups of this species are found both along the southeastern U.S. Atlantic coast and the Gulf of Mexico, it is possible that multiple isolated breeding stocks exist. Restriction fragment length polymorphism analysis of mitochondrial DNA was used to test the hypothesis that Atlantic sharpnose sharks from the U.S. Atlantic coast and the western Gulf of Mexico have identical mitochondrial haplotype frequencies and therefore no apparent genetic stock structure. Seven mitochondrial haplotypes were detected among 52 individuals. The distribution of haplotypes between samples did not differ significantly from homogeneity (P= 0.694), indicating that the null hypothesis of a single breeding population could not be rejected.

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Mitochondrial DNA diversity and divergence among sharpnose sharks, *Rhizoprionodon terraenovae,* from the Gulf of Mexico and Mid-Atlantic Bight*

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The Atlantic sharpnose shark, *Rhizoprionodon terraenovae,* is a small (maximum length 110 cm total length) coastal shark that inhabits the east coast of North America from New Brunswick, Canada, to Yucatan, Mexico (Compagno, 1984). This species is abundant along the southern U.S. Atlantic coast and is second only to the sandbar shark, *Carcharhinus plumbeus,* in longline catches in Virginia (Musick et al., 1993). It supports a large recreational fishery off Texas (Parrack[1]) and is an important species in the Mexican shark longline fishery (Applegate et al., 1993). In addition to being caught in directed fisheries, the Atlantic sharpnose shark is frequently taken by shark longliners targeting large coastal species (Branstetter and McEachran, 1986; Russell, 1993) as well as by commercial shrimp trawlers (Branstetter, 1981; Parrack[1]); however, the implementation of turtle excluder devices (TED's) has produced the additional benefit of reducing bycatch of sharks (Branstetter[2]). Atlantic sharpnose sharks travel in sex-segregated schools, as noted by the disparate sex ratios of adults captured by longlines (Branstetter, 1981; Musick et al., 1993). The gestation period for this species is about ten to twelve months, and parturition takes place from April to June in the northern Gulf of Mexico (Branstetter, 1981; Parsons, 1983) and from May to June in South Carolina (Castro, 1993).

The most recent fishery management plan for sharks in the coastal Atlantic waters of the United States (NMFS[3]) divides sharks into three categories for management purposes: pelagic species, large coastal species, and small coastal species. Currently catches of small coastal species (predominantly the Atlantic sharpnose shark) are not regulated

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1 Parrack, M. L. 1990. A study of shark exploitation in U.S. Atlantic coastal waters during 1986–1989. NOAA, Natl. Mar. Fish. Serv., Southeast Fisheries Science Center, Miami, Florida.

2 Branstetter, S. 1995. Gulf and South Atlantic Fisheries Development Foundation, Suite 997, Lincoln Center, 5401 W. Kennedy, Tampa, Florida 33609. Personal commun.

3 NMFS. 1993. Fishery management plan for sharks of the Atlantic Ocean. U.S. Dep. Commer., NOAA, Southeast Regional Office, St. Petersburg, FL, p. 1–167.

because catch rates are assumed to be at or below maximum sustainable yield and because life history parameters predict a relatively high recruitment rate for this species in comparison to the large coastal species targeted by the U.S. Atlantic shark longline fishery (NMFS[3]). Recently Cortés (1995) challenged this assessment on the basis of a reevaluation of life history characteristics relevant to recruitment (age at maturity, fecundity, and longevity) and suggested that the Atlantic sharpnose shark may be more vulnerable to overfishing than was previously assumed.

Proper management of this species requires not only accurate estimates of standing stock and recruitment values but also an understanding of the reproductive population structure of the species. The observation that pups of this species are found both in the South Atlantic Bight as well as in the Gulf of Mexico, coupled with the small size and apparent lack of significant longshore migration, suggests that there may be isolated breeding populations of this species. Information on stock structure of marine fishes has traditionally relied on two approaches: tag and recapture studies and analyses of genetic variation. Although considerable information has been obtained on the movements of large sharks by means of tagging (Casey and Kohler, 1990), these tagging studies have generally neglected smaller species of sharks. Furthermore, to our knowledge the genetic structure of any population of small coastal shark has not been investigated. This study tests the hypothesis of genetic homogeneity in allele frequency in Atlantic sharpnose sharks between the Gulf of Mexico and Mid-Atlantic Bight by using restriction fragment haplotypes of mitochondrial DNA (mtDNA).

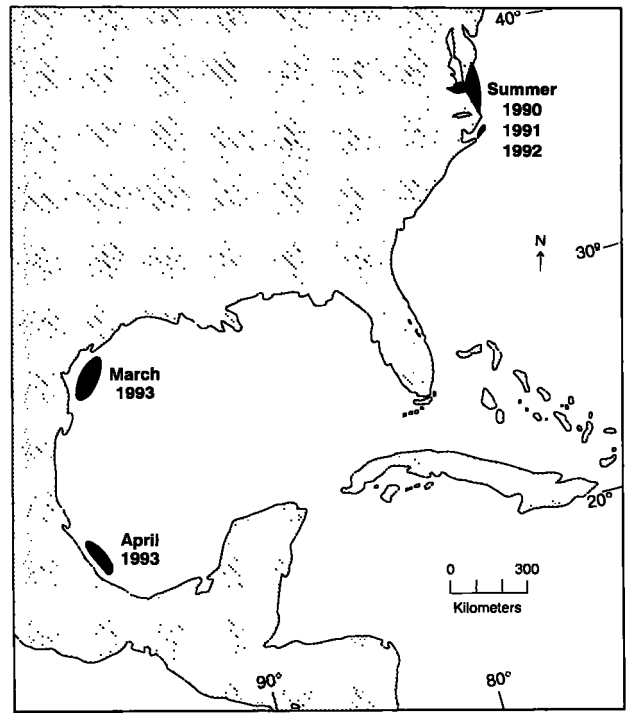

Figure 1

Locations and dates for collection of sharpnose shark, *Rhizoprionodon terraenovae*.

Materials and methods

Atlantic sharpnose sharks were collected with research longlines in the Mid-Atlantic Bight (n=23) as part of an ongoing shark research program of the Virginia Institute of Marine Science, from the recreational fishery of southern Texas (n=21) and from artisanal longline vessels from Veracruz, Mexico (n=8) (Fig. 1). Heart tissue samples from Atlantic sharpnose sharks caught in the Mid-Atlantic Bight were placed into cryovials and stored under liquid nitrogen in the field. In Texas and Mexico, whole hearts were collected on wet ice and stored frozen at (–20°C) until shipped to Virginia. All samples were stored at –70°C.

Mitochondrial DNA was isolated from tissue by following the rapid isolation protocol of Chapman and Powers (1983). Aliquots of mtDNA were digested with ten restriction enzymes (*Ava* I, *Ava* II, *Ban* I, *Bcl* I, *Bst*E II, *Dra* I, *Hin*d III, *Hpa* I, *Sca* I, and *Xho* I) by following the manufacturers' instructions. Restriction fragments were separated on 1.0% horizontal agarose gels run at 2V/cm overnight, then transferred after electrophoresis to a nylon membrane by means of Southern transfer according to the protocols of Sambrook et al. (1989). Filters were hybridized with highly purified mtDNA from tiger shark, *Galeocerdo cuvier*, nick-translated with biotin-14-dATP, and visualized with the BRL BlueGene Nonradioactive Nucleic Acid Detection System.

Fragment patterns were scored for each restriction enzyme and each individual was assigned a composite genotype based on the fragment patterns for all enzymes (Tables 1 and 2). The nucleon (haplotype) diversity was calculated for each sample and for the composite of all samples following Nei (1987). Nucleotide sequence diversity was calculated following the site approach of Nei and Miller (1990). Chi-square significance of the difference in genotypic frequencies between samples was computed by using the randomization protocol of Roff and Bentzen (1989). Nucleotide sequence diversities and divergences were calculated by using the REAP statistical analysis package (McElroy et al., 1991).

Table 1

Estimated size in kilobase pairs of mitochondrial DNA restriction fragments for various restriction enzymes in the Atlantic sharpnose shark, *Rhizoprionodon terraenovae*.

Ava I		*Ava* II	*Ban* I	*Bcl* I		*BstE* II	*Dra* I		*Hind* III	*Hpa* I				*Sca* I	*Xho* I
(A)	(B)	(A)	(A)	(A)	(B)	(A)	(A)	(B)	(A)	(A)	(B)	(C)	(D)	(A)	(A)
7.53	7.53	11.12	11.54	6.62	6.62	6.23	3.14	2.68	6.06	4.84	4.84	5.57	4.84	9.85	11.30
5.17	7.09	2.43	5.44	4.10	4.10	6.09	2.68	2.50	3.83	4.03	3.55	4.03	4.76	5.89	5.32
1.92	1.02	1.60	—	2.26	3.08	1.57	2.08	2.08	2.43	3.43	3.43	3.43	3.43	1.08	—
1.02	8.34	0.64	16.98	1.87	2.26	1.54	2.08	2.08	2.43	2.09	2.09	2.09	2.09	—	16.62
0.83	—	0.55		1.21	0.79	0.84	1.75	1.75	0.80	1.18	1.18	1.18	1.18	16.82	
—	16.48	—		0.79	—	0.65	1.56	1.56	0.68	0.73	0.73	—	—		
16.47		16.33		—	16.85	—	1.14	1.14	—	—	0.45	16.30	16.30		
				16.85		16.92	1.14	0.98	16.23	16.30	—				
							0.98	0.98			16.27				
							—	0.57							
							16.55	—							
								16.32							

Results

Ten restriction enzymes produced an average of 50 restriction fragments with a survey of 288 base pairs (bp) or 1.74% of the 16.6 kb mtDNA molecule (Table 1). Seven haplotypes were detected, resulting in a nucleon diversity of 0.640 and an overall nucleotide sequence diversity (NSD) of 0.13% (Table 2; Fig. 2). Four of the ten restriction enzymes revealed multiple restriction patterns; one enzyme, *Hpa* I, detected four different patterns. The single most common haplotype was found with similar frequencies in each sample and in each year within the Atlantic sample (range=0.50–0.67), and three less common haplotypes also occurred in all three geographic samples. Three rare haplotypes, each found in a different individual, were equally divided among the three sampling locations. Each haplotype differed from the common pattern by the gain or loss of a single restriction site (Fig. 2.) The chi-square probability of haplotype homogeneity among samples (Roff and Bentzen, 1989) was 0.694, indicating that the samples could have been drawn from a single population of mtDNA haplotypes. The nucleotide sequence divergences between the three samples, corrected for within sample diversity, were all less than 0.01%.

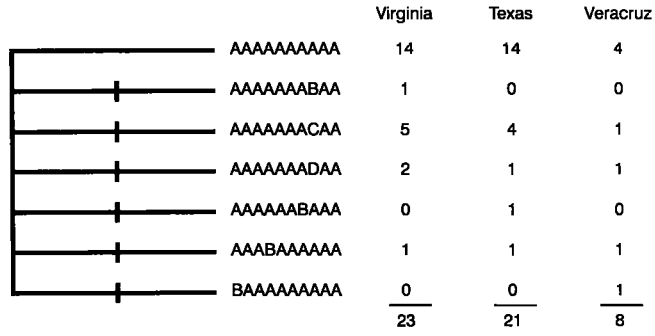

Figure 2

Composite mtDNA haplotypes, inferred phylogenetic relationships among haplotypes (vertical hatches represent restriction site differences), and distribution of haplotypes in samples of Atlantic sharpnose shark, *Rhizoprionodon terraenovae*. Composite haplotypes consist of restriction fragment patterns for the following enzymes (left to right): *Ava* I, *Ava* II, *Ban* I, *Bcl* I, *BstE* II, *Dra* I, *Hind* III, *Hpa* I, *Sca* I, and *Xho* I.

Table 2

Nucleon diversity and percent nucleotide sequence diversity in the Atlantic sharpnose shark, *Rhizoprionodon terraenovae*.

Sample source	Nucleon diversity	Nucleotide sequence diversity (%)
Virginia	0.597	0.120
Texas	0.538	0.105
Veracruz	0.788	0.175
Total	0.640	0.133

Discussion

The results of this study indicate that historically there has been sufficient gene flow among sharpnose

sharks from the Gulf of Mexico to the Mid-Atlantic Bight to prevent significant divergence in mitochondrial DNA haplotypes. The frequencies of the most common alleles, as well as the occurrences of rare alleles, were nearly identical in each of the three samples. The nucleon and nucleotide sequence diversities were also similar among samples. The hypothesis that Atlantic sharpnose sharks collected from locations as distant as Veracruz and Virginia were members of a single homogeneous gene pool could not be rejected.

The distribution of mtDNA haplotypes has been used previously to infer patterns of gene flow in several other commercially important shark species in the Gulf of Mexico and southeastern (U.S.) Atlantic coast (reviewed in Avise, 1992). Gene flow in fishes is accommodated both by the active movement of juveniles and adults, as well as by the passive movement of eggs and larvae. Significant differences in mtDNA haplotype frequencies have been detected in species with limited adult migration and demersal eggs (marine toadfishes, *Opsanus* spp.; Avise et al., 1987) as well as in those with pelagic eggs and larvae (black sea bass, *Centropristis striata;* Bowen and Avise, 1990; and menhaden, *Brevoortia* spp., Bowen and Avise, 1990).

Sharpnose sharks are nektonic from the moment of parturition; therefore, gene flow is accommodated only by the active movements of juveniles and adults. Significant differences in haplotype frequencies were detected in redfish (*Scianops ocellatus*; Gold et al., 1993) of the Gulf of Mexico and southeast U.S. Atlantic coast but not in the hardhead catfish (*Arius felis;* Avise et al., 1987), two species with large active adults but with presumably little passive transport of eggs and larvae. In addition, Heist et al. (1995) detected no heterogeneity in mtDNA haplotype frequencies in the sandbar shark, *Carcharhinus plumbeus*, over the same geographic range.

In menhaden, the presence of two groups of genetically divergent mtDNA haplotypes in the Atlantic was interpreted as indicating complete isolation of these two groups in the past, followed by a mixture of stocks with divergent mtDNA haplotypes (Bowen and Avise, 1990). The close relationships among all haplotypes detected in the Atlantic sharpnose shark is consistent with the hypothesis of a single evolutionary lineage with no historical subdivision.

The lack of genetic divergence among Atlantic and Gulf of Mexico sharpnose sharks can not prove that separate stocks do not exist. An exchange rate of a small number (<20) of females per generation between isolated breeding populations is enough to prevent drift from establishing significant heterogeneity in allele frequencies (Allendorf and Phelps, 1981). Therefore fishery-relevant stocks can be maintained in the absence of statistically significant genetic divergence. Furthermore, if a single population has recently diverged into multiple stocks, there may not have been sufficient time for a significant level of genetic divergence to have become established. Perhaps by examining genetic characters that evolve more rapidly than whole mitochondrial DNA (such as direct sequencing of the mitochondrial control region or microsatellite analysis) stock structure may be eventually detected in this species. The only way, however, to determine the current level of gene flow in this species may be through a tag and recapture program. This information is necessary to determine whether regional exploitation of this species will be compensated by immigration from other regions and whether regional (state) regulations will be an effective means of conservation.

In order to perform robust tests of hypotheses concerning gene flow in organisms, the markers used must have sufficient intraspecific variation so that differences in the frequencies of alleles can be assessed between regions. The level of intraspecific variation in the Atlantic sharpnose shark (NSD= 0.13%) is considerably higher than the NSD of 0.036% reported by Heist et al. (1995) in the sandbar shark, *Carcharhinus plumbeus*, although lower than that detected by Heist et al. (1996) in the shortfin mako, *Isurus oxyrinchus* (NSD=0.38%). Although the number of individuals surveyed in this study is small, the similar amount of variation detected within each sample and the close agreement in frequencies between regions strongly suggest mtDNA haplotype homogeneity between sharpnose sharks of the Mid-Atlantic Bight and Gulf of Mexico. This study has demonstrated that this small coastal shark, with no passive larval transport, nevertheless exhibits mtDNA haplotype homogeneity across a broad geographic range.

Acknowledgments

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Gillnetting in southern New Zealand: duration effects of sets and entanglement modes of fish

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Abstract.—This study examined the catch from gill nets set on nearshore rocky reefs around the Kaikoura Peninsula on the east coast of the South Island of New Zealand. The combined catch of 114 net sets of three net mesh sizes (2.5", 3.5", and 4.5") was analyzed for the mode of entanglement of captured fish and for duration effects on fish. Fusiform species were commonly gilled and wedged, whereas laterally compressed species usually became tangled by fins or spines; these patterns appeared to be a consequence of the behavioral and morphological characteristics unique to each species. The average fork length of caught fish increased with mesh size for gilled and wedged fish but not for those that were tangled. Within each mesh size, entangled fish tended to have the largest mean fork length, gilled fish were intermediate in mean fork length, and wedged fish had the smallest mean fork length. Nets of 2.5" mesh size caught the most fish over all set durations. There was no significant difference between a 6-hour set and a 15-hour set in the number of fish or number of species caught. The proportion of damaged fish in the landed catch was small for nets of all three mesh sizes set for six hours but increased markedly for set times that were longer. Clearly both mesh size, as well as morphological and behavioral differences between species affect the susceptibility of individual fish to gill nets.

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Different species of fish are not equally vulnerable to a given method of fishing. Gill nets, in particular, are highly selective in terms of the sizes and species of fish they catch (Hamley, 1975; Boy and Crivelli, 1988). There are many factors, however, other than the species or size of a fish that can influence the susceptibility of a fish to being caught in a gill net. Hamley (1975) listed these factors as the reaction of fish to nets, the different behavior of fish around nets, the type of net construction, the hanging coefficient, net saturation and characteristics of nets, such as their visibility, elasticity of meshes, and filament size. Dimensional characteristics of fishes, such as length-weight relationships (Kipling, 1957), length-condition relationships (Regier, 1969), and length-girth relationships (Kawamura, 1972), can also influence selectivity.

It is generally agreed that a given mesh size provides a size selection for a particular species that is characterized by a lower size limit, below which fish are small enough to pass through the mesh without hindrance, and by an upper size limit, above which fish are too large to enter the mesh and become entangled (Hamley, 1975). Between these limits the length-frequency distribution of the catch is approximately normal, with a mode at the length where the corresponding girth measure is slightly greater than the mesh perimeter (McCombie and Fry, 1960; Berst, 1961; Garrod, 1961; McCombie and Berst, 1969).

The number of fish caught in gill nets does not necessarily increase in direct proportion to the time that nets are in the water (Kennedy, 1951). Van Oosten (1935) showed that gill nets left for eight nights caught only 47 percent more fish than the same nets left for four nights, whereas if the catch increased in direct proportion to the time fished, the increase would have been 100 percent. The presence of captured, struggling fish and of dead fish may result in the efficiency of gill nets decreasing with time (Kennedy, 1951).

The analysis of catches of fish taken in gill nets is complicated by the passive nature of this type of fishing gear (Berst and McCombie, 1963). Several factors affect gill-net catches, such as the movement of fish, the shape and structure of the fish, and the associative pattern or grouping of the individuals of any species or assemblage of species (Moyle, 1950).

The aim of the present study was to analyse the size range and abundance of the most common fish species in gill-net catches from nearshore reefs in southern New Zealand. The data for this analysis were derived from the catch of nets used for comparison of reef fish populations previously assessed by visual

survey (Hickford and Schiel, 1995) and from gill nets that were used for behavioral observations. By recording the morphological features of the catch, along with the form of entanglement, the primary factors that determine the vulnerability of individual species to particular mesh sizes could be identified. Analysis of the quantity and quality of the catch landed from gill nets set for various periods should yield an optimum set time that will maximize landings and reduce wastage.

Materials and methods

The gillnet catch analyzed in this study was pooled from several experiments. Consequently, the resulting sampling design is not orthogonal. The netting was done on rocky reefs around the Kaikoura Peninsula on the east coast of New Zealand's South Island (42°25'S, 173°42'E) from 8 January 1993 to 26 February 1993. The nets (Table 1) were set from a 6-meter runabout and hauled in by hand. Each net was set in a random direction and the ends were anchored with weights and marked with surface buoys. At least 10 meters separated any two nets. The nets were set on the bottom at depths ranging from 3 to 15 meters and for periods of 11–17 hours. At all sites the benthic habitat type had been described (Hickford and Schiel, 1995) and the fish populations had been surveyed with visual transects by divers immediately before the nets were set. At the end of all sets, the nets were placed in bins and brought back to the laboratory with fish still entangled in the mesh for analysis of the catch. The combined catch of 114 net sets of three mesh sizes over a single known habitat type (rocky pinnacles, mixed algae [Hickford and Schiel, 1995]) was analyzed.

As each fish was removed from the net, its species and fork length (mm) were recorded as was the method by which each fish had become trapped in the mesh. If a fish was held by the mesh encircling its body between the posterior edge of its operculum and the base of its pectoral fin, it was determined to have been "gilled." If the mesh encircling the body was posterior to the base of the pectoral fin, the fish was determined to have been "wedged." If a fish was held because mesh had snagged an appendage, such as the fins, spines, teeth, or maxilla, or if the fish's struggling had simply enveloped it in the mesh, it was described as "tangled." Careful handling of the nets resulted in very few "drop-outs" from the net. However, any fish that were loose in the net were excluded from subsequent entanglement analysis.

Entanglement data were collated for each species in each mesh size. Because the species composition of individual net sets was so variable and because many species were caught only in a small proportion of sets, the analyses of entanglement data were restricted to the five most commonly caught species. This produced a 5×3×3 contingency table, in which the number of fish caught were categorized according to species, mesh size, and entanglement mode. This table was analyzed by using a log-linear model that required thirteen iterations for the G-value to be minimized ($|\Delta G| < 0.001$; Sokal and Rohlf, 1981). The odacid *Odax pullus* was the only species caught in large enough numbers across most net sets for individual statistical analysis of entanglement to be done.

The duration of each net set was recorded. Two set times were chosen for analysis: a 6-h daytime set from late morning to late afternoon and a 15-h night set from late afternoon to early morning. The number of fish and number of species caught during each set were compared. A comparison of the capture rates of common species was also made between day and night sets and between mesh sizes. Each fish caught was given a condition index according to the degree of damage it had sustained while in the net (Table 2).

Results

The 114 net sets caught 1,165 fish from 14 families (Table 3). The odacid *Odax pullus* (46% of the total

Table 1

The dimensions of the gill nets used in fishing during this study. Mesh size is given in inches by the manufacturers and is measured as the diagonal length of a stretched mesh. Filament size is the diameter of the monofilament.

Net and mesh dimension	Measurement		
Net length (m)	30	30	30
Net height (m)	1.80	1.75	1.72
Mesh size (inches)	2.5	3.5	4.5
Filament size (mm)	0.36	0.48	0.58

Table 2

Descriptions of the indices used to categorize the condition of fish landed in gill nets.

Condition index	Damage
No damage	Chafing or scale loss from contact with gill net
Minor damage	Minor lesions; fin or eye damage
Major damage	Major lesions; flesh loss or sea lice damage
Severe damage	Loss of skeletal material

Table 3

The species, common name, fisheries code, and number of fish caught in each of the three mesh sizes and in total. The number of individual net sets are shown in parentheses under the mesh size.

			No. of fish			
			Mesh size			
Family and species	Common name	Fisheries code	2.5" (29)	3.5" (30)	4.5" (55)	Total no. (114)
Myliobatidae						
Myliobatis tenuicaudatus (Hector, 1987)	Eagle ray	EGR	0	1	0	1
Moridae						
Lotella rhacinus (Bloch and Schneider, 1801)	Rock cod	ROC	2	1	0	3
Pseudophycis bachus (Bloch and Schneider, 1801)	Red cod	RCO	2	4	1	7
Carangidae						
Pseudocaranx dentex (Bloch and Schneider, 1801)	Trevally	TRE	0	0	1	1
Trachurus declivis (Jenyns, 1841)	Jack mackerel	JMA	1	1	2	4
Arripidae						
Arripis trutta (Bloch and Schneider, 1801)	Kahawai	KAH	88	6	13	107
Aplodactylidae						
Aplodactylus arctidens Richardson, 1839	Marblefish	GTR	56	45	19	120
Cheilodactylidae						
Cheilodactylus spectabilis (Hutton, 1872)	Red moki	RMO	0	0	5	5
Nemadactylus macropterus (Bloch and Schneider, 1801)	Tarakihi	TAR	0	1	0	1
Latrididae						
Latridopsis ciliaris (Bloch and Schneider, 1801)	Blue moki	MOK	115	40	29	184
Latridopsis forsteri (Castelnau, 1872)	Copper moki	CMO	0	4	2	6
Latris lineata (Bloch and Schneider, 1801)	Trumpeter	TRU	2	0	0	2
Mendosoma lineatum Guichenot, 1849	Telescope fish	TEL	1	0	0	1
Mugilidae						
Aldrichetta forsteri (Cuvier and Valenciennes, 1846)	Yellow-eyed mullet	YEM	22	1	0	23
Labridae						
Notolabrus celidotus (Bloch and Schneider, 1801)	Spotty	STY	7	0	0	7
Notolabrus fucicola (Richardson, 1840)	Banded wrasse	BPF	46	7	5	58
Pseudolabrus miles (Bloch and Schneider, 1801)	Scarlet wrasse	SPF	2	2	0	4
Odacidae						
Odax pullus (Bloch and Schneider, 1801)	Butterfish	BUT	462	72	7	541
Pinguipedidae						
Parapercis colias (Bloch and Schneider, 1801)	Blue cod	BCO	6	3	1	10
Gempylidae						
Thyrsites atun (Euphrasen, 1791)	Barracouta	BAR	0	1	0	1
Istiophoridae						
Seriolella brama (Günther, 1860)	Blue warehou	WAR	45	31	1	77
Monacanthidae						
Parika scaber (Bloch and Schneider, 1801)	Leatherjacket	LEA	0	0	2	2
		Total	857	220	88	1,165

catch), the latrid *Latridopsis ciliaris* (16%), and the aplodactylid *Aplodactylus arctidens* (10%) represented most of the total catch. For the five most commonly caught species, the degree of association between mesh size and method of capture differed for different species (G=81.395, $\chi^2_{0.05[16]}$=26.296, P<0.001). For example, the coastal labrid *Notolabrus fucicola* was mostly gilled in the 2.5" mesh; few of these fish were caught in the larger mesh sizes, and few were caught by wedging and tangling (Table 4). In contrast, the large, slow-moving latrid *L. ciliaris* was mostly tangled in the 2.5" mesh, gilled and tangled in approximately equal numbers in the 3.5" mesh, and mostly gilled in the 4.5" mesh. *Odax pullus* was mostly gilled in the 2.5" and 3.5" meshes and few were caught in the 4.5" mesh. The bottom-dwell-

Table 4

Observed catch frequencies by mode of entanglement for five commonly caught species.

Species	Mesh (inches)		Observed catch			
			Gilled	Wedged	Tangled	Total
Notolabrus fucicola	2.5		39	4	1	44
	3.5		4	1	1	6
	4.5		2	1	1	4
		Total	45	6	3	54
Odax pullus	2.5		317	74	41	432
	3.5		35	25	3	63
	4.5		2	1	1	4
		Total	354	100	45	499
Aplodactylus arctidens	2.5		18	5	28	51
	3.5		24	14	4	42
	4.5		5	10	2	17
		Total	47	29	34	110
Arripis trutta	2.5		61	13	9	83
	3.5		1	1	3	5
	4.5		4	1	3	8
		Total	66	15	15	96
Latridopsis ciliaris	2.5		18	11	60	89
	3.5		15	1	19	35
	4.5		16	5	3	24
		Total	49	17	82	148

ing *A. arctidens* was mostly tangled in the 2.5" mesh, but most fish were gilled and wedged in the 3.5" and 4.5" mesh sizes. The pelagic *Arripis trutta* was mostly gilled in the 2.5" nets, but the number of fish gilled and tangled was approximately equal in the 3.5" and 4.5" nets.

Overall, the mean fork length of each species increased with mesh size for gilled, wedged, and tangled fish (Fig. 1). For example, the mean fork length of gilled *Arripis trutta* was 240 mm in the 2.5" mesh, 310 mm in the 3.5" mesh, and 505 mm in the 4.5" mesh. There was a similar pattern for this species for tangled fish that averaged 460 mm, 560 mm, and 580 mm for the three mesh sizes respectively. There was considerable variation among species in their size interaction among mesh sizes and form of entanglement. However, for most species within each mesh size, the general pattern was that tangled fish had the largest mean fork length, gilled fish had an intermediate mean fork length, and wedged fish had the smallest mean fork length.

There was a clear transition in the proportion of *Odax pullus* captured by each mode as fork length increased in both the 2.5" and 3.5" mesh sizes (Fig. 2). Too few *O. pullus* were caught in the 4.5" mesh for analysis. Gilled fish were significantly larger than wedged fish ($F_{1,104}$=35.77, P<0.001) in both the 2.5" and 3.5" nets. In the 2.5" mesh, tangled fish were significantly larger than gilled fish ($F_{2,453}$=78.41, P<0.001). Overall, the 3.5" mesh caught significantly larger fish than did the 2.5" mesh ($F_{1,104}$=453.36, P<0.001).

With respect to set duration, the 2.5" mesh caught significantly more fish (all species) than the other mesh sizes over both 6 and 15 hours ($F_{2,12}$=36.96, P<0.001) but there was no significant difference between the two set durations in the number of fish caught (Fig. 3A). The 2.5" mesh size also caught a significantly greater number of species over both set durations ($F_{2,12}$=7.60, P=0.007). Again, there was no significant difference between the two set durations in the number of species caught (Fig. 3B).

There was variation among species in the number of fish caught at different set durations (Fig. 4, A–D). The 2.5" mesh caught significantly more *Odax pullus* per hour over both set durations ($F_{2,12}$=5.40, P<0.05). However, there was no significant difference between the two set times in the number of *O. pullus* caught per hour ($F_{2,12}$=3.57, P=0.08). There was also no significant difference between the three mesh sizes

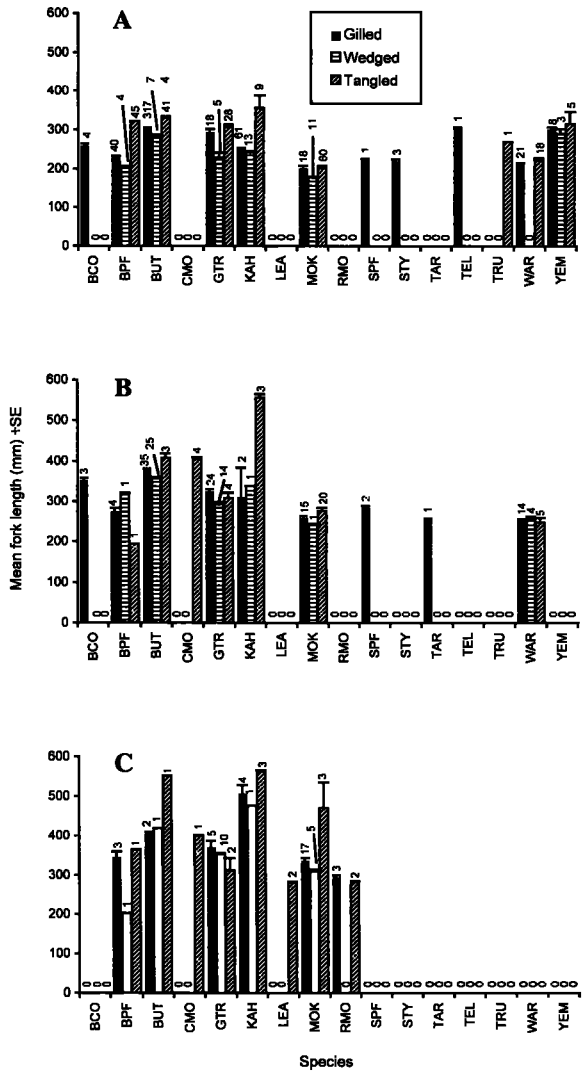

Figure 1

The mean fork length (+1 SE) of fish captured by each entanglement mode in the (**A**) 2.5" mesh, (**B**) 3.5" mesh, and (**C**) 4.5" mesh. n = the number of fish from each species caught in each method. See Table 3 for species codes.

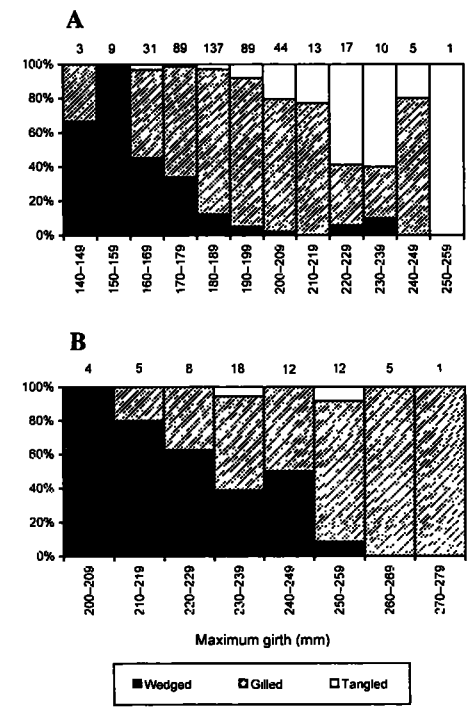

Figure 2

Proportion of butterfish, *Odax pullus*, caught by each entanglement mode in the (**A**) 2.5" mesh and (**B**) 3.5" mesh. n = the number of fish in each size class.

or the two set durations in the number of *Aplodactylus arctidens*, *Latridopsis ciliaris*, or *Arripis trutta* caught per hour (all F values were not significant).

The proportion of damaged fish in the landed catch was small for nets of all three mesh sizes set for six hours but increased markedly for the longer set times (Fig. 5). ANOVA of the condition index of 16 fish selected randomly from each mesh size and each set time showed that fish were significantly more damaged in the longer sets ($F_{1,90}$=19.23, P<0.001), but there was no significant difference among the three mesh sizes in the degree of damage suffered by landed fish ($F_{2,90}$=2.76, P=0.069).

Discussion

Each species showed a distinctive pattern in its form of entanglement in the three mesh sizes. These patterns appear to be a consequence of the behavioral and morphological characteristics unique to each species. For example, *Arripis trutta* were caught mainly by being gilled in the nets. This species is a pelagic carnivore that is dependent on a strong swimming thrust for catching prey. Once gilled, they would be expected to drive forward firmly into the net and to become wedged. The low number of wedged fish for this species may be a result of their firm flesh, which is not easily compressed by the mesh and which may prevent them from entering the net further. Larger fish, despite their greater swimming thrust (Lander, 1969), cannot enter the small mesh sizes far enough to become wedged.

Odax pullus were mostly gilled and wedged in the nets. The low number of *O. pullus* that become tangled was likely the result of the soft fin rays, fused teeth, and small scales typical of this species (Paulin et al., 1989), all of which offer little that will snag on

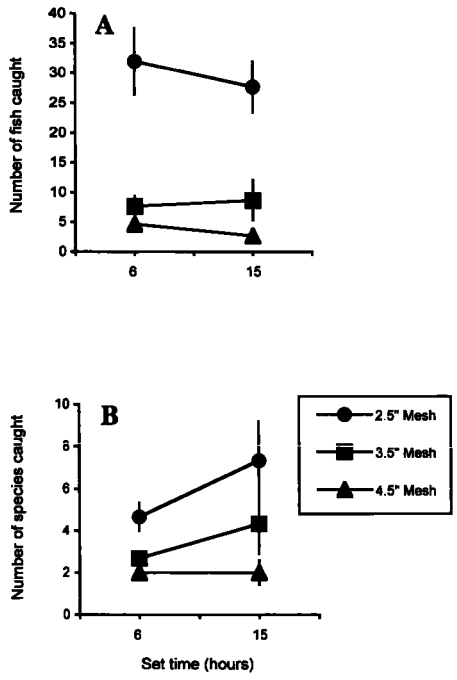

Figure 3

The mean number of fish (**A**) (±1 SE) and the mean number of species (**B**) (±1 SE) landed by the three mesh sizes against time.

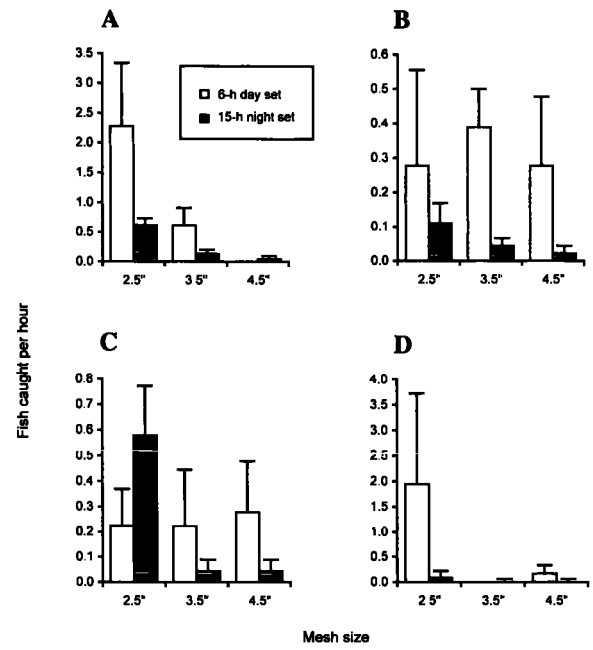

Figure 4

The mean number of fish caught per hour (+1 SE) for four common species in three mesh sizes and in two set durations.

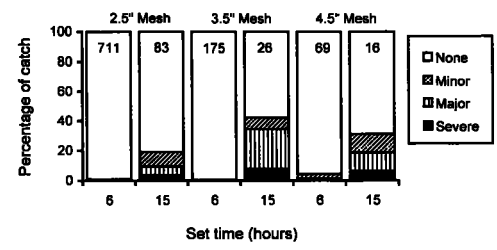

Figure 5

The percentage composition of the catch from nets of three mesh sizes in terms of condition of fish after various set times. n = the number of fish landed by each mesh size after each set duration. See Table 2 for damage categories.

the mesh. However, several other characteristics unique to *O. pullus* make this species very vulnerable to capture by gill nets. The fusiform body shape of this species allows even large individuals to enter the mesh of a gill net to about half their body length before further forward movement is prevented. Their sinuous swimming motion and weak pectorals do not allow them to swim backwards out of a gill net or to stop quickly. This, coupled with the tendency of *O. pullus* to swim below the algal canopy where they are likely to have difficulty detecting the mesh, makes this species one of the most vulnerable to gill nets.

Aplodactylus arctidens were mostly gilled and tangled when caught in the nets. This mode of capture may be due to the strong dorsal spines in this species' anterior dorsal fin which prevent the mesh from passing further along the fish's body. The differences between mesh sizes in the proportions of *A. arctidens* caught by each method may be a result of mesh selectivity. The great number of fish tangled in the 2.5" mesh is probably a result of larger fish becoming tangled by their fins and spines. Small fish caught initially in equivalent numbers in the larger mesh sizes are able to pass through the net unhindered.

Notolabrus fucicola, a labrid species, were mostly gilled when caught in the nets. This is likely to be a result of their labriform swimming motion, which enables them to swim backwards out of the net rather than having to force their way through the mesh. If a labrid's backward motion is not prevented by its gills becoming snagged, it invariably escapes from the mesh. Labrids have also been observed to display a unique rolling motion when first tangled in

the net (Hickford and Schiel, 1995), a motion that often results in a fish freeing itself from the net.

The deep-bodied *Latridopsis ciliaris* were mostly tangled and gilled. The small number of this species that were found wedged in net mesh is probably due to none of the mesh sizes being large enough to allow larger blue moki to enter the nets any further than their gills. The significantly greater number of fish tangled in the 2.5" mesh is a result of larger fish becoming tangled by their large fins and protruding fin rays. Large, laterally compressed fish, such as *L. ciliaris* and *Nemadactylus macropterus*, are not strong swimmers (Doak, 1991). They rely on muscular undulations from head to tail in order to swim, and they brake with their pectoral fins. This weak swimming ability, coupled with their large spiny fins, resulted in *L. ciliaris* often becoming entangled by a single fin rather than being truly enmeshed in the net.

Winters and Wheeler (1990) stated that the difference in fishing power between nets of various mesh sizes may be a result of differences in the proportion of fish caught by each entanglement mode in each mesh size. They stated that the three modes of capture have different fishing powers that may vary with mesh size, but in general, wedging is more effective than gilling, and both these modes are much more effective than tangling. However, the results of our study show that for total fish numbers caught in all mesh sizes combined, most fish were gilled (60%), whereas wedged (17%) and tangled (23%) fish made up significantly lower proportions of the catch. This result suggests that, in the case of our study, gill nets do in fact "gill" fish rather than capture them by tangling or wedging.

Mesh-size selectivity was evident from the mean length of fish captured by each method in each mesh size. Although the fork length of gilled and wedged fish increased with increasing mesh size, the fork length of tangled fish was less uniform in its relationship with mesh size.

The results of our study show that tangling is not the result solely of size selection and is not consistent across mesh sizes. The proportions of *Odax pullus* caught by each method, when plotted against fork length, show a clear transition as fork length increases from most fish being wedged to the majority being tangled. This transition would not occur if the size of tangled fish were independent of mesh size, because fish of all sizes would then become tangled in any given mesh size.

Although the concept of gill net "saturation," or diminishing returns with increasing effort, is generally recognized as a limiting factor in catch per unit of time (Minns and Hurley, 1988), there have been relatively few studies directed at exploring the mechanisms that limit the catch. Our study shows evidence of a set-time saturation effect with all three mesh sizes. Neither the number of fish caught nor the number of species caught were significantly different between the six and fifteen hour sets. However, these different set times had only a small overlap diurnally and saturation may have been influenced by differing periods of fish activity. There was no evidence in either the gill nets or in both underwater observations and videos (Hickford and Schiel, unpubl. data) that predators affected catches.

Space limitation in the gill net itself is regarded as a major component of the saturation effect. Once a fish has been captured, the particular cell that it occupies and the cells immediately surrounding it are not capable of catching other fish. Koike and Takeuchi (1982) examined this feature and found that fish were repulsed around a captured individual for some but not all mesh sizes. Kennedy (1951) cited additional ways in which the efficiency of a gill net decreases with time. These included the presence of captured, struggling fish (which makes the net more obvious and could frighten other fish away) and the presence of dead fish (which may cause other fish to avoid the area). Kennedy speculated that the greater the catch during the initial time period, the greater the difference between the initial (observed) and final (expected) catches.

The effect of set time on total and species catches in gill nets has a direct bearing on the use of this gear in assessing the abundance and species diversity of fish populations. Some studies have focused on comparing multi- to one-night catches (Richards and Schnute, 1986; Minns and Hurley, 1988).The evidence presented here, however, suggests that net saturation can occur during a single night, although this may be confounded by the varying behaviors of the fish species present.

The apparent similarity in catch rates of *Odax pullus*, *Arripis trutta*, *Aplodactylus arctidens*, and *Latridopsis ciliaris* during day and night sets was unexpected. These species are more active during the day and would be expected to be caught in significantly greater numbers in the day sets. Greater average numbers of these species were caught during the daytime, but the catches were so variable that any patterns may have been masked.

The condition of fish in the landed catch is closely related to the length of time a net is in the water. The catch of nets set for longer than six hours will contain a high proportion of damaged fish. The relation between set time and condition is confounded by the fact that nets set for periods longer than six hours were usually left in the water overnight. Dur-

ing the hours of darkness, lobsters (*Jasus edwardsii*) feed more actively (Gunson, 1983) and can severely damage fish. However, lobsters often become tangled in nets while feeding on dead or dying fish in the bottom region of the nets and were frequently caught during nighttime sets in this study. Most intertidal and subtidal marine isopods also peak in their activity rates during the hours of darkness (Jones and Naylor, 1970; Fincham, 1973). Sea lice can completely devour all but the skin and calcified structures of a fish. The fact that both these predators feed predominantly at night means that damage incurred by fish would be greater for overnight sets.

In our study, few fish were damaged in the six hour sets, but up to 40% of fish were damaged in the fifteen hour sets. Therefore, any increase in the number of fish caught beyond six hours may be offset by more fish being severely damaged.

Gill nets do not representatively sample the fish population at reef sites; none of the species in this study was caught in its proportional occurrence in nearshore habitats (Hickford and Schiel, 1995). Behavioral traits, such as swimming motion, and morphological characteristics, such as spines or large fins, act to make some species more vulnerable than others to the fishing action of gill nets. The 2.5" mesh is clearly the most effective at catching most species of fish and is particularly effective at capturing juvenile and resident reef fish. Nets of this small mesh size are commonly available to amateur fishermen in New Zealand, who use them in nearshore waters. Our study clearly shows that although commercially valuable species, such as *Odax pullus, Latridopsis ciliaris,* and *Arripis trutta,* can be caught in great numbers around coastal reefs, the bycatch of resident species, such as *Aplodactylus arctidens, Notolabrus fucicola,* and a broad range of others, is considerable. Most of these species are of no commercial value, but their removal from nearshore waters may well have long-term consequences on resident fish populations in areas where considerable gill netting occurs, such as around the Kaikoura Peninsula.

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Kalman filtering the delay-difference equation: practical approaches and simulations

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Abstract.—Recently, J. J. Pella showed how the Kalman filter could be applied to production modeling to estimate the size and productivity of fish stocks from a time series of catches and relative abundance indices. We apply these methods to the Deriso-Schnute delay-difference equation. The Kalman filter approach incorporates process and measurement error naturally in the model description. When the production model is the delay-difference equation, the error structure is particularly attractive because process error can be interpreted as simply the variance of recruitment, and measurement error as the variance of the relative abundance estimates. We derived prior distributions of initial biomass in order to begin the Kalman filter calculations. Reanalysis of the data from the eastern tropical Pacific for yellowfin tuna, *Thunnus albacares*, shows that modeling results can differ greatly depending on whether error is interpreted to be process error or measurement error. Simulation results show that nonlinear least squares and Kalman filter estimates agree well if data contain only measurement error. In contrast, the Kalman filter was clearly superior if simulated data contained significant amounts of process error. The presence of process error positively biased biomass estimates from both the nonlinear least-squares and Kalman filter methods. The Kalman filter performed well with Schnute's form of the delay-difference equation, even though this model violates the assumption of independent process error vectors. The Kalman filter also performed well when the variance ratio r was assumed known and individual variances were estimated from the data. However, it appeared difficult to estimate r as a parameter in the maximum-likelihood estimation.

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Fishery production models are used to model fishery population dynamics when only catch (measured in biomass units) and relative abundance data are available. Originally, only fishery catch-per-unit-of-effort data (Schaefer, 1954; Pella and Tomlinson, 1969) were used as relative abundance indices for fish populations, but surveys often provide less biased abundance measures. Therefore, both time series of fishery CPUE and survey abundance indices are commonly used estimates of relative abundance.

Production models contrast with age-structured models, such as ADAPT (Gavaris, 1988) and Stock Synthesis (Methot, 1989), that model the population cohort in numbers at age and typically require catch-at-age data. Age-structured models allow for variation in recruitment which has given this class of model greater credence among stock assessment scientists. However, age data are technically difficult to obtain, expensive, and contain biases and variability that can be difficult to interpret. In addition, age-structured models often contain a large number of parameters, and sifting through possible solutions when fitting multiple sources of data can be subjective.

Because of these data requirements and technical problems, production models have remained of interest to stock assessment scientists. Recent production model offerings have included statistical refinements such as bootstrapping (Prager, 1994), Bayesian analysis (Hoenig et al., 1994), and the treatment of statistical error (Polachek et al., 1993). Two of the earliest papers to consider both process and measurement error in population dynamics modeling were those of Ludwig and Walters (1981) followed by Collie and Sissenwine (1983). The Kalman filter approach, which allows the consideration of both process and measurement error, now appears to be becoming standard for assessments by either production or age-structured models (Mendelssohn, 1988; Sullivan, 1992; Pella, 1993; Schnute, 1991, 1994).

The methods described in this paper meld two distinct pieces of technology: the delay-difference equation (Deriso, 1980; Schnute, 1985), and the Kalman filter (Kalman, 1960; Harvey, 1990; Pella, 1993). Collie and Walters (1991) used the Kalman filter to predict and update biomass estimates on the basis of the delay-difference equation but did not use the Kalman filter for parameter estimation. The delay-difference equation has deep roots in fishery modeling. In fact, to a remarkable extent it can encompass the fundamental paradigms of age structure, exponential

survival, and von Bertalanffy growth. The Kalman filter (Kalman, 1960), on the other hand, originated in engineering where it has been widely used in control theory and quality control. The basic idea of Kalman recursive filtering (Meinhold and Singpurwalla, 1983) is that the current state of the system (i.e. the current fish biomass) can be estimated from the system's past (biomass) estimates in two steps: a forecast step and an update step. The forecast estimate is made prior to the current observation of relative abundance; the updated estimate is made following the current observation of relative abundance. The updated estimate of biomass is the modeler's best estimate of the "true" biomass and is, roughly speaking, a weighted average between the forecast and observed abundance values. The updated biomass estimate is used to forecast the next biomass estimate, which then is updated with the next observed value. The absolute and relative magnitude of process and measurement error, which are assumed normal and whose values are generally assumed by the filter, largely determine the result of the update step. If there is little process error assumed by the filter, updating will not substantially change the forecast biomass estimate.

For fishery modeling, the most salient feature of the Kalman filter is its allowance for both process and measurement error. In the implementation of the delay-difference equation with the Kalman filter, process error can be interpreted as the variance of recruitment,[1] and measurement error as the variance of the estimate of relative abundance. Thus the Kalman filter method allows for variation in recruitment, a property that heretofore seemed to be exclusive to age-structured models.

The implementation of the Kalman filter presented here is due to Pella (1993), who applied the method to a simple recruitment model ascribed to Schnute (1991) and to the generalized production model of Pella and Tomlinson (1969). For comparative purposes, we also fitted the delay-difference equation with ordinary nonlinear least squares, which in this case assumes that data contain only measurement error.

The delay-difference population dynamics model

The delay-difference equation is a simple biomass-based model that contains the core dynamics of age-structured models (Deriso, 1980; Schnute, 1985). Thus under many conditions the population dynamics described by the delay-difference equation should agree with that of age-structured models (e.g. virtual population analysis). The applications of the delay-difference equation we propose require the following parameter values and information:

1 The instantaneous natural mortality rate M.
2 Brody[2] growth parameters ρ and ω.
3 Annual catches in biomass c_t, $t=1,...n$.
4 Annual survey biomass estimates y_t, either relative (catchability unknown) or absolute (catchability known) abundance indices, with a few missing values allowed.

The natural mortality rate, M, is always difficult to know but estimates or educated guesses are usually available. The Brody growth parameters can be estimated with nonlinear least squares on relatively small aged samples that provide weight-at-age data (Schnute, 1985):

$$W_{k+j} = \omega_{k-1} + (\omega_k - \omega_{k-1})(1-\rho^{1+j})/(1-\rho) \quad \text{for } j \geq 0. \tag{1}$$

Here, W_{k+j} is the observed weight of a $k+j$ yr-old fish, ω_{k-1}, ω_k, and ρ are parameters to be estimated, and k is the age at recruitment. Our application of the delay-difference equation requires $\omega = \omega_{k-1}/\omega_k$ so that $\hat{\omega} = \hat{\omega}_{k-1}/\hat{\omega}_k$. The difference between Deriso's and Schnute's forms of growth (and hence their delay-difference equations) is that Deriso's original equation requires unrealistically that $\omega_{k-1} = 0$ so that $\omega = 0$. A simple substitution in Schnute's more general formulations of growth and delay-difference equation results in Deriso's forms of growth and delay-difference equation.

Catches and fishing effort are usually among the first statistics collected from a fishery. Survey estimates of stock biomass sometimes come later through significant cost and effort by fisheries management agencies (Gunderson, 1993). If insufficient numbers of survey estimates are available, fishery CPUE can provide the biomass indices. However, fishery CPUE data may bias model estimates because catchability often changes over time. Survey data provide either relative (catchability unknown) or absolute (catchability known) biomass abundance indices. Absolute abundance estimates for a few years will typically

[1] A reviewer noted that process error can also arise from other factors, such as variability in growth and survival, and other sources that make the deterministic delay-difference population dynamics incorrect.

[2] A reviewer pointed out that "Ford" may be a better name for these growth parameters (Ricker, 1975).

constrain an analysis more accurately than will many years of relative abundance indices.

Population dynamics are described by Schnute's (1985, $\omega > 0$) or Deriso's (1980, $\omega = 0$) delay-difference equation:

$$B_t = (1+\rho)s_{t-1}B_{t-1} - \rho s_{t-1}s_{t-2}B_{t-2} + R_t - \rho\omega s_{t-1}R_{t-1}. \quad (2)$$

For the case when $t=2$,

$$B_2 = (1+\rho)s_1B_1 - \rho s_1 s_0 B_0 + R_2 - \rho\omega s_1 R_1. \quad (3)$$

B_t and R_t are the population biomass and recruitment biomass at the beginning of year t, and s_t is total survival during year t (note B_t includes R_t).

The delay-difference equations allow for variable recruitment. In the data analysis and simulations performed in this paper the recruitment process is assumed to have constant mean, i.e. $E(R_t) = R_1$ for all t. The delay-difference Kalman filter method allows for variable recruitment by considering variable recruitment to be process error about the mean recruitment. The nonlinear least-squares estimation method allows only for measurement error, therefore the recruitment process is assumed to be strictly constant with $R_t = R_1$ for all t.

However, both the nonlinear least-squares and Kalman filter methods can be easily generalized to have mean recruitment as a function of stock biomass in earlier years. In this case $E(R_t) = f(B_{t-k})$, where $k \geq 1$ (Kimura, 1988).

Estimating parameters with nonlinear least squares

To fit the delay-difference equation with nonlinear least squares, we must provide biomass projections $\{B_t\}$, from Equations 2 and 3, using as parameters to be estimated, initial values (B_1, R_1). If B_1 is assumed to be virgin biomass and R_1 is in equilibrium with B_1, the expected (i.e. equilibrium) recruitment line (ERL) follows from Equation 2 (Kimura, 1985):

$$R_1 = B_1\{[1-\rho\exp(-M)][1-\exp(-M)]\}/[1-\rho\omega\exp(-M)]. \quad (4)$$

The ERL is a straight line through the origin of the (B_1, R_1) plane.

The initial parameters (B_1, R_1) may be parameterized by either of two assumptions: 1) B_1 is virgin biomass or 2) B_1 is not virgin biomass. If B_1 is virgin biomass, R_1 is determined from Equation 4 (or conversely, B_1 can be determined from R_1). B_2 can then be projected from Equation 3, with $B_0 = B_1$ and $s_0 = \exp(-M)$. Projections of biomass for $t>1$ requires $\{s_t, t = 1, ..., n\}$. These survivals $s_t = \exp(-M-F_t)$, are obtained by iteratively solving the catch equations for F_t (Kimura and Tagart, 1982):

$$c_t = B_t F_t(1-\exp(-M-F_t))/(M+F_t) \quad (5)$$

in a sequential manner (relative to t). If B_1 is not virgin biomass, B_1 and R_1 are independent parameters to be estimated. The initial projection value $B_0 = B_1$ will be used, but with $s_0 = \exp(-M-F_0)$ if information concerning F_0 is available. In either case, further projections of biomass can be made by using Equation 2.

In the simulations to be presented, we assume that the initial population is a virgin biomass (i.e. Equation 4 holds). This allows us to initiate the biomass time series using the results in Appendix 1 and to fit the simulated data without substantial model bias. However, the fits to the simulated data with both nonlinear least squares and the Kalman filter will *not* assume virgin biomass. Instead, the delay-difference equation is fit to a time series of relative abundance data by varying three parameters: B_1, R_1, and a catchability coefficient λ. We assume the catchability coefficient scales the biomass projections from the delay-difference equation $\{B_t\}$ to the expected values of observed relative abundance indices $\{y_t\}$ (i.e. $E(y_t) = \lambda B_t$). For nonlinear least squares, if abundance indices y_t have coefficient of variation cv_t, parameters can be estimated by minimizing

$$SS = \sum[\ln(y_t) - \ln(\lambda B_t)]^2 / cv_t^2. \quad (6)$$

We used a lognormal formulation because of its superior numerical stability in quasi-Newton estimation algorithms. Parameters were estimated in two stages: initial estimates were found by a direct search over a grid of values for B_1, R_1, then refined by using quasi-Newton methods.

The survey catchability λ can be either estimated or fixed depending on whether y_t is thought to be a relative or absolute index of abundance. Differentiating Equation 6 with respect to λ and solving the normal equation shows that λ can be estimated by

$$\hat{\lambda} = \exp\left\{\sum\left[\ln(y_t/\hat{B}_t)/cv_t^2\right]/\sum\left[1/cv_t^2\right]\right\} \quad (7)$$

so that at this stage searches for λ are not necessary. However, the final minimization of Equation 6 with quasi-Newton methods should be based on all three

parameters $\Psi = (\ln(B_1), \ln(R_1), \ln(\lambda))$, because the estimates by using Equation 7 may be suboptimal. If the coefficient of variation is the same for all y_t, then all cv_t can be set equal to one.

We also briefly examined the possibility of estimating nonlinear least-squares parameters by modeling both measurement and process error:

$$SS = \sum\left[(y_t - \hat{\lambda}\hat{B}_t)^2/\sigma_m^2 + (R_t - \hat{R}_1)^2/\sigma_p^2\right]. \quad (8)$$

Here, $\hat{R}_1$ is the estimated mean recruitment as before, but R_t $t > 1$, are allowed to vary. For Deriso's form of the delay difference equation, differentiating Equation 8 with respect to R_t and setting the result equal to zero yields

$$\hat{R}_t = \left[(R_1/r) + \lambda(y_t - \lambda P_t)\right]/\left[(1/r) + \lambda^2\right], \quad (9)$$

where $r = \sigma_p^2/\sigma_m^2$, and P_t is the delay-difference projection of biomass to year t prior to adding recruitment. Estimating parameters by minimizing Equation 8 appeared unstable and was not pursued further. This may be because mean recruitment R_1, and the individual recruitments R_t, both were estimated from the data. With additional constraints, or if recruitment indices were available, such an approach might be useful.

Maximum-likelihood estimation for the Kalman filter

We also applied the Kalman filter as described by Pella (1993) to the delay-difference equation. Pella (1993) credits Harvey (1990) for his own presentation, but we found Pella's presentation to be quite adequate for applying the method. As described earlier, the main reason for using the Kalman filter is that it allows for process error in addition to measurement error. The nonlinear least-squares estimates of the previous section assume constant recruitment and allow only for measurement error.

The state transition equation of the Kalman filter views the delay-difference equation (Eq. 2) as being composed of both deterministic and stochastic components. The determinisitic component of the process assumes that the expected values of R_t and R_{t-1} are constant, say equal to R_1. If desired, we can also assume virgin biomass when applying the Kalman filter, i.e. we can estimate R_1 by using Equation 4. This is analogous to the constant nonrandom recruitment model fit by nonlinear least squares. The biomass prediction given by Equation 2 is in error owing to variability in recruitment. This variability is defined to be process error. Now, even though B_t and λ have definite though unknown values, the abundance index y_t is observed only with error, which we define as measurement error. The Kalman filter method provides maximum-likelihood estimates of B_0, R_1, and λ, almost the same parameters as for the nonlinear least-squares method but for the process and measurement error model we have just described. Note that we estimate B_0 (see below) instead of B_1 because B_0 cannot simply be defined to be equal to B_1 in the equations which initialize the Kalman filter method. For consistency, when comparing parameter estimates for nonlinear least-squares and the Kalman filter methods, we shall compare only estimates of B_1 (i.e. the one year projection of B_0).

Modeling and assumptions in addition to those of nonlinear least squares are needed by the Kalman filter. Because the Kalman filter is essentially a Bayesian procedure (Meinhold and Singpurwalla, 1983), it requires a prior joint distribution for B_0 and B_{-1}. In addition, in order to partition process and measurement error, either the magnitude of process or measurement error (or both) or their ratio must be known or estimated. Nearly all of our simulations will assume that process and measurement error variances are known. Kalman filter estimation without prior information concerning error variances appears to be generally difficult.

Simulating datasets satisfying Kalman filter assumptions

In this section we describe simulation of relative abundance indices that satisfy the assumptions of the delay-difference equation and the Kalman filter. As stated earlier, these simulations assume virgin biomass (i.e. Equation 4 holds with B_0 substituted for B_1). This is the easiest way to avoid an initial modeling bias in the simulation and model fits. Data simulated in this manner will be fitted by using nonlinear least-squares and the delay-difference Kalman filter methods *without* the assumption of virgin biomass. To a large extent we followed the notation of Pella (1993). Note that the "state space" of the system is simply jargon for the unobservable true biomass of the system.

Initial conditions and assumptions The initial state of the system is defined to be

$$\alpha_0 = \begin{pmatrix} B_0 \\ B_{-1} \end{pmatrix}.$$

We assume that α_0 is unknown but has prior distribution with mean

$$\alpha_0 = E(\alpha_0) = \begin{pmatrix} B_0 \\ B_0 \end{pmatrix}$$

and with covariance matrix

$$P_0 = \Sigma(\alpha_0) = \begin{pmatrix} \gamma_0 & \gamma_1 \\ \gamma_1 & \gamma_0 \end{pmatrix}.$$

Estimators for γ_0 and γ_1 are provided in Appendix 1 and only require prior estimates of ρ, ω, σ_p^2 and s_0. To predict α_1, we assumed

$$T_0 = \begin{pmatrix} (1+\rho)s_0 & -\rho s_0 s_0 \\ 1 & 0 \end{pmatrix}, C_0 = \begin{pmatrix} R_1(1-\rho\omega s_0) \\ 0 \end{pmatrix},$$

$$\tilde{R}_0 = \begin{pmatrix} 1 & -\rho\omega s_0 \\ 0 & 0 \end{pmatrix}, \text{and } \eta_0 = \begin{pmatrix} n_1 \\ n_0 \end{pmatrix}.$$

The state of the system at time t=1 is then $\alpha_1 = T_0\alpha_0 + C_0 + \tilde{R}_0\eta_0$, where n_1 is assumed to be a normal random variable with mean zero and variance σ_p^2. For Deriso's form of the delay-difference equation, $\omega = 0$, so that the value of n_0 is irrelevant. However, for Schnute's form of the delay-difference equation we used $n_0 = 0$ because the data contained no information concerning n_0.

Projecting the state space Given the initial conditions (above), and a catch sequence $\{c_t\}$, the state space variable α_t can be projected indefinitely:

$$\alpha_t = \begin{pmatrix} B_t \\ B_{t-1} \end{pmatrix}, T_t = \begin{pmatrix} (1+\rho)s_t & -\rho s_t s_{t-1} \\ 1 & 0 \end{pmatrix}, C_t = \begin{pmatrix} R_1(1-\rho\omega s_t) \\ 0 \end{pmatrix}$$

$$\tilde{R}_t = \begin{pmatrix} 1 & -\rho\omega s_t \\ 0 & 0 \end{pmatrix}, \eta_t = \begin{pmatrix} n_{t+1} \\ n_t \end{pmatrix}$$

so that

$$\alpha_{t+1} = T_t\alpha_t + C_t + \tilde{R}_t\eta_t.$$

The process error vectors η_t are assumed to be independent with

$$E(\eta_t) = \begin{pmatrix} 0 \\ 0 \end{pmatrix}$$

and with covariance matrix

$$Q = \begin{pmatrix} \sigma_p^2 & 0 \\ 0 & \sigma_p^2 \end{pmatrix}.$$

Recall that T_t requires a value for s_t by first solving Equation 5 for F_t.

Addition of measurement error Given a catchability coefficient λ, the observed variables can be described as $y_t = Z\alpha_t + \varepsilon_t$, where $Z = (\lambda\ 0), \varepsilon_t = e_t$, and e_t is assumed to be normally distributed with mean zero and variance $h = \sigma_m^2$.

If expected recruitment is to be a function of stock biomass in earlier years, the state space project vector C_t must become a function of α_t so that

$$C_t(\alpha_t) = \begin{pmatrix} E(R_{t+1}) - \rho\omega s_t E(R_t) \\ 0 \end{pmatrix}.$$

If the delay between hatching and recruitment is to be many years, then the dimension of α_t must be increased, so that the earlier biomass will be available to calculate recruitment.

So far we have described a statistical model which includes process and measurement error and which can be used to compute a realization of relative abundance indices, say $\{\tilde{y}_t\}$. In the implementation of the Kalman filter given here, Deriso's form ($\omega = 0$) of the delay-difference equation fully satisfies the assumptions of the model, but Schnute's ($\omega > 0$) more realistic form does not. This difference is due to the process error vectors

$$\eta_t = \begin{pmatrix} n_{t+1} \\ n_t \end{pmatrix},$$

which represent variability in recruitment and which are assumed to be independent by the Kalman filter. Because η_t and η_{t+1} both contain n_{t+1}, this assumption is clearly violated for Schnute's form of the delay-difference equation. This trade-off between realism in the delay-difference equation and statistical independence required of process error will be examined further with simulation.

Kalman filter estimates

If values of variance for process and measurement error are assumed, parameters $\Psi = \{\ln(B_0), \ln(R_t), \ln(\lambda)]$ can be estimated by the method of maximum likelihood. In principle, the method is very similar to that described for calculating nonlinear least-squares estimates. Given a value for Ψ, initial values for a_0, P_0 can be specified as in the simulations; estimates of biomass and its covariance matrix can then be forecast $\{a_{t|t-1}, P_{t|t-1}\}$. The value of Ψ, whose forecasts maximize the log-likelihood, is taken as the estimate.

Because the Kalman filter incorporates process as well as measurement error, estimation of biomass occurs in two steps.

1 Initial projections $a_{t|t-1} = T_{t-1}a_{t-1} + C_{t-1}$ and $P_{t|t-1} = T_{t-1}P_{t-1}T_{t-1}' + \tilde{R}_{t-1}Q\tilde{R}_{t-1}'$ are calculated on the

basis of the value of Ψ, initial conditions, and the data $(c_1, \ldots, c_{t-1})$and $(y_1, \ldots y_{t-1})$. Recall again that T_{t-1} requires a value for s_{t-1} that can be estimated by first solving the catch equation (Eq. 5) for F_{t-1}. As described earlier, if expected recruitment is to be a function of earlier biomass estimates, then C_{t-1} must be a function of a_{t-1}.

2 If an observation of y_t exists, the initial projections $a_{t|t-1}$ and $P_{t|t-1}$ are updated on the basis of $a_t = a_{t|t-1} + P_{t|t-1}Z' f_t^{-1}(y_t - Za_{t|t-1})$ and $P_t = P_{t|t-1} - P_{t|t-1}Z' f_t^{-1} ZP_{t|t-1}$, where $f_t = ZP_{t|t-1}Z' + h$. If an observation of y_t does not exist, further projections can be made by using Equation 1, with $a_{t|t-1}$ and $P_{t|t-1}$ used in place of a_t and P_t. Therefore, Kalman filter estimation can accommodate missing relative abundance indices provided they are few in number.

3 The log-likelihood is calculated to be

$$\ln(L(y,\Psi)) = -\left(\frac{n}{2}\right)\ln(2\pi) - \frac{1}{2}\sum_{t=1}^{n}\ln(f_t) - \frac{1}{2}\sum_{t=1}^{n}\frac{v_t^2}{f_t},$$

where $v_t = y_t - Za_{t|t-1}$, and $f_t = ZP_{t|t-1}Z' + h$.

As with the nonlinear least-squares method, the Kalman filter estimate of Ψ was also calculated in two stages. First, we searched a grid of possible initial λ_0 values, say from 0.5 to 1.5 at 0.1 intervals. For each fixed λ_0 value, we then estimated the conditional maximum-likelihood estimate $\Psi^* = [\ln(B_0^*), \ln(R_1^*)]$ by a quasi-Newton method. We then picked the λ_0^* and Ψ^* having the largest conditional likelihood, and used that as an initial estimate for finding the unconditional maximum likelihood estimate $\hat{\Psi} = [\ln(\hat{B}_0), \ln(\hat{R}_1), \ln(\hat{\lambda})]$, again by using a quasi-Newton method. The asymptotic covariance matrix of the maximum-likelihood estimates can be estimated from the inverse Hessian of minus the log-likelihood.

Generally, our Kalman filter estimates were made with the assumption that process and measurement error variances were known. However, under the Kalman filter, if $r = \sigma_p^2/\sigma_m^2$ is known, then all model parameters, including σ_m^2 and hence σ_p^2, can be estimated from the data. Following Pella (1993), we reparameterized $h = 1$ and

$$Q = \begin{pmatrix} r & 0 \\ 0 & r \end{pmatrix}.$$

It can be noted that

$$P_0^* = P_0/\sigma_m^2 = \frac{1}{\sigma_m^2}\begin{pmatrix} \gamma_0 & \gamma_1 \\ \gamma_1 & \gamma_0 \end{pmatrix} = rA,$$

where $A = P_0/\sigma_p^2$ is dependent only on ρ, ω, and s_0. The Kalman recursions are then carried forward just as would have been done if no reparametrization had been performed. However, the covariance matrices $\{P_{t|t-1}$ and $P_t\}$ are now automatically scaled versions $\{P_{t|t-1}^* = P_{t|t-1}/\sigma_m^2$ and $P_t^* = P_t/\sigma_m^2\}$, and $f_t^* = f_t/\sigma_m^2$. The vectors $a_{t|t-1}$ and a_t are unaffected by the scaling which cancels in their equations. The parameter estimates are dependent only on the value of r, not the variance components σ_p^2 and σ_m^2. However, σ_m^2 can be estimated from

$$\hat{\sigma}_m^2 = \sum(v_t^2/f_t^*)/n,$$

where n is the number of y_t observed (also $\hat{\sigma}_p^2 = r\hat{\sigma}_m^2$). The log-likelihood to be maximized (see Appendix 2) then becomes

$$\ln(L_c(y,\Psi)) = -\frac{n}{2}[\ln(2\pi)+1] - \frac{1}{2}\sum_{t=1}^{n}\ln(f_t^*) - \frac{n}{2}\ln(\hat{\sigma}_m^2). \quad (10)$$

The question arises whether r can be estimated as just another parameter by using the method of maximum likelihood? Although estimation of r appears possible in theory, our experience suggests that this will be impractical for many data sets. The reason is that the likelihood function appears to be insensitive to r (Fig. 1).

Data analysis and simulations

We reanalyzed the data set for yellowfin tuna, *Thunnus albacares* (Table 1), taken from Pella and Tomlinson (1969) by using methods described in this paper. Ages read from otoliths of yellowfin tuna (Wild, 1986) indicate that length at age is nearly linear. This implies exponential growth in weight at age, but we shall assume linear growth in weight at age (i.e. $\rho = 1.0$, $\omega = 0.0$). Because fish rapidly disappear from the population at age 4 yr, we assume $M = 0.60$. Therefore, we assume constant growth with a large natural mortality rate. Analysis by Pella (1993) indicates a biomass range of from 600 to 1,400 million pounds and an annual sustainable yield of 193 million pounds.

Our data analyses (i.e. fits to the data in Table 1) assume

D1 $\sigma_m^2 = 46, \sigma_p^2 = 32{,}775$ as reported by Pella (1993). These values suggest that most of the error

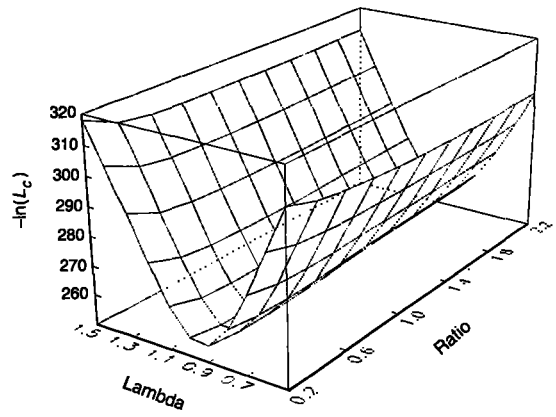

Figure 1

The likelihood profile (minus $\ln(L_c)$) for estimating Kalman filter parameters as a function of the variance ratio ($r = \sigma_p^2/\sigma_m^2$) and lambda ($\lambda$), showing that the likelihood profile appeared insensitive to the value of variance ratio. The assumed parameters were $R_1 = 250$, $\lambda = 1$, $\rho = 1$, $\omega = 0$, $M = 0.60$, $s_0 = \exp(-0.60)$, r=1.0, variances assumed to be $\sigma_m^2 = 100$ $\sigma_p^2 = 100$, with $n = 100$ yr of simulated data.

is process error (i.e. variance of recruitment) as opposed to measurement error (i.e. error in measuring the relative abundance index).

D2 $\sigma_m^2 = 5{,}000$ $\sigma_p^2 = 1{,}000$. These values suggest that most of the error is measurement error as opposed to process error.

Under the heading "Simulating datasets satisfying Kalman filter assumptions," we describe a detailed model for simulating data that satisfy the Kalman filter assumptions. In this paper all simulations are roughly related to the yellowfin tuna dataset (i.e. 34 yr of simulated data with similar model parameter values). To do this we specified values for natural mortality, M, Brody growth parameters ρ and ω, expected recruitment R_1, catchability λ, and variances σ_p^2 and σ_m^2. Assuming virgin biomass (Eq. 4), values for (M, ρ, ω, σ_p^2, R_1) provide us with the mean virgin biomass and its covariance matrix over neighboring years (a_0, P_0). The simulation is initialized by generating biomass estimates, i.e. bivariate normal random deviates having the prior expectation a_0 and covariance matrix P_0. These initializations assumed $s_0 = \exp(-M)$. Because trends in the catch data can affect modeling results, we also simulated the catch data by assuming that catches were lognormal (see Kimura, 1989), $\ln(c_t) \sim N(\mu, \sigma^2)$, with $E(c_t) = \bar{c}$, and $\mathrm{var}(c_t) = cv^2\bar{c}^2$, with $\bar{c} = 141.8$ (average from Table 1), and $cv = 0.2$.

Table 1

Catch (c_t in million pounds) and relative abundance (y_t in pounds per boat day) for yellowfin tuna, *Thunnus albacares*, in the eastern Pacific Ocean (Pella and Tomlinson, 1969).

Year	Catch	Relative abundance
1934	60.9	10,361
1935	72.3	11,484
1936	78.4	11,571
1937	91.5	11,116
1938	78.3	11,463
1939	110.4	10,528
1940	114.6	10,609
1941	76.8	8,018
1942	42.0	7,040
1943	50.1	8,441
1944	64.9	10,019
1945	89.2	9,512
1946	129.7	9,292
1947	160.2	7,857
1948	207.0	8,353
1949	200.1	8,363
1950	224.8	7,057
1951	186.0	10,108
1952	195.3	5,606
1953	140.0	3,852
1954	140.0	5,339
1955	140.9	8,191
1956	177.0	6,507
1957	163.0	6,090
1958	148.5	4,768
1959	140.5	4,982
1960	244.3	6,817
1961	230.9	5,544
1962	174.1	4,120
1963	145.5	4,368
1964	203.9	4,844
1965	180.1	4,166
1966	182.3	4,513
1967	178.9	5,292

Three simulations were replicated 100 times so that we could examine the bias, variance, and root mean square error (i.e. the square root of mean square error) of Kalman filter and nonlinear least-squares parameter estimates when the true parameter values were known. For these simulations we assumed that the stock was initially a virgin biomass ($R_1 = 250$, $\lambda = 1$, $\rho = 1$, $\omega = 0$, $M = 0.60$), and the catch data were generated as lognormal random deviates $LN(\bar{c}=141.8, cv = 0.2)$. We assumed that data sets had only measurement error, only process error, or a mixture of both.

S1 $\sigma_m^2 = 1{,}000$ $\sigma_p^2 = 1$. Measurement error only.

S2 $\sigma_m^2 = 1$ $\sigma_p^2 = 1{,}000$. Process error only.

S3 $\sigma_m^2 = 500$ $\sigma_p^2 = 500$. Measurement and process error.

In order to understand the distribution of bias in the estimated biomass trends, we made histograms of the residuals $Z_t = \hat{B}_t - B_t$ (true) for years t=1, 17, and 34, for both the Kalman filter and nonlinear least-squares estimates.

Finally, two specialized simulations were replicated 100 times:

SP1

$\omega > 0$:

$$R_1 = 250,\ \lambda = 1,\ \rho = 0.75,\ \omega = 0.75,$$
$$M = 0.3,\ \sigma_m^2 = 1,\ \sigma_p^2 = 1{,}000$$

SP2

r fixed:

$$R_1 = 250,\ \lambda = 1,\ \rho = 1,\ \omega = 0,$$
$$M = 0.6,\ \sigma_m^2 = 500,\ \sigma_p^2 = 500.$$

With these simulations the stock was assumed to be initially a virgin biomass. The purpose of simulation SP1 was to examine how severely the correlation in process error (η_t) induced by Schnute's form of the delay-difference equation ($\omega > 0$) degrades the parameter estimates from the Kalman filter. The purpose of SP2 was to examine whether estimating parameters by assuming only $r = \sigma_p^2 / \sigma_m^2 = 1.0$ was known (i.e. by maximizing Equation 10), would degrade the Kalman filter estimates.

Results

Our results from reanalyzing the data set in Table 1 with variance assumptions described as D1 and D2 are shown in Figure 2. The variance assumption D1, that of Pella (1993), is close to assuming only process error. The result is estimated biomass trends that are scaled but that exactly trace the relative abundance indices (Fig. 2A). Our model fit is very similar to that reported by Pella (1993) and indicates that, despite great differences in the underlying state transition models (delay-difference versus generalized production), the Kalman filter method, with large process error, can provide quite similar estimates of biomass trends. The nonlinear least-squares fit assumes only measurement error and differs considerably from the Kalman filter fit. In the analysis with variance assumed to be D2, the Kalman filter assumes that error is predominantly measurement error but also contains a realistic component of process error. The result is Kalman filter estimates of relative abundance that are very similar to nonlinear least-squares estimates (Fig. 2B).

Results from replicated simulations based on assumptions S1–S3 are shown in Table 2. Under the variance assumption S1, we have only measurement error. Under this assumption, the Kalman filter and nonlinear least-squares methods performed similarly. Root mean square error (RMSE) estimates, compared with sample standard deviations of parameter estimates, show that both methods have little bias but that the inverse Hessian of minus the log-likelihood appears to give estimates of the uncertainty of parameter estimates that are biased low (i.e. are more similar to standard deviation than RMSE). Residual plots (Fig. 3) indicate biomass traces have symmetrical error.

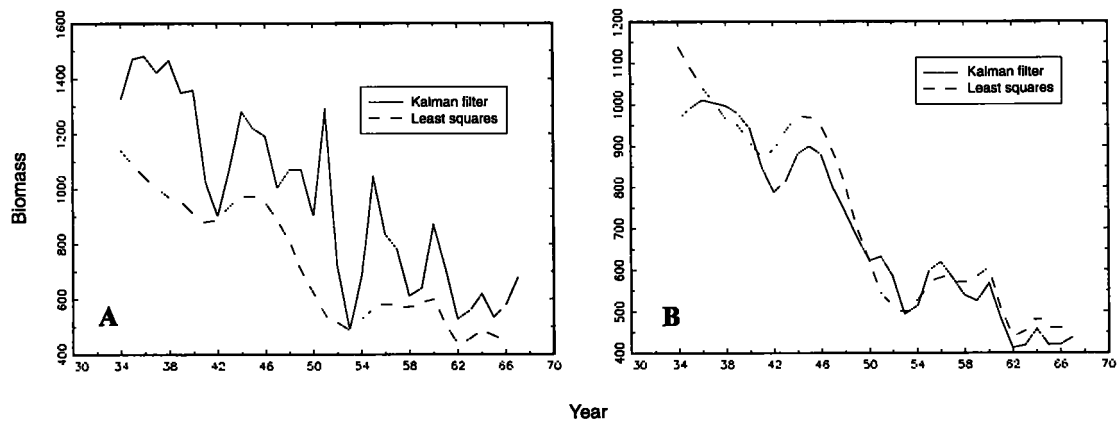

Figure 2

Fits to yellowfin tuna, *Thunnus albacares*, assuming $\rho = 1$, $\omega = 0$, $M = 0.60$, $s_0 = \exp(-0.60)$, and data from the eastern Pacific Ocean (Table1). (**A**) Kalman filter fit assuming $\sigma_m^2 = 46$ $\sigma_p^2 = 32{,}775$ as in Pella (1993). (**B**) Kalman filter by assuming predominantly measurement error $\sigma_m^2 = 5{,}000$ $\sigma_p^2 = 1{,}000$. Nonlinear least-squares estimates are the same in both (A) and (B); biomass is in millions of pounds.

Table 2

Simulation result from 100 replications of the simulations described below. Time series were simulated by assuming virgin biomass with (R_1=250, λ=1), growth parameters (ρ=1, ω=0), s_0=exp(–0.60), σ_m^2, σ_p^2 values given below, and relationships described in Appendix 1. Catches were simulated as lognormal random variables with $\bar{c}$=141.8, cv=0.2). Because the true B_1 value varies in each replication, an average value for each simulation is presented below. Standard errors for Kalman filter (KF) estimates were calculated from the inverse of the Hessian of minus the log-likelihood. RMSE = root mean square error; NLS = nonlinear least squares.

	B_1	R_1	λ
Simulation S1: $\sigma_m^2 = 1{,}000$ $\sigma_p^2 = 1$			
Average true B_1	1,228		
Average of Kalman filter estimates	1,237	250.9	1.004
Standard deviation of KF estimates	135	13.3	0.098
Average standard error of KF estimates	175	16.4	0.120
RMSE of KF estimates	232	23.0	0.169
Average NLS estimates	1,235	250.7	1.007
Standard deviation of NLS estimates	140	14.1	0.106
RMSE of NLS estimates	240	24.3	0.183
Simulation S2: $\sigma_m^2 = 1$ $\sigma_p^2 = 1{,}000$			
Average true B_1	1,222		
Average of Kalman filter estimates	1,282	256.9	0.963
Standard deviation of KF estimates	139	15.5	0.095
Average standard error of KF estimates	154	14.8	0.094
RMSE of KF estimates	244	29.2	0.176
Average NLS estimates	1,332	263.7	1.082
Standard deviation of NLS estimates	618	67.6	0.431
RMSE of NLS estimates	1,072	118.9	0.756
Simulation S3: $\sigma_m^2 = 500$ $\sigma_p^2 = 500$			
Average true B_1	1,230		
Average of Kalman filter estimates	1,287	257.0	0.979
Standard deviation of KF estimates	232	24.5	0.153
Average standard error of KF estimates	228	22.0	0.145
RMSE of KF estimates	400	44.0	0.266
Average NLS estimates	1,304	259.4	1.026
Standard deviation of NLS estimates	481	52.8	0.263
RMSE of NLS estimates	831	92.4	0.455

With variance assumption S2, we have only process error. With this assumption both the Kalman filter and nonlinear least-squares biomass estimates are biased high (Table 2; Fig. 4). However, root mean square errors show that the Kalman filter performance is clearly superior to nonlinear least squares for this case. It is interesting that simulation S2 also shows that nonlinear least-squares estimates are not necessarily more biased under process error but that parameter estimates have larger variances.

Variance assumption S3 represents a combination of process and measurement error. Results from S3 are similar to those from S2, with biomass estimates appearing to be biased high for both the Kalman filter and nonlinear least-squares methods (Table 2; Fig. 5), but with RMSE clearly favoring the Kalman filter method over the nonlinear least-squares method. It should be noted that in simulation S2 and S3, 1 or 2 of the nonlinear least-squares fits failed to converge probably owing to the inclusion of process error. These simulations were thrown out and the runs were repeated.

Results from simulation SP1 (Table 3) indicate that Schnute's form of the delay-difference equation can be used with the Kalman filter, despite the violation of the assumption that process error vectors are independent. And finally, results from simulation SP2 (Table 4) indicate that the Kalman filter parameter estimates have smaller RMSE compared with nonlinear least-squares parameter estimates when only the value of $r = \sigma_p^2 / \sigma_m^2$ is assumed in the model fit.

Conclusions

Simulations show that with the fit of the delay-difference equation, the Kalman filter and nonlinear least-

squares methods give similar results if there is only measurement error. Bias in parameter estimates for both methods tend to be small in this case. The Kalman filter was superior to nonlinear least squares, as measured by RMSE, if there is only process error. Both methods tended to give biomass estimates that were positively biased, and nonlinear least-squares estimates were dramatically skewed to the right. A similar result

Table 3

Simulation result from 100 replications of the simulation described as SP1 in the text. Time series were simulated by assuming virgin biomass (R_1=250, λ=1), growth parameters (ρ=0.75, ω=0.75), s_0=exp (–0.30), (σ_m^2=1, σ_p^2=1,000), and relationships described in Appendix 1. Catches were simulated as lognormal random variables with ($\bar{c}$=141.8, cv=0.2). Because the true B_1 value varies in each replication, an average value for each simulation is presented below. Standard errors for Kalman filter (KF) estimates were calculated from the inverse of the Hessian of minus the log-likelihood. RMSE = root mean square error.

	B_1	R_1	λ
Simulation SP1: $\sigma_m^2 = 1, \sigma_p^2 = 1{,}000$			
Average true B_1	1,262		
Average of Kalman filter estimates	1,287	252.1	0.993
Standard deviation of KF estimates	155	16.4	0.113
Average standard error of KF estimates	159	16.2	0.105
RMSE of KF estimates	257	28.5	0.195

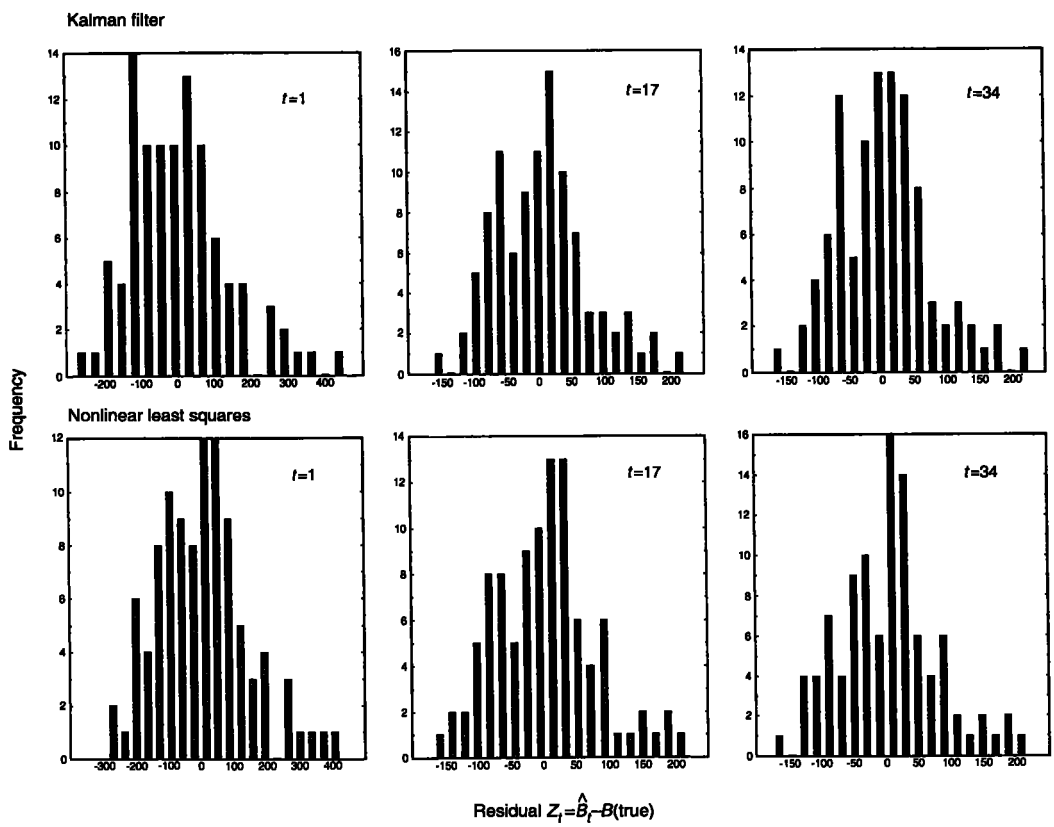

Figure 3

Histograms of the residual between estimated and true biomass, $Z_t = \hat{B}_t - B_t$(true), for simulation S1, with $\sigma_m^2 = 1{,}000$, and $\sigma_p^2 = 1.0$. Top row is for the Kalman filter method; bottom row is for the nonlinear least-squares method; columns are for years t=1, 17, and 34.

occurred when measurement and process error were included in the simulations, the Kalman filter and nonlinear least-squares biomass estimates were positively biased and appeared positively skewed.

We interpret these results to mean that the Kalman filter method provides superior performance in terms of RMSE but provides biased biomass estimates. This is a serious problem for a stock assess-

Table 4

Simulation result from 100 replications of the simulation described as SP2 in the text. Time series were simulated by assuming virgin biomass (R_1=250, λ=1), growth parameters (ρ =1, ω =0), s_0=exp(–0.60), $\sigma_m^2 = 500$ $\sigma_p^2 = 500$, and relationships described in Appendix 1. Catches were simulated as lognormal random variables with ($\bar{c}$ =141.8, cv=0.2). Because the true B_1 value varies in each replication, an average value for each simulation is presented below. KF = Kalman filter; RMSE = root mean square of error; NLS = nonlinear least squares.

	B_1	R_1	λ
Simulation SP2: $\sigma_m^2 = 500$ $\sigma_p^2 = 500$			
Average true B_1	1,226		
Average of Kalman filter estimates	1318	259.9	0.967
Standard deviation of KF estimates	291	28.6	0.173
RMSE of KF estimates	502	55.6	0.313
Average NLS estimates	1310	260.3	1.035
Standard deviation of NLS estimates	565	61.7	0.290
RMSE of NLS estimates	982	107.8	0.503

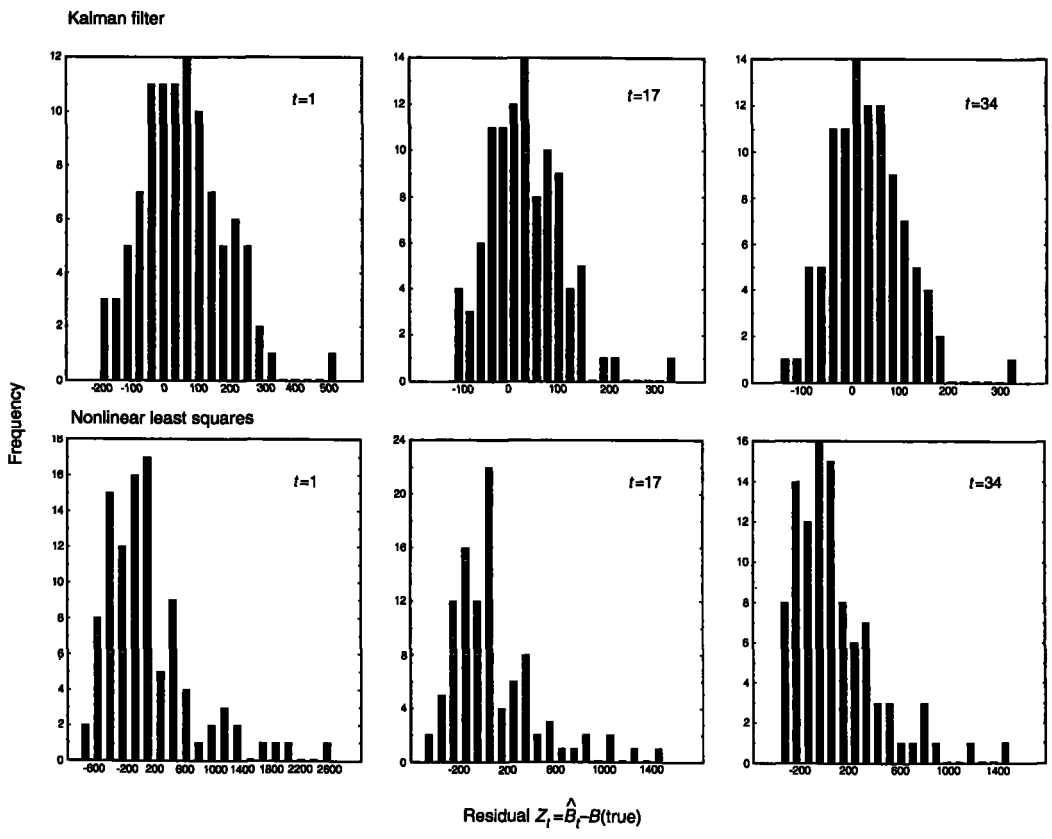

Figure 4

Histograms of the residual between estimated and true biomass, $Z_t = \hat{B}_t - B_t$(true), for simulation S2, with $\sigma_m^2 = 1.0$, and $\sigma_p^2 = 1{,}000$. Top row is for the Kalman filter method; bottom row is for the nonlinear least-squares method; columns are for years t=1, 17, and 34.

ment model because it can lead to overfishing. However, simulation results also indicate that under the presence of process error, nonlinear least-squares methods provide biomass estimates with comparable bias, and have much poorer RMSE properties. We therefore conclude that the Kalman filter method provides superior parameter estimates in the face of process error.

Simulation results indicate that Schnute's form of the delay-difference equation can be used with the Kalman filter despite violation of the independent process error assumption. Although it appears difficult to estimate r directly with maximum-likelihood estimation, simulation results indicate that the Kalman filter can be used to estimate biomass when only $r = \sigma_p^2 / \sigma_m^2$ is known, rather than the individual variances.

It is important to acknowledge that simulation results will differ if natural mortality, catch levels, growth parameters, biomass, and recruitment, or error variances, are changed. We believe that customized simulation studies should be a routine part of production modeling. The simulations performed in this paper favored the Kalman filter in that the true measurement and process error variances were assumed to be known to the Kalman filter fitting algorithm. Under these circumstances, the performance of the Kalman filter method might be described as less than fully satisfactory.

There appears to be few published simulation studies describing the performance of production models in the presence of process error. Process error is particularly troublesome because errors are propagated through the years rather than being quickly forgotten as is measurement error. Our results, and those of Polacheck et al. (1993), indicate that parameter estimation in the presence of process error is inherently difficult for production models. However, the process error method of Polacheck et al. (1993) is regression-based and may not provide fully efficient parameter estimates. Because real data contain process error, we feel process error must be dealt with,

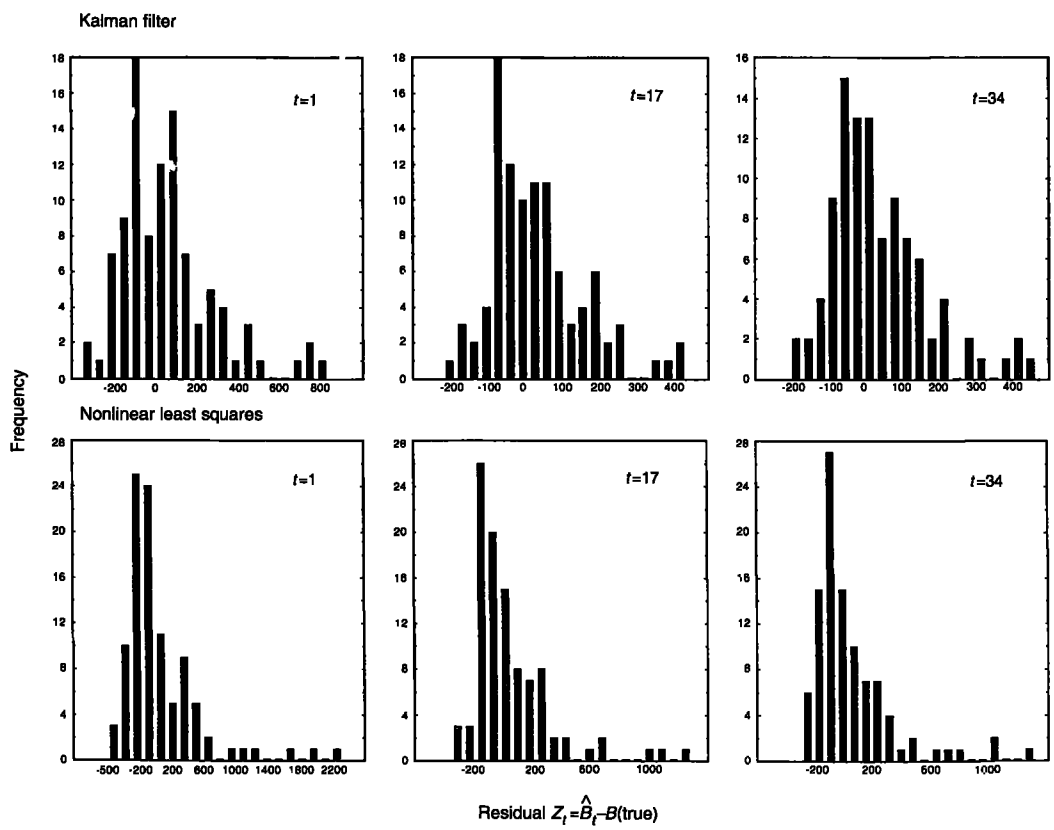

Figure 5

Histograms of the residual between estimated and true biomass, $Z_t = \hat{B}_t - B_t$ (true), for simulation S3, with $\sigma_m^2 = 500$, and $\sigma_p^2 = 500$. Top row is for the Kalman filter method; bottom row is for the nonlinear least-squares method; columns are for years t=1, 17, and 34.

at least to the extent of investigating the effects of such errors on modeling results.

One final note. In this paper we have not emphasized model output beyond biomass traces and basic parameter estimates. For example, annual estimates of fishing mortality rates and exploitation rates were obvious byproducts of the model fits we presented. The models presented here can be thought of as extensions to what we earlier called Stock Reduction Analysis (Kimura and Tagart, 1982; Kimura et al., 1984; Kimura 1985, 1988). These papers contain various methods of analysis that are useful for providing fishery management advice. For example, output from both the Kalman filter and nonlinear least-squares models can be treated as a constant recruitment model, and target ABC's (allowable biological catches) or target biomass levels can be made on the basis of this assumption.

Acknowledgments

This paper was inspired by J. J. Pella's lucid application of the Kalman filter method (Pella, 1993). We thank J. J. Pella for reviewing the manuscript, and providing numerous corrections, clarifications, and improvements. Also, we thank two anonymous reviewers for helpful comments and corrections.

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Appendix 1: Time series properties of the delay-difference equation

If recruitments $\{R_t\}$ are assumed to be uncorrelated with $E(R_t) = R_1$ and $V(R_t) = \sigma_p^2$, then the delay-difference equation (Eq. 2) is close to being a standard ARMA time series model (Box and Jenkins, 1970). Let $\phi_1 = (1+\rho)s_0, \phi_2 = -\rho s_0^2$, and $\theta = \rho\omega s_0$. Then Equation 2 can be written as

$$B_t = \phi_1 B_{t-1} + \phi_2 B_{t-2} + R_t - \theta R_{t-1}. \quad (1')$$

Defining $B_1 = (R_1 - \theta R_1)/(1-\phi_1-\phi_2)$, and substituting $R_t = n_t + R_1$ and $B_t = \tilde{B}_t + B_1$ into Equation 1', yields the process

$$\tilde{B}_t = \phi_1 \tilde{B}_{t-1} + \phi_2 \tilde{B}_{t-2} + n_t - \theta n_{t-1}, \quad (2')$$

where n_t the are now white noise. Thus under the assumption of constant growth parameters (ρ, ω), constant survival s_0, and random recruitment (R_t), the displaced process $\{\tilde{B}_t\}$ is an ARMA time series model with the same statistical properties of $\{B_t\}$.

The stationarity and invertibility of this time series can easily be established by considering the roots of the characteristic polynomials (see Box and Jenkins, 1970):

$$1 - \phi_1 X - \phi_2 X^2 = 0, \text{ and} \quad (3')$$

$$1 - \theta X = 0. \quad (4')$$

The stationarity and invertibility of $\{\tilde{B}_t\}$ follows from the observation that the roots $1/s_0$ and $1/(\rho s_0)$ of Equation 3' and $1/(\rho\omega s_0)$ of Equation 4' are all almost surely greater than unity.

Let $c_0 = (1-\theta\phi_1+\theta^2)\sigma_p^2$, and $c_1 = -\theta\sigma_p^2$. The autocovariance terms (i.e. the γ_k in standard notation) of the process $\{B_t\}$can then be shown to be

$$\begin{aligned}
\gamma_0 &= [c_0 + (1+\phi_2)\phi_1 c_1/(1-\phi_2)]/[(1-\phi_2^2) - \\
&\quad (1+\phi_2)\phi_1^2/(1-\phi_2)], \\
\gamma_1 &= (c_1 + \phi_1\gamma_0)/(1-\phi_2), \\
\gamma_2 &= \phi_1\gamma_1 + \phi_2\gamma_0, \text{ and} \\
\gamma_k &= \phi_1\gamma_{k-1} + \phi_2\gamma_{k-2}, \text{ for } k \geq 3.
\end{aligned}$$

Two interesting correlation coefficients that can be estimated using the γ_k are

$$\rho(B_t, R_t) = \sqrt{\sigma_r^2/\gamma_0} \text{ and } \rho(B_{t-k}, B_t) = \gamma_k/\gamma_0.$$

Appendix 2: Derivation of the log-likelihood when only the variance ratio $r = \sigma_p^2/\sigma_m^2$ is known.

Source: Pella, J. J. 1995. Auke Bay Laboratory, National Marine Fisheries Service, NOAA, 11305 Glacier Highway, Juneau, AK 99801. Personal communication.

We start with the usual log-likelihood when variances are assumed known

$$\ln(L(y,\Psi)) = -\frac{n}{2}\ln(2\pi) - \frac{1}{2}\sum_{t=1}^{n}\ln(f_t) - \frac{1}{2}\sum_{t=1}^{n}\frac{v_t^2}{f_t}. \quad (1'')$$

Substituting $f_t = \sigma_m^2 f_t^*$ into (1''), we have

$$\begin{aligned}
\ln(L(y,\Psi)) &= -\frac{n}{2}\ln(2\pi) - \frac{n}{2}\ln(\sigma_m^2) - \\
&\frac{1}{2}\sum_{t=1}^{n}\ln(f_t^*) - \frac{1}{2\sigma_m^2}\sum_{t=1}^{n}\frac{v_t^2}{f_t^*}.
\end{aligned} \quad (2'')$$

By differentiating with respect to σ_m^2, and by setting this result equal to zero, we obtain the estimator

$$\hat{\sigma}_m^2 = \frac{1}{n}\sum_{t=1}^{n}\frac{v_t^2}{f_t^*},$$

which we substitute into Equation 2'' to arrive at the function to be maximized

$$\begin{aligned}
\ln(L_c(y,\Psi)) &= -\frac{n}{2}[\ln(2\pi)+1] - \\
&\frac{1}{2}\sum_{t=1}^{n}\ln(f_t^*) - \frac{n}{2}\ln(\hat{\sigma}_m^2).
\end{aligned} \quad (3'')$$

Genetic variation and phylogenetic relationships of seven oreo species (Teleostei, Oreosomatidae) inferred from allozyme analysis

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Abstract.—Fishing pressure on deepwater oreosomatids has increased recently in Australian and New Zealand waters, and yet little is known about these fish. Genetic variation and phylogenetic relationships among Australian species was examined. Allozyme variation at 26 loci was examined in seven species: six from Australasia (*Allocyttus niger*, black oreo; *A. verrucosus*, warty oreo; *Neocyttus rhomboidalis*, spiky oreo; *Oreosoma atlanticum*, oxeye oreo; *Pseudocyttus maculatus*, smooth oreo; and a new species *Neocyttus* sp., rough oreo, infrequently captured with the smooth oreo and black oreo) and one from the North Atlantic (*N. helgae*). Two phenetic trees were constructed: an unweighted pair-group method with arithmetic averaging (UPGMA) tree derived from Nei's unbiased genetic distances and a distance-Wagner tree derived from Rogers' distances. A maximum parsimony cladistic analysis, with loci as characters and alleles as unordered states, was also performed. Outgroup species came from three related families: Acanthuridae, Berycidae, and Zeidae.

Mean heterozygosity per locus for the seven oreo species was relatively high for teleosts (11.8%), with *O. atlanticum* having the lowest value (8.3%) and *N.* sp. having the highest value (18.1%). *Oreosoma atlanticum* was the most divergent, with a mean genetic identity (I) of 0.371. The two most closely related species—*N. rhomboidalis* and *N. helgae* (I=0.973)—did not have any diagnostic allozyme loci, although the muscle protein patterns, after Coomassie blue staining, were distinctive. There was little evidence to support the inclusion of *A. niger* and *A. verrucosus* in the same genus; these two species had a genetic identity of 0.695. *Allocyttus niger* appeared to be more closely related to members of the genus *Neocyttus* than to *A. verrucosus*. Phenetic analyses revealed only minor differences in the Oreosomatidae grouping with respect to the three outgroups, whereas cladistic analyses revealed the Zeidae as the most closely related family.

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Oreos are laterally compressed, deep-bodied fish with large heads and large eyes. They are found in deepwater (below 500 m) over the continental slopes of most temperate, and some tropical and subtropical, regions. They appear to be more common in the Southern Hemisphere, but this may reflect a greater deepwater trawling effort in such regions as New Zealand and Australia.

The family Oreosomatidae (order Zeiformes) contains four genera. In a revision of oreos from the southern oceans, James et al. (1988) reported that, although the family is well defined and recognizable, its generic relationships are less clear: the genera *Allocyttus*, *Neocyttus*, and *Oreosoma* need redefining. The fourth genus, *Pseudocyttus*, is well defined and distinguishable.

Oreos are among the most abundant benthopelagic fishes on the continental slope of southern Australia, yet little is known of their biology, stock structure, or phylogeny. In New Zealand waters, oreos have been fished commercially since the late 1970's. A peak catch of 26,500 metric tons (t) was taken in 1981–82; the fishery has since moderated to around 19,000 t per year (Lyle et al., 1992). The New Zealand fishery comprises two main species: the smooth oreo (*Pseudocyttus maculatus* Gilchrist, 1906) and the black oreo (*Allocyttus niger* James et al., 1988). In Australian waters oreos have been caught largely as a bycatch of the deepwater fisheries for blue grenadier (*Macruronus novaezelandiae* (Hector, 1871)) and orange roughy (*Hoplostethus atlanticus* Collett, 1889) and were generally discarded. However, recent drastic reductions in orange roughy catch limits, the development of new deepwater fishing grounds off southern Tasmania, and growing market awareness have resulted in increased targeting of species aggregations and a rapid growth and retention of Australian catches of oreos (Lyle et al., 1992). The retained catch of oreo from the southeast fishery (the main deepwater trawl fishery in Australia) was less than 100 metric tons (t) per annum before 1987, around 2,000 t in 1990 and 1991, over 3,000 t in 1992, and over 1,000 t in 1993 and 1994 (Australian Fisheries Management Authority[1]). Actual catches are prob-

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[1] Australian Fisheries Management Authority. 1995. Burns Centre, 28 National Circuit, Forrest Act 2603, Australia. Unpubl. data.

ably higher because some are not reported and others discarded (Lyle et al., 1992). The recorded tonnages of individual species are unreliable owing to confusion over species identification in the catch log books. As in New Zealand, the smooth and black oreos dominate the Australian catch, whereas the spiky oreo (*Neocyttus rhomboidalis* Gilchrist, 1906) and the warty oreo (*Allocyttus verrucosus* (Gilchrist, 1906)) are also important. A fifth species, the oxeye oreo (*Oreosoma atlanticum* Cuvier, 1829), is commonly caught but discarded because of its small size and low commercial value.

This paper presents the results of an allozyme survey of the five described Australasian species (*Allocyttus niger*, *A. verrucosus*, *Neocyttus rhomboidalis*, *Oreosoma atlanticum*, and *Pseudocyttus maculatus*) and a new species (the rough oreo, *Neocyttus* sp., Yearsley and Last[2]) often captured with *A. niger* and *P. maculatus*. A third *Neocyttus* species, *N. helgae* (Holt and Byrne, 1908), from the North Atlantic, was also examined.

Oreosomatids not included in this study are the North Pacific *Allocyttus folletti* Myers, 1960, the southern Atlantic and Indian Ocean *Allocyttus guineensis* Trunov and Kukuev in Trunov, 1982, and the Indian Ocean *Neocyttus acanthorhyncus* (Regan, 1908). Another member of the family, the Southern Ocean *Pseudocyttus nemotoi* (Abe, 1957), was recently resurrected by Miller (1993).

The intrarelationships of zeiforms have not been discussed in the literature; thus outgroup selection for this phylogenetic study is difficult. Many authors consider the beryciforms to be more primitive than the zeiforms but closely related to them (e.g. Greenwood et al., 1966). Zehren (1979) found the Berycidae to be more primitive than the remaining beryciform families and, thus, a berycid may be a suitable outgroup. However, Rosen (1984) dramatically changed the placement of the zeiforms, including them in the order Tetraodontiformes, with the Caproidae as the sister group to all other tetraodontiforms (the caproids' placement within the Zeiformes was questioned by others [Tighe and Keene, 1984]). A caproid may therefore be a suitable outgroup. Furthermore, Rosen placed the zeids immediately before the oreosomatids in his new division Zeomorphi. He used "acanthurids plus chaetodontids" to establish character polarities. Consequently, a zeid or an acanthurid are also possible outgroups. In the absence of caproid specimens, three outgroups were selected for analysis: the berycid *Beryx splendens* Lowe, 1833 (alfonsino), the zeid *Cyttus australis* (Richardson, 1843) (silver dory), and the acanthurid *Naso tuberosus* Lacepède, 1802 (humphead unicornfish).

Genetic variation present in the Australasian oreosomatids and diagnostic allozyme loci for each species are presented in this paper to assist in future management plans for the developing deepwater fishery. The phylogenetic relationships of previously known species, as well as a new species from Australia and a species from the North Atlantic, are discussed in an effort to understand more fully the systematics of the family Oreosomatidae.

Materials and methods

Samples of muscle and liver tissue were collected from seven oreosomatids (*Allocyttus niger*, *Allocyttus verrucosus*, *Neocyttus* sp. (voucher specimen: CSIRO H2865.01), *Neocyttus helgae*, *Neocyttus rhomboidalis*, *Oreosoma atlanticum* and *Pseudocyttus maculatus*), and from the three outgroup species (*Beryx splendens*, *Cyttus australis*, and *Naso tuberosus*). Sample details and species abbreviations are given in Table 1.

Whole fish were frozen after capture and transported frozen to the laboratory, where tissues were dissected and held at –80°C. Small pieces of tissue were placed in 1.5-mL microcentrifuge tubes, homogenized manually with a few drops of distilled water, and spun at 11,000 rpm in a microcentrifuge for 2 minutes. The supernatant was used for electrophoresis.

Allozyme variation was examined with three gel systems: gel system A—Helena Titan III cellulose acetate plates run at 200 V with a Tris-glycine buffer (0.020 M tris and 0.192 M glycine, Hebert and Beaton[3]); gel system B—Helena Titan III cellulose acetate plates run at 150 V with a Tris-citrate buffer (0.075 M tris and 0.025 M citric acid, pH 7.0); gel system C—8% Connaught starch gels with a histidine/citrate buffer (gel buffer: 0.005 M histidine HCl, pH 7.0; electrode buffer: 0.41 M trisodium citrate, pH 7.0). Standard staining procedures were followed (Richardson et al., 1986; Hebert and Beaton[3]).

In all, 19 enzymes, representing 27 loci, were examined (Table 2) and allele frequencies determined (Table 3). However, the locus *GPI-A** was not included in the phylogenetic analyses because of poor resolution in three species (*A. niger*, *N.* sp., and *P. maculatus*). Loci and alleles are designated by the nomenclature system outlined in Shaklee et al. (1990), except that peptidase loci were identified as *PEP1** and

[2] Yearsley, G. K., and P. R. Last. 1995. CSIRO Division of Fisheries, Castray Esplanade, Hobart, Tasmania 7000, Australia.

[3] Hebert, P. D. N., and M. J. Beaton. 1989. Methodologies for allozyme analysis using cellulose acetate electrophoresis: a practical handbook. Helena Laboratories, Beaumont, Texas.

Table 1

Collection details for specimens analyzed in this study and species abbreviations adopted in this paper.

Species	Abbrev.	Collection area	No. of fish	Collection date
Allocytus niger	AN	Tasmania	202	May 1993
		South Tasman Rise	41	January/June 1992
		New Zealand	100	January 1994
			Total = 343	
Allocytus verrucosus	AV	Western Australia	336	January 1991/March 1992/August 1993
		Great Australian Bight	134	March–June 1992
		Tasmania	126	February 1992/November 1992/April 1994
		New South Wales	32	April 1994
		Lord Howe Rise	83	June 1992
		South Africa	11	September 1993
			Total = 722	
Neocyttus sp.	NA	Southern Tasmania	Total = 16	May 1993
Neocyttus helgae	NH	North Atlantic (ca. 61°39'N, 13°11'W)	Total = 35	February 1993
Neocyttus rhomboidalis	NR	Western Australia	145	October 1993
		Great Australian Bight	31	March 1992
		South Australia	114	October 1993
		Tasmania	451	May 1993–April 1994
		New South Wales	59	February/April 1994
		Lord Howe Rise	98	August 1993
		New Zealand	101	January 1994
			Total = 999	
Oreosoma atlanticum	OA	Southern Tasmania	19	October 1994
		Great Australian Bight	6	March 1992
			Total = 25	
Pseudocyttus maculatus	PM	Western Australia	99	October 1993
		Tasmania	200	May 1993
		New Zealand	100	January 1994
			Total = 399	
Beryx splendens	BS	Western Australia	Total = 6	June 1992
Cyttus australis	CA	Gabo Island, Bass Strait	Total = 6	September 1994
Naso tuberosus	NT	Queensland	Total = 2	March 1994

*PEP2**. Multiple loci encoding the same enzyme were designated by consecutive numbers, with '1' denoting the fastest migrating system. Alleles within each locus were identified by the anodal electrophoretic mobility (rounded to nearest 5%, except for *FH*113*) of their product relative to that of the most common allele observed in the spiky oreo, *N. rhomboidalis*, which was designated '100' (cathodal migration being designated negative). In addition, muscle protein patterns were examined after Coomassie Blue staining. These results are not included in the phylogenetic analyses because of uncertain homologies between species, but patterns were species-specific. The *CK-A** product was one of several protein products visualized by this general protein stain. The mean sample sizes per locus for the seven oreo species had a wide range (from 14 to 598, Table 4) because polymorphic loci for the four main commercial species (*A. niger*, *A. verrucosus*, *N. rhomboidalis*, and *P. maculatus*) were examined in large numbers for stock delineation studies (unpubl. data).

Species relationships were analyzed with BIOSYS-1 software (Swofford and Selander, 1981) and PAUP (phylogenetic analysis using parsimony) 3.0s soft-

Table 2

Details of enzymes used in this study. EC = Enzyme Committee; Tissue: l = liver, m = muscle; Gel: A = cellulose acetate with a Tris-glycine buffer, B = cellulose acetate with a Tris-citrate buffer, C = starch (see text). Multiple loci encoding for the same enzyme are designated by consecutive numbers, with '1' denoting the fastest migrating system. # = loci not included in analyses (see text).

Enzyme	EC number	Locus abbrev.	Locus no.	Tissue	Gel
Aspartate aminotransferase	2.6.1.1	*sAAT-1**	1	m	A
		*sAAT-2**	2	l	A
		*mAAT**	3	m/l	A
Alcohol dehydrogenase	1.1.1.1	*ADH**	4	l	A
Adenylate kinase	2.7.4.3	*AK**	5	m	B
Creatine kinase	2.7.3.2	*CK-A**	6	m	A
Esterase-D (UV, umb. acetate)	3.1.-.-	*ESTD**	7	m/l	A
Fumarate hydratase	4.2.1.2	*FH**	8	m	A
Glyceraldehyde-3-phosphate dehydrogenase	1.2.1.12	*GAPDH-1**	9	m	B
		*GAPDH-2**	10	m	B
Glucose-6-phosphate isomerase	5.3.1.9	*GPI-A**	#	m	A
		*GPI-B**	11	m	A
Glycerol-3-phosphate dehydrogenase	1.1.1.8	*G3PDH-2**	12	m	B/C
Isocitrate dehydrogenase	1.1.1.42	*sIDHP**	13	m	C
		*mIDHP**	14	l	B
l-Lactate dehydrogenase	1.1.1.27	*LDH-C**	15	l	A
		*LDH-1**	16	l	A
		*LDH-2**	17	m	A
Malate dehydrogenase	1.1.1.37	*sMDH-1**	18	m	C
		*sMDH-2**	19	m	C
Mannose-6-phosphate isomerase	5.3.1.8	*MPI**	20	l	A
Peptidase (l-leucyl-l-tyrosine)	3.4.-.-	*PEP1-1**	21	l	A
Peptidase (leu-leu-leu)	3.4.-.-	*PEP2**	22	l	A
Phosphogluconate dehydrogenase	1.1.1.44	*PGDH**	23	m	B/C
Phosphoglucomutase	5.4.2.2	*PGM-1**	24	l	A
		*PGM-2**	25	m/l	A
Superoxide dismutase	1.15.1.1	*sSOD**	26	l	A
General protein		*PROT*	#	m	A

ware (Swofford, 1991). Two phenetic methods of analysis of genetic distance obtained from the allele frequency data were examined with BIOSYS-1. First, Nei's (1978) unbiased genetic distance measure between each species was calculated, and trees were constructed by cluster analysis and the unweighted pair-group method with arithmetic averaging (UPGMA). Second, Rogers' (1972) distance measures were calculated and trees constructed by the distance-Wagner procedure (Farris, 1972) with outgroup rooting. The Wagner procedure, unlike the UPGMA analysis, does not assume a constant rate of evolution. For the cladistic maximum-parsimony analysis (PAUP), the loci were coded as characters and the most common alleles as unordered character states. When two common alleles were at equal frequencies (0.5), they were treated as multiple states and interpreted in the analysis as a polymorphism. The "branch and bound" and "exhaustive" routines were applied to search for the most parsimonious tree.

Results

Several measures of genetic variation were examined (Table 4). Four of the seven oreo species had average sample sizes per locus exceeding 200, but the average sample size for three species was less than 30. Two of the genetic variation parameters, mean number of alleles per locus and percentage of variable loci, are clearly dependent on sample size: both will increase as increasingly rare alleles are detected. Percentage of polymorphic loci, especially with use of the 0.95 rather than 0.99 criterion, will be less sample-size dependent, and mean heterozygosity per locus is little affected by rare alleles. In fact, estimates of heterozygosity (and genetic distance) are influenced more by numbers of loci than by numbers of individuals (Nei, 1978; Gorman and Renzi, 1979), and all estimates of heterozygosity given here are based on the same 26 loci. All oreos showed high levels of variation, with average

Table 3

Allele frequencies. Alleles are presented as allozyme electrophoretic mobilities relative to the most common allele recorded from spiky oreo (NR), *Neocyttus rhomboidalis*. Locus details are presented in Table 2 and species abbreviations are presented in Table 1. *n* = number of individuals scored, — = allele not detected, # = locus not scored due to poor resolution.

			Oreosomatids							Outgroup		
Locus		Allele	AN	AV	NA	NH	NR	OA	PM	BS	CA	NT
1	*sAAT-1**	115	—	—	—	—	—	1.000	—	—	—	—
		110	—	1.000	0.192	0.121	0.246	—	—	—	—	—
		100	1.000	—	0.808	0.879	0.754	—	0.962	—	—	—
		80	—	—	—	—	—	—	0.038	—	—	—
		75	—	—	—	—	—	—	—	—	1.00	—
		65	—	—	—	—	—	—	—	1.00	—	—
		35	—	—	—	—	—	—	—	—	—	1.00
		n	24	24	13	33	778	21	395	6	6	2
2	*sAAT-2**	125	—	—	0.125	0.014	0.001	—	—		—	
		120	—	—	—	—	0.001	—	—		—	
		100	1.000	0.994	0.875	0.986	0.996	—	0.988		—	
		90	—	—	—	—	—	1.000	—		—	
		80	—	0.003	—	—	0.002	—	0.008		0.83	
		60	—	0.003	—	—	—	—	0.004		—	
		55	—	—	—	—	—	—	—		0.17	
		n	226	178	16	35	422	21	248	#	6	#
3	*mAAT**	100	—	—	—	—	0.001	—	—	—	—	—
		0	—	—	—	—	0.007	—	—	—	—	—
		–100	1.000	1.000	0.962	0.958	0.884	1.000	0.959	—	—	—
		–110	—	—	—	—	—	—	—	—	—	1.00
		–150	—	—	—	—	—	—	—	1.00	—	—
		–200	—	—	0.038	0.042	0.107	—	0.041	—	1.00	—
		–250	—	—	—	—	<0.001	—	—	—	—	—
		n	226	178	13	36	971	25	413	6	6	2
4	*ADH**	125	—	—	—	—	—	—	1.000	—	—	—
		100	1.000	1.000	1.000	1.000	1.000	—	—	—	—	—
		35	—	—	—	—	—	0.024	—	—	—	—
		30	—	—	—	—	—	—	—	1.00	—	—
		10	—	—	—	—	—	0.976	—	—	1.00	—
		–30	—	—	—	—	—	—	—	—	—	1.00
		n	226	178	16	35	422	21	248	6	6	2
5	*AK**	100	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.00	—	1.00
		80	—	—	—	—	—	—	—	—	1.00	—
		n	226	24	13	23	24	25	248	6	6	2
6	*CK-A**	110	—	0.845	0.269	—	<0.001	—	—	—	—	—
		100	0.872	0.155	0.731	1.000	0.952	1.000	—	—	—	—
		90	0.128	—	—	—	0.047	—	1.000	—	—	—
		80	—	—	—	—	<0.001	—	—	—	—	—
		75	—	—	—	—	—	—	—	—	—	1.00
		60	—	—	—	—	—	—	—	1.00	—	—
		50	—	—	—	—	—	—	—	—	1.00	—
		n	337	700	13	35	987	25	248	6	6	2
7	*ESTD**	135	—	—	—	—	—	—	—	—	1.00	—
		120	—	—	—	—	—	—	—	1.00	—	—
		115	1.000	1.000	0.846	—	—	—	1.000	—	—	1.00
		100	—	—	0.154	1.000	0.998	1.000	—	—	—	—
		85	—	—	—	—	0.002	—	—	—	—	—
		n	226	178	13	23	422	22	248	4	2	2

Table 3 (continued)

			Oreosomatids							Outgroup		
Locus		Allele	AN	AV	NA	NH	NR	OA	PM	BS	CA	NT
8	*FH**	120	0.003	—	—	—	—	—	—	—	—	—
		115	—	0.002	—	—	—	—	0.007	—	—	—
		113	—	—	—	—	0.006	—	—	—	—	—
		110	—	—	—	0.030	—	—	0.027	—	—	—
		100	0.990	0.747	0.962	0.940	0.982	—	0.838	—	—	—
		95	—	—	—	—	—	—	—	—	—	1.00
		80	0.007	0.247	0.038	0.030	0.011	1.000	0.128	1.00	—	—
		65	—	0.004	—	—	—	—	—	—	1.00	—
		n	294	672	13	33	935	23	413	6	6	2
9	*GAPDH-1**	105	—	—	—	—	—	—	—	1.00	—	—
		100	1.000	1.000	1.000	1.000	1.000	—	1.000	—	1.00	—
		90	—	—	—	—	—	1.000	—	—	—	1.00
		n	24	24	13	23	24	22	24	6	6	2
10	*GAPDH-2**	100	1.000	1.000	1.000	1.000	1.000	1.000	1.000	—	—	—
		75	—	—	—	—	—	—	—	1.00	1.00	—
		30	—	—	—	—	—	—	—	—	—	1.00
		n	24	24	16	23	24	25	24	6	6	2
11	*GPI-B**	140	—	0.001	—	—	0.004	—	—	—	—	—
		125	—	—	—	—	—	—	—	0.50	—	0.50
		120	—	0.071	—	—	—	—	—	—	—	—
		115	—	—	—	0.030	—	—	—	—	—	—
		110	—	—	—	—	—	—	—	0.42	—	0.50
		100	1.000	0.584	0.692	0.849	0.550	1.000	1.000	—	—	—
		95	—	—	—	—	—	—	—	0.08	—	—
		85	—	—	—	—	—	—	—	—	0.33	—
		80	—	0.343	0.269	0.121	0.446	—	—	—	—	—
		65	—	—	—	—	—	—	—	—	0.67	—
		60	—	0.001	0.039	—	<0.001	—	—	—	—	—
		n	226	694	13	33	983	25	248	6	6	2
12	*G3PDH-2**	165	—	—	—	—	0.002	—	—	—	—	—
		160	—	—	—	0.080	—	—	—	—	—	—
		145	—	—	—	—	—	1.000	—	—	—	—
		130	0.118	0.007	—	—	0.052	—	—	—	—	—
		100	0.561	0.526	0.846	0.355	0.900	—	—	—	—	—
		75	0.321	0.459	0.154	0.565	0.046	—	—	1.00	—	—
		70	—	—	—	—	—	—	1.000	—	—	—
		65	—	0.008	—	—	—	—	—	—	—	—
		25	—	—	—	—	—	—	—	—	1.00	—
		15	—	—	—	—	—	—	—	—	—	1.00
		n	279	291	13	31	918	18	248	6	6	2
13	*sIDHP**	120	—	—	—	—	—	1.000	—	—	—	—
		110	—	—	—	—	—	—	—	—	1.00	—
		105	—	—	—	—	—	—	—	1.00	—	—
		100	1.000	1.000	1.000	1.000	0.998	—	1.000	—	—	—
		65	—	—	—	—	—	—	—	—	—	1.00
		50	—	—	—	—	0.002	—	—	—	—	—
		n	226	178	13	18	494	21	248	6	6	2
14	*mIDHP**	105	—	—	—	—	—	1.000	—	—	—	—
		100	1.000	1.000	1.000	1.000	1.000	—	1.000	—	—	—
		95	—	—	—	—	—	—	—	0.33	0.08	—
		85	—	—	—	—	—	—	—	0.42	0.92	1.00
		75	—	—	—	—	—	—	—	0.25	—	—
		n	226	178	15	22	422	24	248	6	6	2

Table 3 (continued)

			Oreosomatids							Outgroup		
Locus		Allele	AN	AV	NA	NH	NR	OA	PM	BS	CA	NT
15	*LDH-C**	100	1.000	1.000	1.000	1.000	0.994	—	0.802	—	0.90	
		85	—	—	—	—	0.006	1.000	0.198	—	0.10	
		80	—	—	—	—	—	—	—	1.00	—	
		n	226	178	16	35	494	24	413	4	5	#
16	*LDH-1**	100	1.000	1.000	0.594	1.000	0.999	—	0.776	—	—	—
		40	—	—	0.406	—	0.001	—	0.224	1.00	—	—
		–15	—	—	—	—	—	1.000	—	—	1.00	—
		–35	—	—	—	—	—	—	—	—	—	1.00
		n	226	178	16	35	422	25	415	6	6	2
17	*LDH-2**	100	0.052	1.000	1.000	1.000	1.000	1.000	1.000	1.00	—	—
		50	0.948	—	—	—	—	—	—	—	—	—
		30	—	—	—	—	—	—	—	—	—	1.00
		–35	—	—	—	—	—	—	—	—	1.00	—
		n	336	178	13	23	422	25	248	6	6	2
18	*sMDH-1**	130	—	—	—	—	—	—	—	1.00	—	—
		125	—	—	—	—	—	1.000	—	—	—	—
		110	—	1.000	—	—	—	—	—	—	—	1.00
		100	1.000	—	1.000	1.000	1.000	—	1.000	—	—	—
		50	—	—	—	—	—	—	—	—	1.00	—
		n	226	178	13	23	422	22	248	6	6	2
19	*sMDH-2**	160	—	—	—	—	—	1.000	—	—	—	—
		100	1.000	1.000	1.000	1.000	1.000	—	1.000	—	1.00	—
		95	—	—	—	—	—	—	—	—	—	1.00
		80	—	—	—	—	—	—	—	1.00	—	—
		n	226	178	16	23	422	25	248	6	6	2
20	*MPI**	110	—	0.219	—	0.071	0.049	—	—		—	—
		100	—	0.765	0.318	0.804	0.779	0.476	0.122		—	1.00
		90	1.000	0.016	0.682	0.125	0.170	0.524	0.878		1.00	—
		80	—	—	—	—	0.002	—	—		—	—
		n	226	276	11	28	903	21	388	#	6	2
21	*PEP1-1**	100	1.000	1.000	1.000	1.000	1.000	1.000	—	1.00	—	—
		90	—	—	—	—	—	—	0.998	—	—	—
		85	—	—	—	—	—	—	—	—	1.00	—
		80	—	—	—	—	—	—	0.002	—	—	1.00
		n	226	178	13	23	422	25	248	6	6	2
22	*PEP2**	105	—	1.000	—	—	—	—	—		—	
		100	1.000	—	1.000	1.000	0.999	1.000	0.507		—	
		85	—	—	—	—	0.001	—	0.493		—	
		80	—	—	—	—	—	—	—		1.00	
		n	226	24	13	23	422	21	402	#	6	#
23	*PGDH**	160	—	—	0.750	—	—	—	—	—	—	—
		150	—	—	0.208	—	—	—	—	—	—	—
		130	—	—	0.042	—	<0.001	—	—	—	—	—
		120	—	—	—	—	0.005	—	—	—	—	—
		115	—	—	—	—	—	1.000	—	—	—	—
		110	0.644	—	—	—	0.184	—	—	—	—	—
		105	—	—	—	—	—	—	—	1.00	—	—
		100	0.286	1.000	—	1.000	0.803	—	0.934	—	0.83	—
		90	—	—	—	—	0.007	—	0.033	—	0.17	—

Table 3 (continued)

			Oreosomatids							Outgroup		
Locus		Allele	AN	AV	NA	NH	NR	OA	PM	BS	CA	NT
		85	—	—	—	—	—	—	0.033	—	—	—
		75	0.070	—	—	—	—	—	—	—	—	—
		60	—	—	—	—	—	—	—	—	—	1.00
		n	287	178	13	31	916	14	412	6	6	2
24	*PGM-1**	115	—	—	—	—	<0.001	—	—		—	—
		110	—	—	—	—	0.004	—	—		—	—
		105	—	0.137	—	—	0.099	—	—		—	—
		100	0.011	0.624	—	0.517	0.609	—	—		0.08	—
		95	0.696	0.222	0.433	0.450	0.242	—	0.017		0.83	—
		90	0.273	0.017	0.500	0.033	0.043	—	0.623		0.08	—
		85	0.020	—	0.067	—	0.003	0.250	0.025		—	—
		80	—	—	—	—	—	0.500	0.335		—	—
		75	—	—	—	—	—	0.250	—		—	1.00
		n	276	259	15	30	911	2	395	#	6	2
25	*PGM-2**	130	—	0.005	—	—	—	—	—	—	—	—
		125	—	—	—	—	0.002	—	—	—	—	—
		120	0.006	0.220	0.077	0.043	0.029	0.060	0.002	—	—	—
		100	0.591	0.749	0.923	0.943	0.925	0.840	0.874	—	—	—
		95	—	—	—	—	—	—	—	1.00	—	—
		80	0.282	0.016	—	0.014	0.040	0.060	0.123	—	—	—
		65	0.111	0.009	—	—	0.004	0.040	—	—	—	—
		60	—	—	—	—	—	—	—	—	1.00	—
		50	0.011	—	—	—	—	—	—	—	—	—
		40	—	—	—	—	—	—	—	—	—	0.75
		20	—	—	—	—	—	—	—	—	—	0.25
		n	330	676	13	35	972	25	414	6	6	2
26	*SOD**	180	—	—	—	0.014	—	0.021	0.374	—	—	—
		140	0.204	1.000	0.500	0.057	0.487	0.333	0.626	—	—	—
		130	—	—	—	—	—	—	—	—	1.00	—
		100	0.796	—	0.500	0.929	0.513	—	—	—	—	—
		60	—	—	—	—	—	0.646	—	1.00	—	—
		0	—	—	—	—	—	—	—	—	—	1.00
		n	329	178	19	35	983	24	412	6	6	2
Locus not included in analyses (see text):												
*GPI-A**		150		0.012		—	—	—		—	—	—
		140		0.002		—	—	—		—	—	—
		130		0.203		0.016	0.007	—		—	—	—
		125		0.005		—	0.014	—		—	—	—
		115		0.753		0.031	0.338	—		—		—
		110		—		0.484	—	—		—	—	—
		100		0.017		0.469	0.610	1.000		—	—	—
		95		0.007		—	—	—		—	—	—
		90		0.002		—	0.014	—		—	—	—
		85		—		—	0.016	—		—	—	—
		75		—		—	0.001	—		—	—	—
		45		—		—	—	—		1.00	—	—
		20		—		—	—	—		—	—	1.00
		10		—		—	—	—		—	1.00	—
		N	#	711	#	32	987	25	#	6	6	6

Table 4

Comparison of genetic statistical information for 26 loci scored in each oreosomatid species. A locus is considered variable when more than one allele is present, and polymorphic when the frequency of the most common allele is 0.95 or less. Mean and standard errors are presented. Mean heterozygosity per locus is Nei's (1978) unbiased estimate. Species abbreviations are defined in Table 1.

Species	Mean sample size per locus	Mean no. alleles per locus	Percentage of loci		Mean heterozygosity
			Variable	Polymorphic	
AN	228.1 ±16.7	1.6 ±0.2	30.8	26.9	0.105 ±0.038
AV	237.7 ±40.9	1.8 ±0.3	30.8	26.9	0.116 ±0.039
NA	14.0 ±0.3	1.7 ±0.1	53.8	46.2	0.181 ±0.041
NH	28.7 ±1.1	1.7 ±0.2	38.5	30.8	0.093 ±0.032
NR	597.6 ±63.1	2.5 ±0.3	65.4	34.6	0.127 ±0.037
OA	22.0 ±1.0	1.3 ±0.2	19.2	15.4	0.083 ±0.041
PM	297.8 ±22.0	1.8 ±0.2	50.0	34.6	0.121 ±0.034

heterozygosities ranging from 0.083 in *O. atlanticum* to 0.181 in *N.* sp.: the four commercial species (*A. niger*, *A. verrucosus*, *N. rhomboidalis*, and *P. maculatus*) had values ranging from 0.105 to 0.127. Despite the lowest mean sample size, *N.* sp. showed the highest proportion of polymorphic loci (46.2%) and the highest average heterozygosity.

Oreosoma atlanticum was the most divergent of the oreosomatids (Table 5). Its average genetic identity (Nei, 1978) (0 indicates complete dissimilarity and 1 complete similarity) with the other species was 0.371 (range 0.313 to 0.426 for 26 loci). The two most similar species were *N. rhomboidalis* and *N. helgae*, with a high genetic identity of 0.973. The third *Neocyttus* species, *N.* sp., had a relatively lower identity with the other two *Neocyttus* species: 0.903 with *N. rhomboidalis* and 0.884 with *N. helgae*. The two *Allocyttus* species had a genetic identity of only 0.695.

The three outgroup species were very divergent from both the oreosomatids and each other (Table 5). The acanthurid *N. tuberosus* diverged most from the oreosomatids, with an average genetic identity of 0.112 (range 0.085 to 0.180, from 23 loci). *Cyttus australis* had a mean identity with the oreosomatids of 0.171 (range 0.108 to 0.199, 26 loci) and *B. splendens* a mean identity of 0.164 (range 0.115 to 0.222, 22 loci).

In the acanthurid *N. tuberosus*, 16 of the 23 scorable loci were diagnostic (no shared alleles with any oreosomatid); in the zeid *C. australis*, 15 of 26 loci; and in the berycid *B. splendens*, 15 of 22 loci were diagnostic (Table 3). In a comparison of oreosomatids with one another, *O. atlanticum* had eleven diagnostic loci, *P. maculatus*, three, *A. verrucosus*, two, whereas the other four species revealed that only the muscle protein patterns were diagnostic (Table 3; Fig. 1). However, when the seven oreosomatids were compared pair-wise, each pair (except *N. rhomboidalis* with either *N.* sp. or *N. helgae*) had at least one and up to fourteen diagnostic allozyme loci, other than the general protein difference (Table 6). With the addition of between 4 and 13 loci showing significant allele frequency differentiation ($P<0.05$, with Bonferroni adjustment for multiple tests) (Table 6), even the closely related *N. rhomboidalis* and *N. helgae* were found to differ at five loci (*FH**, *GPI-A**, *GPI-B**, *G3PDH-2**, and *sSOD**) and *N. rhomboidalis* and *N.* sp. at eight loci (*sAAT-2**, *CK-A**, *ESTD**, *GPI-B**, *LDH-1**, *MPI**, *PGDH**, and *PGM-1**). The locus *PGDH** was diagnostic between *N.* sp. and *N. helgae*, with significant allele frequency differences at a further seven loci (*CK-A**, *ESTD**, *G3PDH-2**, *LDH-1**, *MPI**, *PGM-1**, and *sSOD**). *Oreosoma atlanticum* differed from

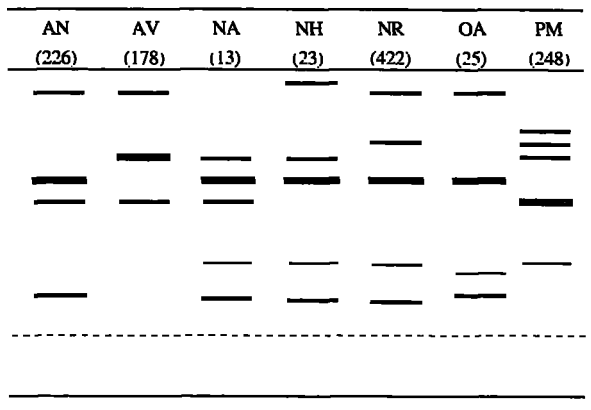

Figure 1

Banding pattern observed for each oreosomatid species with a general protein Coomassie blue stain (*PROT**). Dashed line indicates sample origin. Boldest band represents most common *CK-A** product in each species. Species abbreviations are defined in Table 1. Numbers in parentheses are number of individuals scored.

Table 5

Pairwise comparison of Nei's (1978) unbiased genetic identity (above diagonal) and genetic distance (below diagonal) between species for 26 loci, except for BS (22 loci) and NT (23 loci). Species abbreviations are defined in Table 1.

Species	AN	AV	NA	NH	NR	OA	PM	BS	CA	NT
AN	—	0.695	0.903	0.852	0.841	0.342	0.738	0.118	0.199	0.095
AV	0.364	—	0.773	0.761	0.788	0.313	0.659	0.183	0.169	0.180
NA	0.102	0.257	—	0.884	0.903	0.402	0.764	0.184	0.177	0.108
NH	0.160	0.273	0.123	—	0.973	0.426	0.711	0.174	0.180	0.085
NR	0.173	0.238	0.102	0.027	—	0.422	0.711	0.152	0.174	0.086
OA	1.073	1.161	0.913	0.853	0.864	—	0.319	0.222	0.108	0.128
PM	0.304	0.417	0.269	0.341	0.342	1.143	—	0.115	0.191	0.100
BS	2.138	1.700	1.694	1.749	1.885	1.505	2.159	—	0.068	0.095[1]
CA	1.614	1.780	1.734	1.714	1.748	2.227	1.653	2.689	—	0.042
NT	2.353	1.714	2.229	2.465	2.456	2.057	2.303	2.355[1]	3.168	—

[1] 21 loci common to both species.

the other six species at 17 to 22 loci, in addition to the general protein difference.

Two loci—*AK** and *GAPDH-2**—were invariant across all seven oreosomatid species, but only *GAPDH-2** differed in all three outgroup species; *AK** was different only in *C. australis*. These loci are consistent with a monophyletic origin of the oreosomatids. Three loci (*GAPDH-1**, *mIDHP**, and *sMDH-2**) were monomorphic for the same allele in six of the seven oreo species, with *O. atlanticum* fixed for alternative alleles; these putative synapomorphies indicate that these six species are probably monophyletic.

It is therefore not surprising to find that *O. atlanticum* was clearly separated from the other oreosomatid species on the phenogram constructed by the UPGMA method from Nei's (1978) unbiased genetic distances (Fig. 2). Branching order and significance of the branching nodes did not differ with the choice of outgroup. The three *Neocyttus* species and *A. niger* formed a distinct cluster. There was a very close association of the Southern Hemisphere *N. rhomboidalis* and the Northern Hemisphere *N. helgae*.

The phylogenetic tree constructed by the distance-Wagner procedure from Rogers' (1972) distances, rooted by the outgroup *C. australis*, also showed the divergence of *O. atlanticum* from the other oreosomatids (Fig. 3). Although the closeness of *N. rhomboidalis* and *N. helgae* was maintained, and again the two *Allocyttus* species were not grouped together, *P. maculatus* was found to be grouped with *A. niger* and *N.* sp. A similar tree was produced, by this procedure, with *N. tuberosus* as the outgroup, whereas the tree produced with *B. splendens* as the outgroup resembled those from the UPGMA cluster analyses (with *P. maculatus* divergent from the *Neocyttus* and *Allocyttus* species); a similar tree was produced when all three outgroups were applied together.

Cladistic analysis (PAUP) with all three outgroup species together produced 55 most parsimonious trees, all of which showed the divergence of *O. atlanticum* from other members of the family, but failed to define any structure for the other six species. Analysis with *C. australis* as the outgroup produced eleven most parsimonious trees of 52 units in

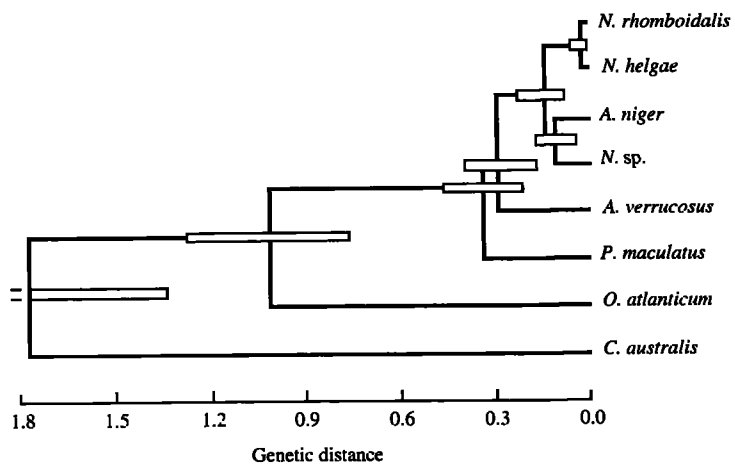

Figure 2

Unweighted pair-group method with arithmetic averaging (UPGMA) phenogram constructed from Nei's (1978) unbiased genetic distance. Open boxes represent standard errors (Nei, 1987) of the branch nodes.

Table 6

Allozyme differences between pairs of oreo species. Above the diagonal: diagnostic loci (no shared alleles); below the diagonal: loci at which significant differences (χ^2 test, $P<0.05$ with Bonferroni adjustment) exist in allele frequencies at loci where alleles are shared, including the GPI-*A** locus. Note that the general protein (PROT) staining patterns (not included here but see Fig. 1) are diagnostic for all species. Total numbers are shown in bold and each locus is identified by the reference number shown in Tables 2 and 3. Species abbreviations are defined in Table 1.

	AN	AV	NA	NH	NR	OA	PM
AN		**3** 1,18,22	**1** 23	**1** 7	**1** 7	**13** 1,2,4, 7,9 12,13,14,15 16,18,19,23	**3** 4,12,21
AV	**10** 6,8,11,12 17,20,23 24,25,26		**3** 18,22,23	**3** 7,18,22	**3** 7,18,22	**14** 1,2,4,7,9,12 13,14,15,16 18,19,22,23	**7** 1,4,6,12 18,21,22
NA	**9** 2,6,7,11 16,17,20 25,26	**8** 1,2,6,7 16,20,24 26		**1** 23	**0**	**12** 1,2,4,9,12,13 14,15,16,18, 19,23,24	**5** 4,6,12,21 23
NH	**9** 3,11,12 17,20,23 24,25,26	**9** 1,6,8,11 12,20,24 26,*GPI-A**	**7** 6,7,12,16 20,24,26		**0**	**13** 1,2,4,9,12,13, 14,15,16,18, 19,23,24	**5** 4,6,7,12 21
NR	**11** 1,3,6,11 12,17,20 23,24,25 26	**11** 1,3,6,8 11,12,20 23,25,26 *GPI-A**	**8** 2,6,7,11, 16,20,23 24	**5** 8,11,12,26 *GPI-A**		**11** 1,2,4,9,12,13, 14,16,18,19, 23	**4** 4,7,12,21
OA	**6** 8,17,20 24,25,26	**8** 6,8,11,20 24,25,26 *GPI-A**	**6** 6,7,8,11, 24,26	**4** 8,20,26 *GPI-A**	**8** 8,11,15,20 24,25,26 *GPI-A**		**14** 1,2,4,6,7,9 12,13,14,16 18,19,21,23
PM	**12** 3,6,8,15 16,17,20 22,23,24 25,26	**10** 3,8,11,15 16,20,23 24,25,26	**8** 1,2,7,11 15,22,24 26	**9** 1,11,15 16,20,22 24,25,26	**13** 1,3,6,8 11,15,16 20,22,23 24,25,26	**7** 8,15,20,22, 24,25,26	

length, all again showing the divergence of *O. atlanticum* , but this time defining some structure to the other species. The 50% majority-rule consensus tree is shown in Figure 4. The most significant difference in this analysis from the two phenetic analyses is the reversal of the positions of the two *Allocyttus* species. In the cladistic analysis *A. niger* is separated from the other species, whereas *A. verrucosus* was grouped with either *P. maculatus* and *N.* sp. or the other two *Neocyttus* species. Applying a topological constraint to the search (enforcing predetermined groupings and keeping only those trees that satisfy the constraints) for the three *Neocyttus* species or the two *Allocyttus* species produced the shortest trees only one step longer than the most parsimonious under no-constraint searches. A search for near-optimal trees with lengths of 53 units produced 56 trees, with 98% confirming the branch separation of *O. atlanticum*, and 71% supporting the separation of *N. rhomboidalis* and *N. helgae* from the other four species, among which the branching points could not be resolved.

The zeids appear to be the most likely sister family to the oreosomatids after the cladistic analyses.

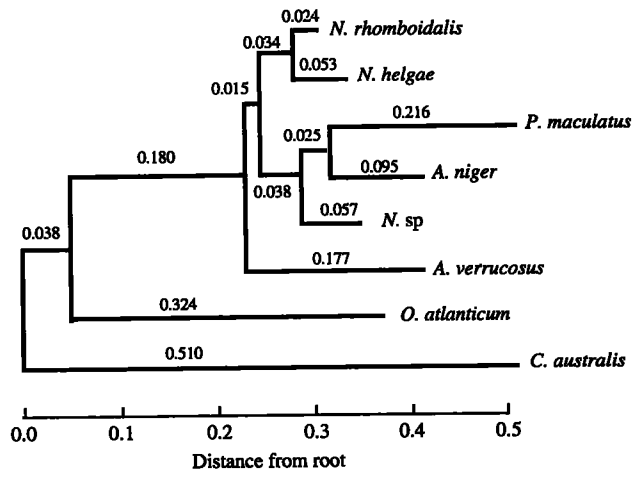

Figure 3

Tree constructed from Rogers' distance by the distance-Wagner procedure. Numbers represent relative branch lengths.

Neither analysis with the berycid or the acanthurid produced the shortest trees that resembled in any way the trees produced from the phenetic analyses or the cladistic analyses with either all three outgroups or *C. australis* alone. *Naso tuberosus* as the outgroup resulted in a single shortest tree (49 units) with *A. verrucosus* as the most divergent oreosomatid and *O. atlanticum* grouped next to the *N. rhomboidalis* and *N. helgae* cluster. Four shortest trees (42 units) resulted from the analysis with *B. splendens*, all of which, although confirming the divergence of *O. atlanticum*, resulted in *N. rhomboidalis* and *N. helgae* diverging independently from the other four species.

Discussion

The mean heterozygosity per locus for the seven oreosomatid species ranged from 8.3% to 18.1%, with an overall mean of 11.8%. These figures are considerably higher than the mean of 5.1% for 195 species of marine and freshwater fish (Ward et al., 1992) and 5.5% for 106 species of marine teleosts (Smith and Fujio, 1982). Three of the seven oreosomatid species had mean heterozygosity values (12.1% to 18.1%) which exceeded the highest value of 11.7% reported by Ward et al. (1994) from comparisons of genetic diversity among populations of 57 species of marine fish. This value was shown by two species, *Fundulus heteroclitus* (Linnaeus, 1766) (15 loci, Ropson et al., 1990) and *Hoplostethus atlanticus* (22 loci, Smith, 1986). Subsequent studies of additional loci in the orange roughy, *H. atlanticus*, raised the estimate of its mean heterozygosity to 13.0% (Elliott and Ward, 1992).

Two or more samples contributed to these heterozygosity estimates for five of the oreo species (Table 1). These estimates of heterozygosity are Hardy-Weinberg expected heterozygosities based on pooled allele frequencies. Had there been substantial differentiation of allele frequencies among samples, such estimates of heterozygosity would have been higher than average sample heterozygosities. In fact, the degree of inter-sample differentiation was, with a single exception, very limited (Lowry et al., unpubl. data). Thus these estimates of total heterozygosity will be very similar to estimates of sample heterozygosity. The one exception was the locus *sSOD** in *N. rhomboidalis*. Variation at this locus was found to be depth-related; samples with a high frequency (>0.6 [cf. <0.2]) of *sSOD**140 came from deeper water (>700 m). The total heterozygosity for this one locus was 0.500, whereas its average sample heterozygosity was 0.285. Use of sample heterozygosity rather than total heterozygosity would effect a small reduction in the overall heterozygosity estimate for this species (from 0.127 to 0.119). Note also that the species with the highest degree of variation, *N.* sp., came from a single sample. The high variability seen in the oreos cannot be attributed to inter-sample differentiation.

It is clear that oreosomatids have higher heterozygosities than most species of teleosts. Interestingly, both oreosomatids and the similarly variable orange roughy occupy deepwater habitats. As speculated by

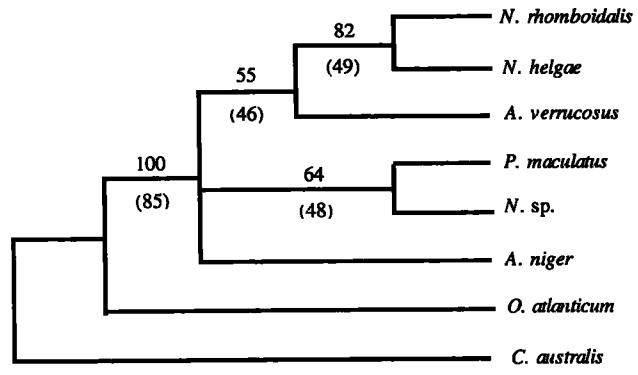

Figure 4

The 50% majority-rule consensus tree of the eleven shortest trees produced by PAUP analysis, with numbers representing the percentage consensus measures for the eleven trees. Numbers in brackets are bootstrapped values (100 replicates).

Elliott and Ward (1992) for the orange roughy, the high heterozygosity shown by these deepwater (500–1200 m) species may reflect their large (prior to exploitation) population sizes and (assuming that deepwater species have been less severely affected by glaciations than shallow water species) a lack of severe bottlenecks in their recent evolutionary past.

As adults, *Pseudocyttus* is the most morphologically distinct oreosomatid genus (James et al., 1988). Its distinguishing characters include the first dorsal-fin spine being longer than the second (vice versa in other species), a pelvic fin with only five rays (usually six or seven in other species), and 40–43 vertebrae (34–41 in other species). However, as juveniles, the genus *Oreosoma* is the most distinctive with prominent cones over the body. Other juvenile oreosomatids have "warts" or protuberances (such structures are absent in at least *N. rhomboidalis)*, but none are quite so pronounced or bizarre as in *O. atlanticum*. Our genetic study confirms the uniqueness of *O. atlanticum*, which has a very low genetic identity (0.371) with the other oreosomatid species—substantially less than the corresponding mean identity (0.650) of *P. maculatus* with other oreosomatids. Morphologically, *O. atlanticum* can be distinguished as an adult by a very large eye (eye diameter 52–60% of head length) and by a prominent horizontal ridge on the operculum.

James et al. (1988) suggested that further study may synonymize the Northern Hemisphere *N. helgae* with the Southern Hemisphere *N. rhomboidalis*. Our allozyme data suggest that, although these two taxa are indeed very closely related (genetic identity I=0.973 for 26 loci and I=0.966 for 27 loci including *GPI-1**), their distinctive muscle protein patterns, not included in the genetic identity values, are consistent with their being separate species. Of the four non-*CK-A** protein bands, two appear to be fixed differently for the two species. However, the amount of genetic differentiation between these two species is only a little greater than that between samples of *H. atlanticus* taken from the same two areas (North Atlantic and off southern Australia) (Elliott et al., 1994). Eleven polymorphic loci were screened in the *H. atlanticus* comparison and just three loci showed significant heterogeneity and gave a genetic identity of 0.990 (N.G.E.'s unpubl. data). Thus the genetic data do not unequivocally validate the recognition of *N. rhomboidalis* and *N. helgae* as distinct species. Morphologically they are also very similar, although there are some differences (Yearsley and Last[2]).

As mentioned earlier, there is depth-related variation in the *sSOD** polymorphism in *N. rhomboidalis*, with samples derived from deeper water having a high frequency of *sSOD**140. We are uncertain as yet whether this indicates reproductive isolation of two forms or selection acting on *sSOD*, although the lack of detectable mitochondrial DNA differentiation (Grewe, Innes, and Evans[4]) suggests that if reproductive isolation is responsible, it is likely to be recent in origin. These data and analyses will be presented in full elsewhere.

The new species *N.* sp., infrequently captured with *P. maculatus* and *A. niger* in southern Australian waters and morphologically similar to *N. rhomboidalis*, showed quite a high degree of genetic similarity to the other two *Neocyttus* species (I=0.903 with *N. rhomboidalis* and 0.884 with *N. helgae*). However, it was genetically distinct from them at several loci (Table 6), and numerous meristic and morphological characters (Yearsley and Last[2]) confirm that it is a separate species. Although it clustered with *A. niger* (I=0.903) in the two phenetic trees constructed from the genetic distance data, in the cladistic analyses it grouped more often with *P. maculatus*. However, classical taxonomic techniques suggest a close association with *Neocyttus* species, particularly the western Indian Ocean *N. acanthorhynchus* (Yearsley and Last[2]).

The two *Allocyttus* species were found to be genetically quite distinct from one another (I=0.695); there was no evidence from either phenetic or cladistic analyses that they made up an exclusive monophyletic group. James et al. (1988) gave no justification for placing *A. niger* in *Allocyttus*. However, they drew attention to problems with generic diagnoses of the oreosomatids. *Allocyttus*, as it currently stands, but excluding *A. niger* (i.e. *A. verrucosus*, *A. guineensis*, and *A. folletti*), may be a natural grouping, with *A. niger* more akin to, but probably not congeneric with, *Neocyttus*. Ongoing morphological work should elucidate these problems.

Whereas the branch node for *O. atlanticum* is clearly resolved to be ancestral to the remaining oreosomatids, the phenetic and cladistic analyses could not resolve unambiguously all the internal nodes for the remaining species. There is strong evidence for a branch node separating *N. rhomboidalis* and *N. helgae* from the other four species, but there is no evidence supporting two species in *Allocyttus*.

Several problems in the family Oreosomatidae remain to be resolved. They include the formal description of the rough oreo, *N.* sp. (Yearsley and Last[2]), a reassessment of the generic affinities of *A. niger* and *A. verrucosus,* and further examination of the two depth-related *sSOD** forms of *N. rhomboidalis* and their relationship to *N. helgae*. As intimated by

[4] Grewe, P. M., B. H. Innes, and B. S. Evans. 1995. CSIRO Division of Fisheries, Castray Esplanade, Hobart, Tasmania 7000, Australia.

James et al. (1988), there remains a clear need for a full and thorough revision of the family Oreosomatidae.

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Abstract.—We analyzed 364 spawner-recruitment time series to determine whether recruitment is related to spawner abundance. We pose three questions: 1) Does the highest recruitment occur when spawner abundance is high? 2) Does the lowest recruitment occur when spawner abundance is low? and 3) Is the mean recruitment higher if spawner abundance is above rather than below the median? We found that when there is a sufficient range in spawner abundance the answer to all three questions is almost always "yes." Thus, spawner abundance cannot be ignored in the management of fish populations. Recruitment overfishing appears to be a common problem.

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Is fish recruitment related to spawner abundance?

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Perhaps the most fundamental issue for the study and management of fish populations is the relation between spawner abundance and subsequent recruitment. There is surprisingly little consensus on this issue; many researchers believe that there is no relevant relationship between species abundance and recruitment (reviewed by Wooster and Bailey, 1989; Koslow et al., 1987) whereas others believe it to be fundamental (e.g. Ricker, 1954; Beverton and Holt, 1957; Cushing, 1971; Myers et al., 1995a). The assumed absence of a relationship between spawner abundance and recruitment has prompted some scientists to claim that recruitment overfishing is almost impossible (Laevastu, 1993). This divergence of opinion has practical consequences for the management of fisheries: many fisheries are managed without consideration of maintaining a sustainable abundance or biomass of spawners (Smith et al., 1993).

The purpose of this paper is to provide conclusive evidence that strong year classes are more likely when spawner abundance is large. We approach the problem using the simplest possible nonparametric methods in order to avoid the many subtle statistical difficulties in fitting spawner-recruitment functions (Walters, 1985, 1990; Hilborn and Walters, 1992). Our approach is to examine systematically 364 data sets from the most recent version of the database compiled by Myers et al. (1995b) as part of an ongoing study of recruitment variability. By analyzing many populations with identical methods, it is possible to arrive at conclusions with greater reliability.

The nonparametric methods we used were devised in order to answer three deliberately simple questions. First: Does the largest recruitment occur when the spawner abundance is high? To answer this question, we examined the rank of spawner abundance associated with the largest recruitment. Second: Does the smallest recruitment occur when spawner abundance is low? This time we examined the rank of spawner abundance associated with the smallest recruitment. Third: Is the mean recruitment higher if spawner abundance is above rather than below the median? To answer this question, we examined the ratio of mean recruitment when spawner abundance is above the median to mean recruitment when spawner abundance is below the median.

Data

By "spawner abundance" we mean any of the following metrics of the size of the spawning stock: spawning stock biomass, the number of spawners, the number of eggs, or some index of spawner abundance (derived from catch per unit of effort or research vessels).

We tried to assemble all time series of reliable data on spawner abundance and recruitment. We started with the 477 time series from the most recent version of the database by Myers et al. (1995b). Of these, 77 series were eliminated because they had less than 5 years of spawner-recruitment data, 5 series were eliminated because they were for invertebrates, 17 pink and chum salmon series were eliminated because they were described as less reliable, and 14 series were eliminated because they were different versions of other series or because they overlapped other series. We were left with 364 series. Sometimes the same population was included more than once because of incompatible time periods or because different life stages were examined.

For each population, Table 1 lists the method used to estimate spawner abundance and recruitment. For most marine populations, spawning biomass and recruitment had been estimated by sequential population analysis (SPA) of commercial catch-at-age data. SPA techniques include virtual population analysis (VPA; Gulland[1]), cohort analysis (Pope, 1972), and related methods that reconstruct population size from catch-at-age data (Deriso et al., 1985, 1989; Megrey, 1989; Gavaris, 1988). For some marine populations, accurate commercial catch-at-age data were not available; therefore research vessel (RV) surveys estimates were used. For a few populations, other types of data were used, e.g. spawning stock biomass was estimated from SPA and recruitment was estimated from research vessel surveys. We did not include populations for which there was only commercial catch-per-unit-of-effort estimates of abundance.

For populations in the family Salmonidae, series were sometimes available for several different life-stage transitions. The life stages are denoted in Table 1 as follows: a = adults (or eggs); f = fry; s = smolts (sea-bound migrating juveniles); and p = parr (juveniles within the river).

For most of the Pacific salmonid populations, the numbers of spawners and recruits were reconstructed from commercial catch-at-age data and independent estimates of fishing mortality or from an independent estimate of escapement from surveys of spawning, or both. In these cases, the method is termed "stock reconstruction," and is denoted as SR in Table 1. Some of the estimates were derived from experiments in which the number of spawners and recruits, e.g. number of parr produced, are direct counts. We analyzed data by families and species separately if there were at least 6 populations per taxa.

[1] Gulland, J. A. 1965. Estimation of mortality rates. Annex to Rep., Arctic Fish. Working Group ICES Council Meeting 1965(3), 9 p.

Methods and results

In evaluating the relationship between spawners and recruitment, the range of the spawner data will clearly be important. For near constant spawner levels, changes in recruitment will reflect only variability in density-independent mortality. As an index of the range spanned by the spawner data, we used the ratio S_{max}/S_{min}, where S_{max} is the maximum observed spawner abundance and S_{min} is the minimum observed spawner abundance. When this ratio is near 1, the spawner level is nearly constant; the larger its value, the greater the range of spawner data. Values of S_{max}/S_{min} for the data series examined in this paper are listed in Table 1.

Hypothesis 1: Does the largest recruitment occur when spawner abundance is high?

For each spawner-recruitment series we asked whether the highest recruitment, R_{max}, occurred when spawner abundance was high. We computed the rank of the spawner abundance that gave rise to the highest recruitment, S_{Rmax}. In order to compare ranks across populations, we computed a "relative rank" $r_{max} = (\text{rank}(S_{Rmax}) - 1)/(n - 1)$, where n is the number of observations in the spawner-recruitment series (Fig. 1A). The relative rank therefore lies between 0 and 1, with $r_{max} = 0$ implying that the highest recruitment occurs for the lowest spawner abundance, and conversely, with $r_{max} = 1$ implying that the highest recruitment occurs for the highest spawner abundance.

To help summarize the data and to test hypotheses, cumulative weighted means were calculated. The weighted mean of k relative ranks $r_{max,i}$ is

$$\frac{\sum_{i=1}^{k} n_i r_{\max,i}}{\sum_{i=1}^{k} n_i}, \qquad (1)$$

where n_i is the number of observations in the ith spawner-recruitment series. The cumulative weighted mean was calculated by starting with the relative rank associated with the largest value of S_{max}/S_{min} and by continuing through the relative rank associated with the smallest value of S_{max}/S_{min}.

If, for a given population, spawner abundance and highest recruitment were independent, each possible relative rank would be equally likely, i.e. the expected value of $r_{max,i}$ would be 0.5. If this were true for each population, then the expected value of the weighted mean relative rank would also be 0.5. Therefore we

Table 1

Statistics for each population. "Population" lists the order, family, species, and location; n lists the number of common years of spawner-recruitment data; S_{max}/S_{min} lists the ratio of maximum quantity of spawners to minimum quantity of spawners; r_{max} lists the relative rank of the quantity of spawners for the maximum recruitment; r_{min} lists the relative rank of the quantity of spawners for the minimum recruitment; $\overline{R}_{above}/\overline{R}_{below}$ lists the ratio of mean recruitment above the median quantity of spawners to mean recruitment below the median quantity of spawners; and "Method" lists the stock assessment method used (SPA=sequential population analysis, Count=direct count, RV=research vessel, SR=stock reconstruction, MR=mark recapture). For populations within the family Salmonidae, series were sometimes available for several different life-stage transitions. The life stages are denoted as follows: a = adults (or eggs), f = fry, s = smolt, and p = parr. They are shown in the table with an arrow notation so that "a ⇒ f" means spawners were "adults" and recruits were "fry."

Population	n	$\frac{S_{max}}{S_{min}}$	r_{max}	r_{min}	$\frac{\overline{R}_{above}}{\overline{R}_{below}}$	Method
Aulopiformes						
Synodontidae						
Greater lizardfish (*Saurida tumbil*)						
East China Sea	10	6.8	0.67	0.22	1.7	CPUE
Clupeiformes						
Clupeidae						
Blueback herring (*Alosa aestivalis*)						
Saint John River	14	65.2	0.77	0.08	2.9	Count
Alewife (*Alosa pseudoharengus*)						
Damariscotta Lake, Maine	8	5.6	0.21	0.43	1.0	Count
Lake Ontario	7	7.4	0.50	0.00	0.3	RV
Saint John River	16	54.8	1.00	0.33	2.2	Count
Anadromous American shad (*Alosa sapidissima*)						
Connecticut River	16	4.5	0.67	0.20	1.2	MR and count
Gulf menhaden (*Brevoortia patronus*)						
Gulf of Mexico	19	11.2	0.78	0.17	1.2	SPA
Atlantic menhaden (*Brevoortia tyrannus*)						
U.S. Atlantic	35	39.8	0.79	0.32	1.5	SPA
Herring (*Clupea harengus*)						
Archipelago and Bothnian Seas	13	1.3	0.33	1.00	0.7	SPA
Baltic, Bothnian Sea	15	1.6	0.93	0.79	0.9	SPA
S.W. Baltic	19	2.8	0.39	0.94	0.8	SPA
S. Baltic	15	1.2	0.57	0.07	1.0	SPA
Central Baltic	16	1.4	0.67	0.53	1.4	SPA
Baltic, Bothnian Bay	15	1.7	0.93	0.29	1.8	SPA
Central Coast B.C.	38	16.4	0.78	0.16	1.0	SPA
Craig, Alaska	16	13.4	0.53	0.73	2.6	SPA
Downs stock	65	470.5	0.84	0.02	5.5	SPA
Eastern Bering Sea	26	16.7	0.20	0.68	0.6	SPA
Georges Bank	15	9.9	0.50	0.14	1.2	SPA
Gulf of Finland	18	1.8	0.94	1.00	0.9	SPA
Gulf of Maine	23	6.6	0.09	0.95	0.8	SPA
Gulf of Riga	19	2.2	0.11	0.44	1.3	SPA
West of Scotland	18	10.4	0.76	0.53	1.2	SPA
West of Ireland	19	2.5	0.78	1.00	0.8	SPA
Iceland (spring spawners)	23	630.0	0.45	0.00	1.4	SPA
Iceland (summer spawners)	46	39.6	0.91	0.04	2.9	SPA
N. Gulf of St. Lawrence (fall spawners)	13	4.7	0.33	0.67	0.2	SPA
N. Gulf of St. Lawrence (spring spawners)	13	6.0	0.33	0.75	0.3	SPA
S. Gulf of St. Lawrence (fall spawners)	9	9.1	0.62	0.38	1.2	SPA
S. Nova Scotia	11	6.2	0.90	0.40	1.4	SPA
North Sea	41	76.1	0.68	0.15	1.7	SPA
North Strait of Georgia	38	22.4	0.65	0.27	1.4	SPA
North West Coast Vancouver Island	38	13.0	0.95	0.54	1.0	SPA
Northern Irish Sea	18	5.5	0.94	0.12	1.3	SPA
Norway (spring spawners)	41	8,986.4	1.00	0.03	5.5	SPA

Continued on next page

Table 1 (continued)

Population	n	$\frac{S_{max}}{S_{min}}$	r_{max}	r_{min}	$\frac{\overline{R}_{above}}{\overline{R}_{below}}$	Method
Prince Rupert District	38	11.3	0.97	0.35	1.2	SPA
Queen Charlotte Islands	38	34.2	0.73	0.14	1.2	SPA
Revilla Channel (Kah Shakes), Alaska	16	3.1	0.33	0.47	0.6	SPA
S.E. Alaska	30	6.0	0.03	0.52	1.2	SPA
Seymour Canal, Alaska	16	8.4	0.73	0.33	1.0	SPA
Sitka, Alaska	21	14.8	0.95	0.15	3.2	SPA
South West Coast Vancouver Island	38	42.0	0.86	0.22	1.0	SPA
Southern Central Baltic	11	1.9	0.80	0.00	1.4	SPA
Southern Strait of Georgia	38	8.4	0.49	0.05	0.9	SPA
Yellow Sea or Huanghai Sea	15	51.2	0.93	0.79	1.9	SPA
Spanish sardine (*Sardina pilchardus*)						
Iberian Atlantic Coast	14	5.7	0.96	0.46	0.9	SPA
Brazilian sardine (*Sardinella brasiliensis*)						
South Eastern Brazil	15	3.4	0.57	0.00	1.6	Length-based SPA
Sardine (*Sardinops sagax*)						
California	31	134.4	0.87	0.00	6.4	SPA
Chile-Northern zone	13	4.1	1.00	0.25	1.0	SPA
Gulf of California	13	15.1	0.75	0.17	2.2	SPA
Eastern Japan	14	6.4	0.15	0.77	0.6	SPA
Sea of Japan	13	26.2	0.58	0.92	1.7	SPA
South Africa	31	19.0	0.53	0.83	1.7	SPA
South Africa	8	69.2	0.00	1.00	0.8	SPA
Sprat (*Sprattus sprattus*)						
Central Baltic	15	5.6	0.93	0.43	0.7	SPA
S.E. Baltic	19	19.7	0.11	0.50	1.7	SPA
Engraulidae						
S.A. anchovy (*Engraulis capensis*)						
South Africa	18	3.5	0.00	0.53	1.3	SPA
South Africa	10	3.7	0.67	0.06	2.5	Acoustics
Northern anchovy (*Engraulis mordax*)						
California	25	4.7	0.79	0.33	0.9	SPA
Peruvian anchoveta (*Engraulis ringens*)						
Northern and central stock, Peru	19	18.4	0.61	0.00	2.2	SPA
Cypriniformes						
Cyprinidae						
Bream (*Abramis brama*)						
Lake Tjeukemeer, the Netherlands	11	4.5	0.50	0.30	0.5	RV
Golden shiner (*Notemigonus crysoleucas*)						
Lake St. George, Ontario	8	6.7	0.43	0.29	0.2	MR and beach seine
Roach (*Rutilus rutilus*)						
Klicava Reservoir	11	1.9	0.00	0.40	0.8	MR
Gadiformes						
Gadidae						
Pacific cod (*Gadus macrocephalus*)						
Eastern Bering Sea	10	5.8	0.33	0.22	0.8	SPA
Hecate Strait	14	2.9	0.62	0.15	1.5	SPA
Cod (*Gadus morhua*)						
S.E. Baltic	22	5.3	0.43	0.10	1.4	SPA
Central Baltic	22	5.4	0.52	0.24	1.7	SPA
Celtic Sea	20	4.4	0.89	0.53	1.6	SPA
Faroe Plateau	31	6.7	0.58	0.20	0.9	SPA
Eastern English Channel	12	4.3	0.73	0.18	1.4	SPA
West of Scotland	27	3.7	0.10	1.00	0.8	SPA

Continued on next page

Table 1 (continued)

Population	n	$\frac{S_{max}}{S_{min}}$	r_{max}	r_{min}	$\frac{\bar{R}_{above}}{\bar{R}_{below}}$	Method
Iceland	38	7.3	0.49	0.08	1.2	SPA
Irish Sea	25	3.6	0.17	1.00	0.8	SPA
Kattegat	21	12.7	1.00	0.10	1.8	SPA
W. Coast of Greenland	31	55.7	0.83	0.30	2.3	SPA
Labrador and N.E. Newfoundland	28	17.2	0.93	0.28	2.7	SPA
Flemish Cap	10	18.7	0.56	0.78	2.6	RV
S. Grand Banks	31	9.0	0.67	0.53	1.9	SPA
N. Gulf of St. Lawrence	17	4.7	0.31	0.06	1.0	SPA
St. Pierre Bank	31	4.2	0.83	0.00	1.2	SPA
S. Gulf of St. Lawrence	41	5.9	0.66	0.19	1.1	SPA
E. Scotian Shelf	33	4.7	0.75	0.25	1.1	SPA
S.W. Scotian Shelf	45	2.0	0.64	0.66	1.0	SPA
Gulf of Maine	7	1.8	0.17	0.50	0.6	SPA
Georges Bank	14	1.7	0.00	0.15	1.2	SPA
North East Arctic	43	15.8	0.81	0.02	1.6	SPA
North Sea	28	4.4	1.00	0.22	1.2	SPA
Skagerrak	13	2.3	0.50	0.42	1.1	SPA
Haddock (*Melanogrammus aeglefinus*)						
Faroe Plateau	30	4.1	0.72	0.00	1.1	SPA
West of Scotland	28	10.9	0.41	0.33	0.7	SPA
Iceland	28	8.6	0.48	0.52	0.8	SPA
E. Scotian Shelf	38	23.2	0.84	0.32	2.9	SPA
S.W. Scotian Shelf	24	3.7	0.91	0.00	1.2	SPA
Georges Bank	58	17.2	0.93	0.02	2.7	SPA
North East Arctic	41	12.0	0.93	0.12	2.0	SPA
North Sea	31	23.4	0.52	0.17	0.8	SPA
Rockall Bank	6	4.1	0.20	0.80	0.5	SPA
Whiting (*Merlangius merlangus*)						
Celtic Sea	9	2.9	0.75	0.88	1.1	SPA
Eastern English Channel	14	3.9	0.46	0.38	1.2	SPA
West of Scotland	27	4.1	0.56	0.23	1.2	SPA
Irish Sea	13	3.2	0.58	1.00	1.0	SPA
North Sea	27	2.7	0.38	0.62	0.9	SPA
Silver hake (*Merluccius bilinearis*)						
Mid Atlantic Bight	33	27.1	0.88	0.31	2.9	SPA
Scotian Shelf	13	2.0	0.67	0.75	1.2	SPA
Georges Bank	33	25.3	0.78	0.28	5.1	SPA
S.A. hake (*Merluccius capensis*)						
South Africa	20	5.6	0.74	0.58	1.1	SPA
South Africa South Coast	12	1.5	0.64	1.00	1.0	SPA
Peruvian hake (*Merluccius gayi*)						
Chile-South Central zone	14	1.7	0.15	1.00	0.8	SPA
Chile-Northern zone	14	2.4	0.85	0.54	1.3	SPA
Peru	8	3.0	0.43	1.00	0.6	SPA
Hake (*Merluccius merluccius*)						
West of France and British Isles	14	1.8	1.00	0.31	1.0	SPA
Iberian Atlantic Coast	9	3.2	0.88	0.00	2.0	SPA
Jabuka Pit, Adriatic Sea	26	8.5	1.00	0.20	1.1	CPUE
Pacific hake (*Merluccius productus*)						
W. U.S. + Canada	33	2.2	0.06	1.00	1.0	SPA
Blue whiting (*Micromesistius poutassou*)						
N.E. Atlantic (North)	20	3.5	0.21	0.79	0.6	SPA
N.E. Atlantic (South)	10	1.2	1.00	0.72	1.1	SPA
Pollock or saithe (*Pollachius virens*)						
Faroe	30	2.4	0.03	0.93	0.8	SPA

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Table 1 (continued)

Population	n	$\frac{S_{max}}{S_{min}}$	r_{max}	r_{min}	$\frac{\overline{R}_{above}}{\overline{R}_{below}}$	Method
West of Scotland	20	3.2	0.39	0.79	0.8	SPA
Iceland	26	4.1	0.56	0.26	1.0	SPA
Scotian Shelf and Georges Bank	10	1.7	0.78	0.33	1.5	SPA
North East Arctic	32	8.9	0.19	0.06	1.3	SPA
North Sea	22	7.0	0.95	0.10	1.1	SPA
Walleye pollock (*Theragra chalcogramma*)						
E. Bering Sea	24	5.9	0.26	0.83	0.8	SPA
East Kamchatka	12	24.0	1.00	0.27	2.0	SPA
Gulf of Alaska, Alaska	25	4.3	0.38	0.50	0.5	SPA
Japan-Pacific Coast of Hokkaido	15	3.8	0.29	0.43	0.9	SPA
West Bering Sea	8	2.8	1.00	0.00	2.1	SPA
Norway pout (*Trisopterus esmarkii*)						
North Sea	12	4.3	0.45	0.27	1.2	SPA
Red hake (*Urophycis chuss*)						
Gulf of Maine and N. Georges Bank	13	8.6	0.50	0.17	1.4	SPA
S. New England	15	5.7	0.64	0.07	2.6	SPA
White hake (*Urophycis tenuis*)						
S. Gulf of St. Lawrence	14	2.7	0.08	0.38	0.7	SPA
Lophiformes						
Lophiidae						
Monkfish (*Lophius piscatorius*)						
Celtic Sea and West of France	6	1.6	1.00	0.40	2.7	SPA
Perciformes						
Ammodytidae						
Sandeel (*Ammodytes marinus*)						
West of Scotland	10	8.5	0.44	0.78	0.8	SPA
Northern North Sea	14	7.1	0.08	0.23	0.7	SPA
Shetland	16	4.4	0.93	0.47	1.3	SPA
Southern North Sea	14	6.1	0.77	1.00	1.6	SPA
Branchiostegidae						
Branquillo (*Branchiostegus japonicus*)						
Wakasa Bay	7	2.4	0.50	0.92	0.4	Leslie
Carangidae						
Cape horse mackerel (*Trachurus capensis*)						
Namibian Coast	17	3.9	0.31	0.94	0.5	SPA
Horse mackerel (*Trachurus symetricus murphyi*)						
South Pacific Ocean	15	5.5	0.50	0.79	1.1	SPA
Horse mackerel (*Trachurus trachurus*)						
Iberian Atlantic Coast	8	1.7	0.14	0.43	0.6	SPA
N.E. Atlantic	8	4.3	0.14	0.00	0.2	SPA
Lactariidae						
False trevally (*Lactarius lactarius*)						
Gulf of Thailand	8	521.8	0.43	0.00	0.9	CPUE
Lutjanidae						
Silk snapper (*Lutjanus synagris*)						
Cuba	17	2.8	0.44	0.38	1.0	SPA
Mugilidae						
Grey mullet (*Mugil cephalus*)						
Taiwan	7	2.3	1.00	0.17	1.3	SPA
Pentacerotidae						
Pelagic armourhead (*Pseudopentaceros wheeleri*)						
Southeast Hancock Seamount, Hawaii	11	19.1	1.00	0.70	7.1	Leslie
Percidae						
Yellow perch (*Perca flavescens*)						

Continued on next page

Table 1 (continued)

Population	n	$\frac{S_{max}}{S_{min}}$	r_{max}	r_{min}	$\frac{\overline{R}_{above}}{\overline{R}_{below}}$	Method
Oneida Lake, New York	7	1.6	0.00	0.67	0.3	Seine
South Bay, Lake Huron	27	582.9	0.62	0.58	1.6	Research nets
Eurasian perch (*Perca fluviatilis*)						
Lake Ijssel, the Netherlands	16	6.2	0.50	0.77	0.8	SPA, RV
Pikeperch (*Stizostedion lucioperca*)						
Lake Ijssel, the Netherlands	17	43.0	0.50	1.00	0.5	SPA, RV
Walleye (*Stizostedion vitreum*)						
Escanaba Lake, Wisconsin	16	3.9	0.07	0.60	0.4	MR
Lake Erie	14	23.7	0.23	0.77	0.6	SPA
Lake Erie, Michigan	22	452.7	0.81	0.14	3.6	CPUE
Mille Lacs Lake, Minnesota	12	3.3	0.91	0.45	5.2	SPA
Rainy Lake, Minnesota	15	2.1	0.93	0.00	1.6	CPUE
Scianidae						
White croaker (*Argyrosomus argentatus*)						
East China Sea	15	1.9	0.79	0.64	1.1	SPA
Black croaker (*Argyrosomus nibe*)						
East China Sea	13	61.0	0.58	0.17	2.3	CPUE
Yellow croaker (*Pseudociaena polyactis*)						
East China Sea	10	15.0	0.78	0.22	2.7	Catch curve
Scombridae						
Chub mackerel (*Scomber japonicus*)						
Pacific Coast of Japan	16	33.5	0.27	0.53	0.4	Egg survey
Pacific Coast of Japan	12	33.5	1.00	0.09	2.6	Egg survey
Southern California	36	64.1	0.89	0.23	2.5	SPA
Mackerel (*Scomber scombrus*)						
N.W. Atlantic	28	10.7	0.30	0.44	1.1	SPA
N.E. Atlantic	19	1.9	0.56	0.50	1.0	SPA
Yellowfin tuna (*Thunnus albacares*)						
Eastern Pacific Ocean	25	3.4	0.88	0.58	1.4	SPA
Indian Ocean	25	9.1	0.83	0.04	2.2	SPA
Southern bluefin tuna (*Thunnus maccoyii*)						
Southern Pacific	26	4.2	0.64	0.04	1.2	SPA
Atlantic bluefin tuna (*Thunnus thynnus*)						
West Atlantic	23	8.2	0.91	0.00	2.2	SPA
Sparidae						
Sea bream (*Chrysophrys major*)						
Yellow Sea	17	440.3	0.81	0.00	2.2	CPUE
Red porgy (*Pagrus pagrus*)						
Atlantic Ocean off North Carolina	14	3.0	0.23	0.00	1.2	SPA
Yellow sea bream (*Taius tumifrons*)						
Central East China Sea	20	4.3	0.26	0.00	1.7	Catch curve
East China Sea	8	3.2	0.00	0.57	0.7	CPUE
Japan Coast	20	6.2	0.89	0.05	2.1	Catch curve
South East China Sea	18	9.9	1.00	0.00	3.8	Catch curve
Pleuronectiformes						
Bothidae						
Summer flounder (*Paralichthys dentatus*)						
Middle Atlantic Bight	9	3.1	1.00	0.12	1.8	SPA
Pleuronectidae						
American plaice (*Hippoglossoides platessoides*)						
Grand Banks	19	4.0	0.72	0.28	1.3	SPA
Georges Bank	11	6.3	0.00	0.70	0.6	SPA
Pacific halibut (*Hippoglossus stenolepis*)						
Pacific	47	2.8	0.39	0.46	0.9	SPA
Rock sole (*Lepidopsetta bilineata*)						

Continued on next page

Table 1 (continued)

Population	n	$\frac{S_{max}}{S_{min}}$	r_{max}	r_{min}	$\frac{\overline{R}_{above}}{\overline{R}_{below}}$	Method
Hecate Strait, B.C.	24	4.6	0.39	0.70	1.0	CPUE
Yellowfin sole (*Limanda aspera*)						
E. Bering Sea	12	1.9	0.91	0.45	1.3	SPA
Yellowtail flounder (*Limanda ferruginae*)						
Grand Banks	15	3.1	0.50	0.00	1.0	SPA
Georges Bank	20	11.8	0.95	0.21	2.7	SPA
Southern New England	20	16.7	0.63	0.00	1.1	SPA
Plaice (*Pleuronectes platessa*)						
Celtic Sea	14	3.4	0.85	0.31	1.2	SPA
Skagerrak and Kattegat	12	2.2	0.45	0.73	0.5	SPA
Eastern English Channel	11	2.2	0.60	0.10	1.3	SPA
Western English Channel	15	2.9	0.71	0.00	1.4	SPA
Irish Sea	28	3.7	0.00	0.56	0.9	SPA
Kattegat	22	10.7	0.67	0.14	2.4	SPA
North Sea	35	1.9	0.35	0.63	0.8	SPA
Skagerrak	10	2.2	0.56	0.44	0.9	SPA
Greenland halibut (*Reinhardtius hippoglossoides*)						
W. Greenland and Iceland	14	2.5	0.31	0.92	0.9	SPA
North East Arctic	21	4.3	0.40	0.10	1.3	SPA
Northwest Atlantic	15	2.6	0.14	0.86	0.8	SPA
Scophthalmidae						
Megrim (*Lepidorhombus whiffiagonis*)						
West of France and British Isles	7	1.5	0.83	0.50	1.1	SPA
Iberian Atlantic Coast	6	1.6	0.20	1.00	0.2	SPA
Soleidae						
Sole (*Solea vulgaris*)						
Bay of Biscay (VIII)	13	2.0	0.17	0.75	0.9	SPA
Celtic Sea	18	2.4	0.00	0.88	0.4	SPA
Skagerrak and Kattegat	5	2.2	1.00	0.50	1.4	SPA
Eastern English Channel	20	5.4	0.42	1.00	1.1	SPA
Western English Channel	22	2.7	0.90	0.48	1.3	SPA
Irish Sea	21	2.0	0.00	0.65	0.5	SPA
North Sea	36	5.7	0.96	0.19	1.1	SPA
Salmoniformes						
Esociadae						
Pike (*Esox lucius*)						
North Basin, Windermere Lake	35	7.3	0.74	0.13	1.6	SPA
South Basin, Windermere Lake	35	5.8	0.57	0.07	1.5	SPA
Osmeridae						
Capelin (*Mallotus villosus*)						
Barents Sea	20	138.0	0.79	0.84	2.2	RV
Iceland	12	5.2	0.27	0.36	0.9	SPA
Plecoglossidae						
Ayu (*Plecoglossus altivelis*)						
Lake Biwa, Japan	12	19.3	0.82	0.00	1.0	SPA
Salmonidae						
Lake Whitefish (*Coregonus clupeaformis*)						
Lake Huron (a ⇒ a)	28	77.3	0.78	0.89	1.4	Research nets
Bloater (*Coregonus hoyi*)						
Lake Michigan (a ⇒ a)	11	49.5	0.90	0.10	37.1	RV
Whitefish (*Coregonus lavaretus*)						
Lake Constance, Europe (a ⇒ a)	21	7.9	0.65	0.00	3.2	SPA
Pink salmon (*Oncorhynchus gorbuscha*)						
Auke Creek, Alaska (f ⇒ a)	14	10.4	0.92	0.00	1.6	Count
Auke Creek, Alaska (a ⇒ f)	16	15.5	0.73	0.00	1.6	Count

Continued on next page

Table 1 (continued)

Population	n	$\frac{S_{max}}{S_{min}}$	r_{max}	r_{min}	$\frac{\overline{R}_{above}}{\overline{R}_{below}}$	Method
Bakhura River, Sakhalin Is. (a ⇒ f)	26	54.0	0.24	0.04	0.7	Count
Bakhura River, Sakhalin Is. (f ⇒ a)	24	35.1	0.65	0.22	1.4	Count
Bakhura River, Sakhalin Is. (a ⇒ a)	24	54.0	0.91	0.13	1.4	Count
Bentinck, B.C. (a ⇒ a)	11	76.4	0.70	0.10	2.4	SR
Brown's Peak Creek, Cook Inlet, Alaska (a ⇒ a)	22	280.0	0.48	0.12	1.1	SR
Bruin Bay, Cook Inlet, Alaska (a ⇒ a)	17	252.4	0.88	0.06	15.1	SR
Central Alaska (a ⇒ a)	25	310.0	0.75	0.17	2.9	SR
Central B.C. (Areas 6–8) (a ⇒ a)	14	4.1	0.77	0.69	1.1	SR
Central Coast Area 7, B.C. (a ⇒ a)	11	4.2	0.80	0.20	1.4	SR
Central Coast Area 9, B.C. (a ⇒ a)	11	51.5	0.70	0.20	4.5	SR
Dagi River, Sakhalin Is. (a ⇒ f)	11	81.0	0.90	0.00	2.3	Count
Desire Lake, Cook Inlet, Alaska (a ⇒ a)	8	12.5	0.14	0.86	0.5	SR
Douglas, B.C. (a ⇒ a)	11	5.2	0.80	0.50	3.4	SR
Fraser River, B.C. (a ⇒ a)	16	6.0	0.93	0.00	1.8	SR
Gardner, B.C. (a ⇒ a)	11	54.0	0.50	0.20	1.5	SR
Hooknose Creek, B.C., Canada (a ⇒ f)	14	35.8	0.85	0.69	4.1	Count
Humpy Creek, Cook Inlet, Alaska (a ⇒ a)	27	37.0	0.85	0.27	1.3	SR
Island Creek, Cook Inlet, Alaska (a ⇒ a)	25	350.0	0.83	0.92	3.9	SR
James Lagoon, Cook Inlet, Alaska (a ⇒ a)	8	12.7	0.43	0.71	0.3	SR
Kitimat, B.C. (a ⇒ a)	11	69.8	0.90	0.10	5.9	SR
Kodiak Archipelago, Alaska (a ⇒ a)	42	37.2	0.76	0.15	2.0	SR
Kodiak Archipelago, Alaska (a ⇒ f)	19	9.6	0.78	0.22	1.5	SR
Lakelse River, B.C. (a ⇒ f)	8	10.8	0.71	0.00	1.9	MR and count
Lakelse River, B.C. (f ⇒ a)	8	4.4	1.00	0.43	2.0	MR and count
Lakelse River, B.C. (a ⇒ a)	9	10.8	0.75	0.88	1.2	MR and count
Lesnaya River, Sakhalin Is. (a ⇒ f)	9	36.1	0.75	0.00	1.4	Count
Lower Skeena, B.C. (a ⇒ a)	11	7.6	0.70	0.30	1.8	SR
Lutoga River, Sakhalin Is. (a ⇒ f)	20	29.7	0.95	0.11	2.4	Count
Lutoga River, Sakhalin Is. (f ⇒ a)	19	17.6	0.94	0.06	2.1	Count
Lutoga River, Sakhalin Is. (a ⇒ a)	19	29.7	1.00	0.33	2.8	Count
North Coast Area 4, B.C. (a ⇒ a)	11	8.9	0.50	0.90	1.1	SR
Northern Panhandle, Alaska (a ⇒ a)	34	6.0	0.92	0.11	2.0	SR
Pokosnaya River, Sakhalin Is. (a ⇒ f)	25	384.6	0.88	0.06	8.1	Count
Pokosnaya River, Sakhalin Is. (f ⇒ a)	24	244.2	0.57	0.04	4.9	Count
Pokosnaya River, Sakhalin Is. (a ⇒ a)	23	384.6	0.82	0.00	6.5	Count
Poronal River, Sakhalin Is. (a ⇒ a)	21	84.1	0.95	0.10	3.1	Count
Port Chatham, Cook Inlet, Alaska (a ⇒ a)	15	69.3	0.86	0.07	4.4	SR
Port Dick, Cook Inlet, Alaska (a ⇒ a)	27	77.3	0.96	0.04	2.3	SR
Port Graham, Cook Inlet, Alaska (a ⇒ a)	27	33.3	0.69	0.58	1.7	SR
Prince William Sound, Alaska (a ⇒ a)	25	17.0	0.58	0.00	2.4	SR
Rocky River, Cook Inlet, Alaska (a ⇒ a)	20	85.0	0.32	0.03	1.4	SR
Sashin Creek, Alaska (a ⇒ f)	25	11,084.8	0.83	0.08	17.1	Count
Seldovia, Cook Inlet, Alaska (a ⇒ a)	27	14.8	0.15	0.23	1.1	SR
Southern Panhandle, Alaska (a ⇒ a)	34	8.3	0.94	0.15	2.3	SR
Sunday Creek, Cook Inlet, Alaska (a ⇒ a)	18	1,090.0	0.71	0.26	2.9	SR
Upper Skeena, B.C. (a ⇒ a)	11	19.6	1.00	0.20	1.5	SR
Utka River, Kamchatka (a ⇒ f)	12	182.0	0.45	0.00	2.0	Count
Utka River, Kamchatka (f ⇒ a)	10	7.7	0.78	0.06	10.4	Count
Utka River, Kamchatka (a ⇒ a)	10	124.7	0.67	1.00	2.9	Count
Windy Left, Cook Inlet, Alaska (a ⇒ a)	27	748.0	0.96	0.08	7.0	SR
Windy Right, Cook Inlet, Alaska (a ⇒ a)	27	187.0	0.88	0.19	3.6	SR
Chum salmon (*Oncorhynchus keta*)						
Central Coast, B.C. (a ⇒ a)	30	4.8	1.00	0.24	1.5	SR
Fraser River, B.C. (a ⇒ a)	14	5.0	1.00	0.00	2.0	SR
Hooknose Creek, B.C. (a ⇒ f)	14	15.4	0.92	0.00	2.5	Count
Johnstone Strait (a ⇒ a)	28	4.7	0.89	0.63	2.0	SR

Continued on next page

Table 1 (continued)

Population	n	$\frac{S_{max}}{S_{min}}$	r_{max}	r_{min}	$\frac{\overline{R}_{above}}{\overline{R}_{below}}$	Method
Minter Creek, Washington (a ⇒ f)	14	352.5	1.00	0.08	4.2	Count
North Coast, B.C. (a ⇒ a)	30	4.6	0.48	0.24	1.0	SR
Queen Charlotte Islands, B.C. (a ⇒ a)	25	11.0	0.21	0.04	1.0	SR
West Coast Vancouver Island, B.C. (a ⇒ a)	25	6.0	0.83	0.21	1.6	SR
Coho salmon (*Oncorhynchus kisutch*)						
Minter Creek, Washington (a ⇒ s)	10	14.2	0.39	0.00	1.1	Count
Steelhead trout (*Oncorhynchus mykiss*)						
Keogh River, B.C. (s ⇒ a)	7	5.7	1.00	0.00	3.3	Count
Keogh River, B.C. (a ⇒ f)	7	5.6	1.00	0.00	3.4	MR and removal
Keogh River, B.C. (a ⇒ s)	7	5.6	1.00	0.33	1.2	MR and count
Sockeye salmon (*Oncorhynchus nerka*)						
Adams Complex, B.C. (a ⇒ a)	39	7,498.8	0.95	0.00	160.8	SR
Ayakulik, Kodiak Island, Alaska (a ⇒ a)	22	25.6	0.95	0.00	2.9	SR
Babine Lake, B.C. (s ⇒ a)	23	14.6	0.86	0.36	1.8	MR and count
Babine Lake, B.C. (f ⇒ s)	23	10.0	0.86	0.23	3.0	MR and count
Babine Lake, B.C. (a ⇒ s)	10	14.7	1.00	0.22	3.6	MR and count
Birkenhead River, B.C. (a ⇒ a)	39	33.0	0.95	0.05	1.4	SR
Black Lake, Alaska (a ⇒ a)	38	22.3	0.69	0.22	2.3	SR
Branch River, Alaska (a ⇒ a)	33	35.5	0.94	0.31	1.5	SR
Bristol Bay, Alaska (a ⇒ a)	45	13.1	0.98	0.00	2.5	SR
Chignik Lake, Alaska (a ⇒ a)	38	7.2	0.31	0.08	0.9	SR
Chilko Lake, B.C. (a ⇒ s)	44	88.2	1.00	0.00	3.5	Count
Chilko River, B.C. (a ⇒ a)	39	72.5	0.68	0.11	2.9	SR
Chilko River, B.C. (s ⇒ a)	41	29.6	0.65	0.03	3.5	Count
Chilko South End, B.C. (s ⇒ a)	14	485.1	1.00	0.15	8.3	Count
Columbia River (a ⇒ a)	19	126.3	0.50	0.00	1.2	SR
Early Stuart Complex, B.C. (a ⇒ a)	39	305.8	0.97	0.00	4.7	SR
Egegik River, Alaska (a ⇒ a)	32	8.3	0.95	0.13	2.0	SR
Egegik River, Alaska (a ⇒ a)	39	8.9	0.84	0.08	2.6	SR
Egegik River, Alaska (a ⇒ s)	12	4.0	0.64	0.36	1.4	SR
Frazer Lake, Alaska (a ⇒ a)	24	54.0	0.63	0.00	3.2	SR
Fulton River, B.C. (a ⇒ f)	28	25.3	0.70	0.22	1.3	Count
Fulton River, Channel 1, B.C. (a ⇒ f)	21	48.1	0.80	0.00	1.8	Count
Fulton River, Channel 2, B.C. (a ⇒ f)	17	6.3	0.94	0.62	1.1	Count
Gates Creek, B.C. (f ⇒ a)	16	741.2	0.80	0.00	6.9	Count
Horsefly River, B.C. (a ⇒ a)	39	27,562.1	1.00	0.05	714.8	SR
Igushik River, Alaska (a ⇒ a)	39	124.2	0.55	0.24	1.6	SR
Karluk River, Alaska (a ⇒ a)	62	8.7	0.66	0.56	1.3	SR
Karymaisky Spring, Kamchatka (a ⇒ f)	8	34.0	1.00	0.00	5.0	Count
Kasilof River, Alaska (a ⇒ a)	21	13.0	0.90	0.10	2.3	SR
Kenai River, Alaska (a ⇒ a)	21	27.1	1.00	0.20	2.5	SR
Kvichak River, Alaska (a ⇒ s)	23	77.3	0.82	0.05	3.9	Count
Kvichak River, Alaska (a ⇒ a)	38	107.2	0.95	0.14	7.6	SR
Lake Dalnee, Kamchatka (a ⇒ s)	12	7.6	0.55	0.27	1.3	Count
Lakelse Lake, B.C. (a ⇒ s)	8	14.8	0.86	0.14	1.8	Count
Late Nadina River, B.C. (f ⇒ a)	11	15.6	0.60	0.00	5.9	Count
Late Stuart Complex, B.C. (a ⇒ a)	38	18,441.8	0.92	0.16	27.9	SR
Little Kitoi Lake, Afognak Is., Alaska (a ⇒ s)	7	9.2	0.50	0.00	1.4	Count
Naknek, Alaska (a ⇒ a)	38	26.4	0.92	0.07	1.9	SR
Naknek-Kvichak Rivers, Alaska (a ⇒ a)	32	16.2	0.95	0.00	1.9	SR
Nushagak River, Alaska (a ⇒ a)	32	33.7	0.58	0.00	1.3	SR
Nuyakuk River, Alaska (a ⇒ a)	20	30.9	0.84	0.47	3.4	SR
Pinkut Channel, B.C. (a ⇒ f)	17	3.2	0.94	0.69	1.5	Count
Pinkut Creek, B.C. (a ⇒ f)	26	27.4	0.44	0.08	1.5	Count
Port John Lake, B.C. (a ⇒ s)	9	30.9	0.50	0.62	0.5	Count
Quesnel Lake, Fraser River, B.C. (a ⇒ f)	10	7,211.9	0.67	0.00	2.7	Acoustics

Continued on next page

Table 1 (continued)

Population	n	$\frac{S_{max}}{S_{min}}$	r_{max}	r_{min}	$\frac{\bar{R}_{above}}{\bar{R}_{below}}$	Method
Red River, Alaska (a ⇒ a)	23	22.8	0.95	0.00	3.1	SR
Rivers Inlet, B.C. (a ⇒ a)	42	9.8	0.98	0.77	1.0	SR
Shuswap Lake, Fraser River, B.C. (a ⇒ f)	14	256.0	0.62	0.23	2.7	Acoustics
Skeena River, B.C. (a ⇒ a)	39	16.0	0.87	0.03	1.4	SR
Smith Inlet, B.C. (a ⇒ a)	10	2.8	0.72	1.00	1.3	SR
Stellako River, B.C. (a ⇒ a)	39	17.1	0.97	0.11	2.6	SR
Tahltan Lake, B.C. (a ⇒ f)	9	26.5	0.12	0.75	0.6	Count
Tahltan Lake, B.C. (a ⇒ s)	9	26.5	0.12	0.88	0.5	Count
Tahltan Lake, B.C. (a ⇒ a)	12	8.3	0.18	0.36	0.8	SR
Tally Creek, B.C. (a ⇒ f)	11	6.7	0.70	0.20	2.4	Count
Togiak River, Alaska (a ⇒ a)	14	9.0	0.85	0.62	1.3	SR
Togiak River, Alaska (a ⇒ a)	33	21.1	0.78	0.34	1.8	SR
Ugashik River, Alaska (a ⇒ a)	30	9.2	0.90	0.72	2.0	SR
Ugashik River, Alaska (a ⇒ a)	38	85.5	1.00	0.05	2.8	SR
Ugashik River, Alaska (a ⇒ s)	9	3.8	0.50	0.38	0.9	SR
Upper Pinkut Creek, B.C. (a ⇒ f)	9	3.4	1.00	0.75	1.2	Count
Weaver Creek, B.C. (a ⇒ a)	39	190.1	1.00	0.11	3.1	SR
Weaver Creek, B.C. (f ⇒ a)	26	16.4	1.00	0.44	1.9	Count
Wood River, Alaska (a ⇒ a)	40	12.9	0.38	0.03	1.5	SR
Chinook salmon (*Oncorhynchus tshawytscha*)						
Wild Canadian Coastwide (a ⇒ a)	26	2.1	0.28	0.88	0.9	SR
Atlantic salmon (*Salmo salar*)						
Bec-Scie, Canada (a ⇒ s)	5	2.5	1.00	0.50	1.5	Count
Ellidaar River, Iceland (a ⇒ a)	37	7.7	0.25	0.69	1.0	Count
Girnock Burn, Scotland (a ⇒ p)	9	5.2	0.25	0.00	1.3	Count
Little Codroy River, Canada (a ⇒ s)	7	16.6	1.00	0.00	1.5	Count
Margaree River, N.S., Canada (a ⇒ a)	37	13.3	0.94	0.22	1.4	Count
Miramichi River, N.B., Canada (a ⇒ p)	13	5.7	0.92	0.00	1.8	Count
Pollett River, Canada (a ⇒ s)	8	28.7	1.00	0.71	2.4	Count
Restigouche River, Canada (a ⇒ p)	11	6.8	0.50	0.20	1.6	Count
River Bush, Northern Ireland (a ⇒ f)	12	4.5	0.27	0.00	0.8	Count and electrofishing
River Bush, Northern Ireland (a ⇒ s)	17	4.5	0.56	0.00	1.1	Count
Shelligan Burn, Section D, Scotland (f ⇒ a)	6	12.0	0.20	0.00	0.9	Count
Tobique River, Canada (a ⇒ a)	9	57.8	0.75	0.00	1.7	Count
Trinite, Canada (a ⇒ s)	8	2.9	1.00	0.57	0.9	Count
Western Arm Brook, Canada (a ⇒ a)	16	13.2	0.47	1.00	0.7	Count
Western Arm Brook, Canada (a ⇒ s)	15	13.2	1.00	0.14	1.4	Count
Brook trout (*Salvelinus fontinalis*)						
Hunt Creek, Michigan (a ⇒ f)	9	2.0	0.88	0.62	1.0	Count
Scorpaeniformes						
Scorpaenidae						
Pacific ocean perch (*Sebastes alutus*)						
Aleutian Is.	30	6.8	0.97	0.79	0.8	SPA
Gulf of Alaska	31	17.1	0.97	0.57	1.9	SPA
U.S. West Coast	29	7.6	0.86	0.07	2.9	SPA
Widow rockfish (*Sebastes entomelas*)						
W. U.S. + Canada	12	5.3	0.73	0.82	1.0	SPA
Redfish (*Sebastes marinus*)						
W. Greenland and Iceland	10	2.9	0.22	0.67	0.2	RV and SPA
Iceland	7	1.4	1.00	0.50	1.2	SPA
Redfish (*Sebastes mentella*)						
North East Arctic	23	19.6	0.91	0.05	3.9	SPA and RV
Squaliformes						
Squalidae						
Spiny dogfish (*Squalus acanthias*)						
Northwest Atlantic	21	11.2	0.85	0.05	1.3	RV

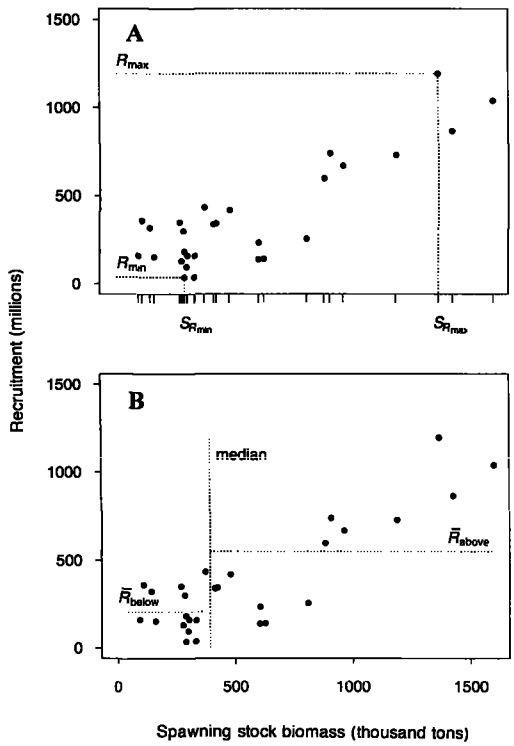

Figure 1

Illustration of the three nonparametric methods applied to spawner-recruitment data for Labrador–Newfoundland cod (Cod NAFO 2J3KL, Table 1). Here spawner abundance is measured as spawning stock biomass. (**A**) The maximum recruitment is R_{max} and the corresponding spawner abundance is S_{Rmax}, which ranks 26th out of 28. Hence r_{max} = (26–1)/(28–1) ≈ 0.93. Similarly, the minimum recruitment is R_{min} and the corresponding spawner abundance is S_{Rmin} which ranks 8.5 out of 28 (since there is a tie). Hence r_{max} = (8.5 –1)/(28 –1) ≈ 0.28. (**B**) The mean recruitment below the median spawner abundance is $\bar{R}_{below}$ whereas the mean recruitment above the median spawner abundance is $\bar{R}_{above}$.

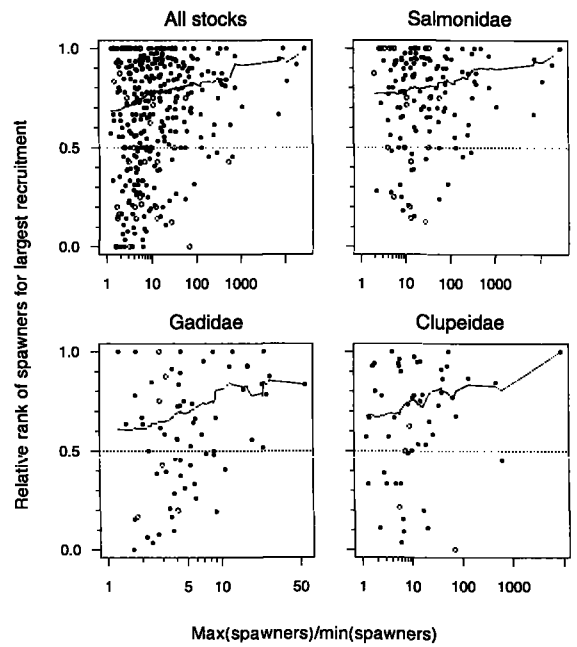

Figure 2

Scatter plots of the relative rank of spawner abundance for the highest recruitment versus the ratio S_{max}/S_{min} for all stocks and for three major families. Data points from series with fewer than 10 pairs of observations are shown as open circles. The horizontal axis has a logarithmic scale. If spawner abundance and recruitment were independent, the distributions would be expected to have a median of 0.5. To help summarize the data, we superimposed curves representing cumulative (from the right) weighted means on the plots in each figure.

tested the null hypothesis that the weighted mean relative rank is less than or equal to 0.5 versus the alternative hypothesis that it is greater than 0.5. A sampled randomization test (Manly, 1991) of the null hypothesis of independence was easily performed. For the ith series, a random rank between 1 and n_i was selected, and the corresponding relative rank computed. This was performed for each series, and the weighted mean of the relative ranks was then computed. Repetition of this procedure (10,000 times sampling with replacement) gives an empirical null distribution of weighted mean relative ranks. If m of these 10,000 weighted means were greater than or equal to the observed weighted mean, we then assigned a one-sided P-value of $\frac{m+1}{10{,}001}$. The smallest one-sided P-value is thus $\frac{1}{10{,}001}$.

As with the cumulative weighted means, we took into account the varying reliability of the data based on the range of spawner abundance. Therefore, we performed significance tests beginning with the data having large values of S_{max}/S_{min} and progressively including data with smaller values of S_{max}/S_{min}.

For each family, the highest recruitment tends to occur when spawner abundance is high (Fig. 2). The cumulative weighted means never fell below 0.5 for any family. The cumulative weighted mean began on the right-hand side and accumulated to the left-hand side because we had greater confidence in the relative ranks obtained from time series having wide ranges of spawner abundance. Consequently, the value of the cumulative weighted mean on the extreme left-hand side encompassed all the data shown in the plot. Using the sample size as a weighting factor, we incorporated a greater confidence in the relative ranks obtained from long time series. The randomized test showed that the null hypothesis that

the weighted mean relative rank is less than or equal to 0.5 can be rejected for all stocks combined and for most of the taxonomic groups considered (Table 2A). In moving from left to right in the figure, the sample size used in the test decreased, whereas the reliability of the data (as gauged by S_{max}/S_{min}) increased. The tests were performed for all stocks, and separately for 3 major families. The overall trend of increase from left to right was due to the loss of power as the sample size used in the test decreased.

Hypothesis 2: Does the smallest recruitment occur when spawner abundance is low?

Next, we examined r_{min}, the relative rank of spawner abundance for the lowest recruitment (Fig. 1A). This time, $r_{min} = 0$ implies that the lowest recruitment occurs for the lowest spawner abundance, whereas $r_{min} = 1$ implies that the lowest recruitment occurs for the highest spawner abundance. As before, cumulative weighted means were calculated and a randomization test was performed.

The lowest recruitment tended to occur when spawner abundance was low (Fig. 3). Again, the pattern held for all stocks combined and for most of the taxonomic groups considered. The effect for the lowest recruitment appeared to be less than the effect for highest recruitment. The statistical significance of the results is usually less than 0.05, but there is a tendency for the significance to be reduced if the range of spawners is small (Table 2B).

Hypothesis 3: Is recruitment greater if spawner abundance is above rather than below the median?

Finally, for each spawner-recruitment series we asked whether the mean recruitment is the same when the spawner abundance is below or above the median. We split each spawner-recruitment series into two sections: the first section at or below the median spawner abundance, and the second section above the median spawner abundance. We then computed the mean recruitment for each section, which we denote as $\overline{R}_{above}$ and $\overline{R}_{below}$ respectively. When the mean recruitment is identical on both sides of the median spawner abundance, the ratio $\overline{R}_{above}/\overline{R}_{below}$ equals 1, or equivalently $\log(\overline{R}_{above}/\overline{R}_{below}) = 0$. A distribution-free test of this null hypothesis is the one-sample Wilcoxon signed rank test (Conover, 1980; Lehmann, 1975). We computed the ranks of the absolute values of the log ratios. The test statistic was given by the sum of the ranks of the positive log ratios. The logarithm was used because ratios of (for example) 1:2 and 2:1 would result in ties.

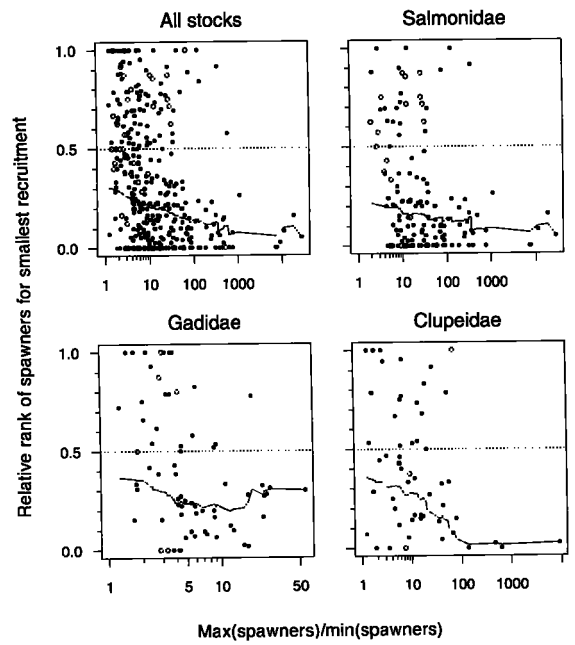

Figure 3

Scatter plots of the relative rank of the spawner abundance for the lowest recruitment versus the ratio S_{max}/S_{min} for all stocks and for three major families. See Figure 2 for explanation of data points, axis labels, and lines.

Our alternative hypothesis was that the median of the distribution of log ratios was greater than 0. For this one-sided test, in order to reject the null hypothesis (at the 5% significance level), we required at least 5 observations. When there were 25 or fewer log ratios, an exact probability for the test was computed; otherwise a normal approximation was used. Note that there were no ties in the absolute values of the log ratios.

This test is conservative because errors in the estimates of the range will bias the estimate of the slope downward (Judge et al., 1984). The ratio of the mean recruitment above the median level of spawners to that below, $\overline{R}_{above}/\overline{R}_{below}$, is greater than 1 for all families if the range of observed spawners is large (Fig. 4). For narrow ranges of spawner data, the ratio is closely clustered. When the data are grouped taxonomically, the pattern holds. The Wilcoxon signed rank test shows that the null hypothesis that the median of the distribution of $\overline{R}_{above}/\overline{R}_{below}$ is 1 can be rejected for all stocks combined and for most of the taxonomic groups considered.

Taxonomic variation

The Clupeidae show strong evidence of greater recruitment at large spawner-abundance levels. This

Table 2

Observed levels of significance for tests based on the data shown in Figure 2 (A) in Figure 3 (B), and in Figure 4 (C). The tests were conducted by using the data with $S_{max}/S_{min} \geq 1$, 2, 5, 10, 50, and 100. As this lower limit increases, the reliability of the data improves; however, the number of samples (shown in parentheses) decreases, thereby decreasing the power of the test. Empty cells indicate that there were no observations with the specified values of S_{max}/S_{min}. For populations within the family Salmonidae, series were sometimes available for several different life-stage transitions. The life stages are denoted as follows: a = adults (or eggs); f = fry; s = smolt; and p = parr. They are shown in the table with an arrow notation so that "a ⇒ f" means spawners were adults and recruits were fry or smolts.

A *P*-values corresponding to Figure 2 from one-sided randomization tests with 10,000 samples (with associated numbers of data sets in parentheses). The null hypothesis is that the weighted mean relative rank is less than or equal to 0.5. The alternative hypothesis is that the weighted mean relative rank is greater than 0.5.

	S_{max}/S_{min}											
Group	≥1		≥2		≥5		≥10		≥50		≥100	
All stocks	< 0.0001	(364)	< 0.0001	(338)	< 0.0001	(243)	< 0.0001	(162)	< 0.0001	(61)	< 0.0001	(35)
Clupeidae	< 0.0001	(55)	0.0002	(48)	0.0001	(40)	< 0.0001	(26)	0.0044	(9)	0.014	(4)
Herring	0.0007	(37)	0.0018	(30)	0.0006	(25)	< 0.0001	(16)	0.017	(5)	0.04	(3)
Sardine	0.18	(7)	0.18	(7)	0.31	(6)	0.2	(5)	0.28	(2)	0.16	(1)
Gadidae	0.004	(68)	0.0025	(61)	0.0003	(28)	< 0.0001	(13)	0.19	(1)		
Cod	0.023	(23)	0.014	(21)	0.024	(11)	0.0042	(5)	0.19	(1)		
Haddock	0.012	(9)	0.012	(9)	0.028	(6)	0.021	(5)				
Merluccius	0.043	(12)	0.047	(9)	0.0082	(4)	0.074	(2)				
Pollock or saithe	0.74	(6)	0.78	(5)	0.49	(2)						
Percidae	0.34	(9)	0.25	(8)	0.33	(5)	0.32	(4)	0.19	(2)	0.19	(2)
Scombridae	0.024	(9)	0.025	(8)	0.06	(6)	0.26	(4)	0.14	(1)		
Sparidae	0.23	(6)	0.23	(6)	0.008	(3)	0.24	(1)	0.24	(1)	0.25	(1)
Pleuronectidae	0.63	(19)	0.63	(17)	0.21	(4)	0.079	(3)				
Plaice	0.63	(8)	0.53	(7)	0.36	(1)	0.36	(1)				
Soleidae	0.45	(7)	0.45	(7)	0.13	(2)						
Salmonidae	< 0.0001	(150)	< 0.0001	(149)	< 0.0001	(133)	< 0.0001	(101)	< 0.0001	(44)	< 0.0001	(26)
Pink salmon	< 0.0001	(53)	< 0.0001	(53)	< 0.0001	(50)	< 0.0001	(42)	< 0.0001	(24)	0.0007	(13)
(a ⇒ a)	< 0.0001	(36)	< 0.0001	(36)	< 0.0001	(34)	< 0.0001	(28)	0.0001	(18)	0.0018	(9)
(a ⇒ f)	0.0098	(11)	0.0094	(11)	0.0091	(11)	0.017	(10)	0.15	(5)	0.067	(3)
(f ⇒ a)	0.023	(6)	0.022	(6)	0.041	(5)	0.059	(4)	0.46	(1)	0.45	(1)
Chum salmon	0.0092	(8)	0.0082	(8)	0.049	(5)	0.29	(3)	0.074	(1)	0.074	(1)
Sockeye salmon	< 0.0001	(65)	< 0.0001	(65)	< 0.0001	(60)	< 0.0001	(46)	< 0.0001	(17)	< 0.0001	(12)
(a ⇒ a)	< 0.0001	(37)	< 0.0001	(37)	< 0.0001	(36)	< 0.0001	(27)	< 0.0001	(11)	< 0.0001	(8)
(a ⇒ f,s)	0.0009	(21)	0.0014	(21)	0.0042	(17)	0.01	(13)	0.012	(4)	0.28	(2)
(f,s ⇒ a)	0.007	(6)	0.0079	(6)	0.008	(6)	0.0081	(6)	0.032	(2)	0.03	(2)
Atlantic salmon	0.065	(15)	0.068	(15)	0.091	(11)	0.0055	(7)	0.33	(1)		
Scorpaenidae	0.0007	(7)	0.0017	(6)	0.0005	(5)	0.012	(2)				

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relationship clearly holds for herring, whereas the evidence for sardines is not as strong.

The Gadidae, and particularly cod, show strong evidence for all three hypotheses. Haddock show strong evidence for the first two hypotheses, and weak nonsignificance for the third. The hakes of the genus *Merluccius*, show strong evidence for the hypothesis that strong year classes result from relatively high spawner abundance, fair evidence that the mean recruitment is greater for larger spawner abundances, and no evidence for the second hypothesis, except if there is a wide range of spawner abundances.

There is a relatively small range in observed spawner abundances for pollock, known as "saithe" in the eastern Atlantic. Given the narrow range of observed spawner abundances, there is evidence against the first hypothesis, some evidence for the second hypothesis, and no evidence for the third. An examination of the spawner recruitment curves for this species shows stronger evidence for overcompensation, i.e. reduced recruitment at high spawner abundances, than for any other group (see plots in Myers et al., 1995b). This species appears to be more cannibalistic than other Gadidae. Whiting, which is also highly cannibalistic, shows a similar narrow

Table 2 (continued)

B *P*-values corresponding to Figure 3 from one-sided randomization tests with 10,000 samples (with associated numbers of data sets in parentheses). The null hypothesis is that the weighted mean relative rank is greater than or equal to 0.5. The alternative hypothesis is that the weighted mean relative rank is less than 0.5.

	S_{max}/S_{min}					
Group	≥1	≥2	≥5	≥10	≥50	≥100
All stocks	< 0.0001 (364)	< 0.0001 (338)	< 0.0001 (243)	< 0.0001 (162)	< 0.0001(61)	< 0.0001 (35)
Clupeidae	0.0004 (55)	0.0003 (48)	0.0002 (40)	0.0004 (26)	0.0003 (9)	(4)
Herring	0.0021 (37)	0.0014 (30)	0.0002 (25)	0.0002 (16)	0.0011 (5)	(3)
Sardine	0.5 (7)	0.52 (7)	0.59 (6)	0.49 (5)	0.15 (2)	0.032 (1)
Gadidae	0.0007 (68)	0.0001 (61)	< 0.0001 (28)	0.0001 (13)	0.32 (1)	
Cod	0.0037 (23)	0.0042 (21)	0.0003 (11)	0.018 (5)	0.33 (1)	
Haddock	0.001 (9)	0.0006 (9)	0.0093 (6)	0.0053 (5)		
Merluccius	0.68 (12)	0.5 (9)	0.13 (4)	0.19 (2)		
Pollock or saithe	0.26 (6)	0.28 (5)	0.018 (2)			
Percidae	0.63 (9)	0.6 (8)	0.78 (5)	0.7 (4)	0.3 (2)	0.29 (2)
Scombridae	0.011 (9)	0.009 (8)	0.013 (6)	0.16 (4)	0.26 (1)	
Sparidae	< 0.0001 (6)	0.0001 (6)	0.0002 (3)	0.059 (1)	0.065 (1)	0.057 (1)
Pleuronectidae	0.11 (19)	0.068 (17)	0.03 (4)	0.01 (3)		
Plaice	0.21 (8)	0.089 (7)	0.18 (1)	0.19 (1)		
Soleidae	0.75 (7)	0.75 (7)	0.45 (2)			
Salmonidae	< 0.0001 (150)	< 0.0001 (149)	< 0.0001 (133)	< 0.0001 (101)	< 0.0001(44)	< 0.0001 (26)
Pink salmon	< 0.0001 (53)	< 0.0001 (53)	< 0.0001 (50)	< 0.0001 (42)	< 0.0001(24)	0.0002 (13)
(a ⇒ a)	< 0.0001 (36)	< 0.0001 (36)	< 0.0001 (34)	< 0.0001 (28)	< 0.0001(18)	0.013 (9)
(a ⇒ f)	< 0.0001 (11)	< 0.0001 (11)	< 0.0001 (11)	< 0.0001 (10)	0.0001 (5)	0.0023 (3)
(f ⇒ a)	0.0005 (6)	0.0004 (6)	0.0001 (5)	0.0015 (4)	0.081 (1)	0.081 (1)
Chum salmon	0.0034 (8)	0.0042 (8)	0.0004 (5)	0.0025 (3)	0.15 (1)	0.14 (1)
Sockeye salmon	< 0.0001 (65)	< 0.0001 (65)	< 0.0001 (60)	< 0.0001 (46)	< 0.0001(17)	< 0.0001 (12)
(a ⇒ a)	< 0.0001 (37)	< 0.0001 (37)	< 0.0001 (36)	< 0.0001 (27)	< 0.0001(11)	< 0.0001 (8)
(a ⇒ f,s)	0.0005 (21)	0.0004 (21)	0.0001 (17)	0.0002 (13)	0.0002 (4)	0.049 (2)
(f,s ⇒ aa)	0.0055 (6)	0.0049 (6)	0.0042 (6)	0.0047 (6)	0.024 (2)	0.026 (2)
Atlantic salmon	0.026 (15)	0.026 (15)	0.099 (11)	0.11 (7)	0.11 (1)	
Scorpaenidae	0.36 (7)	0.36 (6)	0.33 (5)	0.24 (2)		

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range in observed spawner abundance and provides no evidence for our hypotheses.

Within the Perciformes, the freshwater Percidae, represented by perch of the genus *Perca*, and walleye and pikeperch of the genus *Stizostedion*, provide moderate evidence for the three hypotheses only when there is a very wide range of observed spawner abundance. However, for most of the marine species of the order Perciformes (e.g. the Scombridae, the mackerel and tunas, and the Sparidae, the sea breams) there was very strong evidence for all three hypotheses. One explanation for this pattern is that freshwater species for which we had data may have been less subject to overexploitation, but the question certainly deserves further study.

The order that showed the weakest amount of the relationship between the abundance of spawners and subsequent recruitment was the flatfish, i.e. the Pleuronectiformes. There was evidence for this relationship with both Pleuronectidae and Soleidae in all the tests for wider ranges in spawner abundance, i.e. the *P*-values in Table 2 were less than 0.5; however, these relationships were not statistically significant. The relatively weak relationship for flatfish may be caused by the strong density-dependent mortality for these populations (Myers and Cadigan, 1993; Iles, 1994). Furthermore, many of these populations have juvenile nursery grounds in regions where exploitation cannot take place. For these reasons, the range of spawner abundance has been relatively narrow, which reduces our ability to detect any relationship.

For the salmonids included in this analysis, large year classes almost always are associated with high spawner levels. This conclusion is true for the pink, chum, sockeye, and Atlantic salmon for each life-stage transition considered (Table 2). Our conclusion differs from that of Larkin (1977), who stated that for the Pa-

Table 2 (continued)

C *P*-values corresponding to Figure 4 from one-sample Wilcoxon signed-rank tests (with associated numbers of data sets in parentheses). The null hypothesis is that the median of $\log(R_{above}/R_{below})$, is less than or equal to 0. The alternative hypothesis is that the median is greater than 0. For this test, at least 5 observations were required to obtain a *P*-value less than 0.05.

	S_{max}/S_{min}											
Group	≥1		≥2		≥5		≥10		≥50		≥100	
All stocks	< 0.0001	(364)	< 0.0001	(338)	< 0.0001	(243)	< 0.0001	(162)	< 0.0001	(61)	< 0.0001	(35)
Clupeidae	0.0041	(55)	0.0068	(48)	0.0018	(40)	< 0.0001	(26)	0.0039	(9)	0.062	(4)
Herring	0.025	(37)	0.04	(30)	0.0031	(25)	0.0013	(16)	0.031	(5)	0.12	(3)
Sardine	0.15	(7)	0.15	(7)	0.16	(6)	0.062	(5)	0.5	(2)	0.5	(1)
Gadidae	0.0016	(68)	0.0011	(61)	0.00028	(28)	0.00061	(13)	0.5	(1)		
Cod	0.0017	(23)	0.00069	(21)	0.00098	(11)	0.031	(5)	0.5	(1)		
Haddock	0.33	(9)	0.33	(9)	0.22	(6)	0.16	(5)				
Merluccius	0.076	(12)	0.027	(9)	0.062	(4)	0.25	(2)				
Pollock or saithe	0.28	(6)	0.5	(5)	0.25	(2)						
Percidae	0.54	(9)	0.42	(8)	0.59	(5)	0.56	(4)	0.25	(2)	0.25	(2)
Scombridae	0.064	(9)	0.098	(8)	0.22	(6)	0.44	(4)	0.5	(1)		
Sparidae	0.047	(6)	0.047	(6)	0.12	(3)	0.5	(1)	0.5	(1)	0.5	(1)
Pleuronectidae	0.24	(19)	0.24	(17)	0.19	(4)	0.12	(3)				
Plaice	0.32	(8)	0.23	(7)	0.5	(1)	0.5	(1)				
Soleidae	0.53	(7)	0.53	(7)	0.25	(2)						
Salmonidae	< 0.0001	(150)	< 0.0001	(149)	< 0.0001	(133)	< 0.0001	(101)	< 0.0001	(44)	< 0.0001	(26)
Pink salmon	< 0.0001	(53)	< 0.0001	(53)	< 0.0001	(50)	< 0.0001	(42)	< 0.0001	(24)	0.00012	(13)
(a ⇒ a)	< 0.0001	(36)	< 0.0001	(36)	< 0.0001	(34)	< 0.0001	(28)	< 0.0001	(18)	0.002	(9)
(a ⇒ f)	0.00098	(11)	0.00098	(11)	0.00098	(11)	0.002	(10)	0.062	(5)	0.12	(3)
(f ⇒ a)	0.016	(6)	0.016	(6)	0.031	(5)	0.062	(4)	0.5	(1)	0.5	(1)
Chum salmon	0.012	(8)	0.012	(8)	0.031	(5)	0.12	(3)	0.5	(1)	0.5	(1)
Sockeye salmon	< 0.0001	(65)	< 0.0001	(65)	< 0.0001	(60)	< 0.0001	(46)	< 0.0001	(17)	0.00024	(12)
(a ⇒ a)	< 0.0001	(37)	< 0.0001	(37)	< 0.0001	(36)	< 0.0001	(27)	0.00049	(11)	0.0039	(8)
(a ⇒ f,s)	0.0031	(21)	0.0031	(21)	0.0064	(17)	0.02	(13)	0.062	(4)	0.25	(2)
(f,s ⇒ a)	0.016	(6)	0.016	(6)	0.016	(6)	0.016	(6)	0.25	(2)	0.25	(2)
Atlantic salmon	0.021	(15)	0.021	(15)	0.021	(11)	0.11	(7)	0.5	(1)		
Scorpaenidae	0.29	(7)	0.34	(6)	0.094	(5)	0.25	(2)				

cific salmon species of the genus *Oncorhynchus*, "recruitment is maximum at some intermediate stock size." The three hypotheses hold for the four salmon species in Table 2 and for all life-stage transitions.

Discussion

Could our results be an artifact of the necessary relationship between recruitment and subsequent spawner abundance? It has been argued that the observed relationships between spawners and recruitment is a by-product of the high autocorrelations present in some spawner and recruitment series. Consider a simple example in which recruitment is unrelated to the spawner abundance but is completely determined by the environment. Let recruitment be a first-order autoregressive process with autocorrelation parameter ρ, i.e. the correlation of recruitment with lag t is ρ^t. For a semelparous species, or a heavily-exploited species with relatively little survival after reproduction, the amount of variance in recruitment that would be "explained" by this process is ρ^{2a}, where a is the age at maturity. For example, if the age at maturity is $a = 4$ and the autocorrelation in recruitment is $\rho = 0.4$, then only 0.066% of the variance would be explained by spawner abundance. Thus, this mechanism will be important only when there is high environmental autocorrelation in recruitment and low age at maturity. However, when we restricted our analysis to data series with estimated autocorrelation less than 0.4, the observed patterns remained (Fig. 5). Alternative cutoff values for the degree of autocorrelation produced similar results. We conclude that our results are not caused by autocorrelation in recruitment and the necessary relationship between recruitment and subsequent spawner abundance.

In each of our three tests, the hypothesis that there is no practical relationship between spawners and

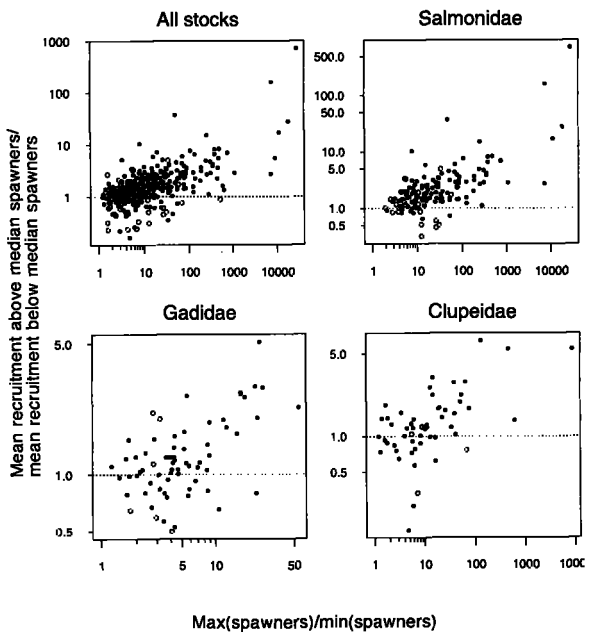

Figure 4

Scatter plots of the ratio $\overline{R}_{above}/\overline{R}_{below}$ versus the ratio S_{max}/S_{min} for all stocks, and for three major families. Data points from series with fewer than 10 pairs of observations are shown as open circles. Both axes have logarithmic scales. If spawner abundance and recruitment were independent, the distribution would be expected to have a median of 1.

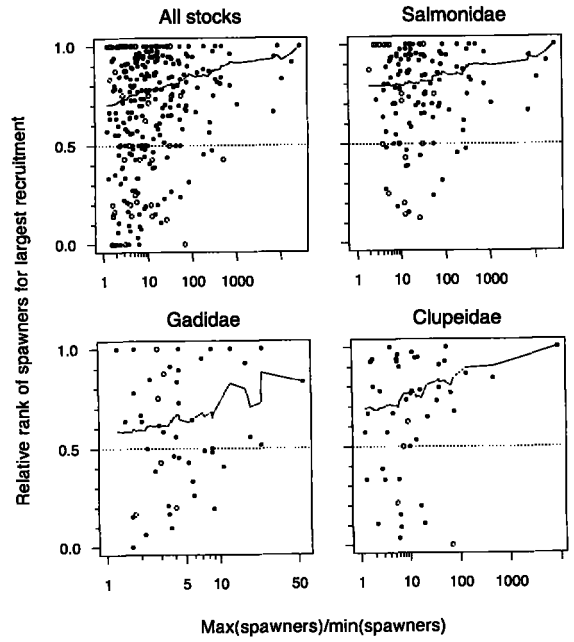

Figure 5

Test of the hypothesis that our results are caused by autocorrelation of recruitment. This scatterplot repeats the analysis shown in Figure 2 (the relative rank of spawner abundance for the highest recruitment versus the ratio S_{max}/S_{min}), except that populations with an autocorrelation in recruitment of 0.4 or greater are eliminated. Data points from series with fewer than 10 pairs of observations are shown as open circles. If spawner abundance and recruitment were independent, the distributions would be expected to have a median of 0.5. To help summarize the data, curves representing cumulative (from the right) weighted means are superimposed on the plots in each figure.

subsequent recruitment can be rejected. These conclusions hold for almost every species and family analyzed. These results also help to explain the widely-held belief that spawner abundance and recruitment are not related. When there is little variation in spawner abundance, no practical relation between spawners and subsequent recruitment may seem to be the case; however, wider ranges of spawner data reveal that the relationship holds. Sadly, many of the populations for which wide ranges of spawner data are available are those that have been fished to low levels, perhaps due, in part, to a rejection of spawner-recruitment relationships.

Our results are robust. We have considered three different approaches to our general question, and in each case the results are consistent with the hypothesis that recruitment is indeed linked to abundance of spawners. Errors in estimation of spawner abundance should have the effect of reducing the significance of our tests (Judge et al., 1984, chapter 5). For example, for our third question, errors in estimating spawner abundance would result in misclassifying observations and would reduce the magnitude of $\overline{R}_{above}/\overline{R}_{below}$. A second potential source of bias arises in the statistical analysis of spawner-recruitment relationships because the "independent" variable, spawners, is not independent of the interannual variation in the spawner-recruitment relationship. For a given spawning population, above-average recruitment tends to result in higher spawning populations, whereas below-average recruitment tends to result in lower spawning populations. This is called "time series bias" and causes the density-dependent mortality to be overestimated (Walters 1985, 1990; Myers and Barrowman, 1995). If this source of bias is important in our problem it will cause our conclusions to be conservative because the importance of density-dependent mortality will be overestimated, and thus recruitment would appear to be less positively related to spawners.

Some, who are not familiar with the fisheries literature, may consider our analysis unnecessary because the results seem obvious. However, the results

are not obvious and are not consistent with many claims that have been based on much less extensive, and less systematic, analyses. If a population is "managed" such that spawner abundance is reduced to low levels, the manager should not be surprised to observe the smallest recruitment ever recorded.

Are our results of practical importance for the management of fish populations? We believe the answer is clearly "yes." The simple observation that recruitment is generally lower at lower spawner abundances implies that recruitment overfishing is a pervasive problem among heavily exploited fish populations. The collapse of many of the fish stocks in the world, e.g. cod in eastern Canada (Myers et al., in press), can be at least partially blamed on reduced recruitment associated with reduction in spawner abundance.

We conclude that fish populations should be managed so as to maintain sufficient spawner abundance to yield high recruitment. Recruitment overfishing appears to be a common problem.

Acknowledgments

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Abstract.—The spawning seasonality of albacore, *Thunnus alalunga*, in the South Pacific was studied by examining ovaries and testes collected from longline vessels operating in the waters off New Caledonia (21°–23°S, 164°–166°E) and Tonga (16°–29°S, 171°–177°W), January 1990 to February 1992. The monthly change in GSI values and mean oocyte diameters indicated that albacore are annual spawners, with most spawning limited to the austral summer months from November to February. Asymmetry in weight of, but not in the reproductive development of, the left and right gonad pairs was apparent in samples from the two collection sites; most right ovaries and testes were heavier and larger than those on the left side.

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Spawning seasonality of albacore, *Thunnus alalunga*, in the South Pacific Ocean

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Albacore, *Thunnus alalunga*, are distributed throughout the Pacific in temperate and tropical waters. The North and South Pacific populations are considered to be separate stocks because 1) catch rates for these two populations are extremely low in the equatorial region, 2) the two populations have nonoverlapping spawning areas and different spawning seasons, and 3) there is no evidence that albacore tagged in the North Pacific move to the South Pacific (Lewis[1]). In the South Pacific, albacore are found from the Equator to 50°S latitude and from the surface to depths of 300 m (Yoneta and Saito, 1973). South Pacific albacore generally are considered to reach sexual maturity in the size range of 85 to 90 cm fork length [FL] (Ueyanagi, 1957; Otsu and Hansen, 1962), when they are usually between 6 and 8 years old (Labelle et al., 1993).

Two major fisheries target albacore in the South Pacific: a longline fishery concentrating on adult fish (80–110 cm) in tropical and subtropical waters (10°–30°S) throughout the year and a surface troll fishery targeting subadults (50–80 cm) in temperate waters (30°–40°S) during the austral summer (Lewis[1]; Rensink[2]). An area of research that was recognized by the second South Pacific Albacore Research (SPAR) workshop as needing further work was delineation of the spawning seasonality of albacore in the South Pacific. A sampling and histological project was organized by the Tuna and Billfish Assessment Programme (TBAP) of the South Pacific Commission (SPC) and the Southwest Fisheries Science Center (SWFSC) to provide a better understanding of albacore reproduction in the South Pacific. Because adult albacore at various stages of reproductive development were needed, sampling was limited to the longline fishery.

The purpose of our study is to report on the spawning seasonality of albacore in the South Pacific Ocean by using oocyte development and gonadosomatic indices as indicators of spawning activity.

* Deceased.

[1] Lewis, A. D. 1990. South Pacific albacore stock structure: a review of available information. Third South Pacific albacore research workshop; Noumea, New Caledonia, 9–12 October 1990, Working Paper 5, 13 p. South Pacific Commission, B.P. D5, Noumea Cedex, New Caledonia.

[2] Rensink, G. 1991. Summary of the 1989–90 U.S. South Pacific albacore fisheries data. Southwest Fish. Sci. Center, National Marine Fisheries Service, P.O. Box 271, La Jolla, CA 92038. Admin. Rep.14:1–21.

Materials and methods

Albacore were sampled from the catches of two longline vessels: a Japanese–New Caledonia joint-venture with longliners fishing in New Caledonia waters (21°–23°S, 164°–166°E) and unloading in Noumea, and 2) the Tonga government-owned longliner, MV *Lofa*, operating in Tonga waters (16°–29°S, 171°–177°W) (Fig.1). These sampling arrangements were selected because these vessels fished throughout the year in known spawning areas. Fishing operations took place during daylight and standard commercial longline gear was used.

Sampling was designed to cause minimum disturbance to commercial operations while providing adequate samples and data. For both sampling operations, sex, fork length (to the nearest centimeter), and gonad weight (to the nearest g, New Caledonia [females]; or to the nearest 5 g, Tonga [females and males]) were measured. In waters near New Caledonia, ovaries from each 10-cm size class (70–79 cm, 80–89 cm, 90–99 cm, and 100–110 cm) were collected each collection day, but actual quantities were dependent on the landings from the commercial operation. However, in waters near Tonga, ovaries were collected only from albacore in the 80–89 cm size class because of sampling limitations. Sampling in waters near New Caledonia was done once a week, May 1990 to February 1992, whereas sampling near Tonga occurred on every second set of the longline during January 1990 to February 1992.

In New Caledonia and aboard *Lofa*, gonads were removed from the gut cavity of albacore and identified as male or female. Each pair was separated into a left and right section and weighed fresh to the nearest 1 g in New Caledonia and to the nearest 5 g on *Lofa* for size comparison. Weights of fresh gonads included the weight of the associated fatbody.

A total of 1,105 albacore were examined and measured (300 females, 799 males, 6 undetermined); of this number, 246 pairs of ovaries and 444 pairs of testes were weighed fresh (Table 1). A subset of 150 ovaries were collected from female albacore in various stages of development for histology. A greater percentage of the ovaries collected came from New Caledonia because ovary collections from waters near Tonga were limited to ovaries from albacore in the 80–89 cm FL size range. In the laboratory, the ovary was removed from a formalin fixative, patted dry, and weighed to the nearest 0.1 g. The associated fatbody was then removed and the ovary reweighed without the fatbody; these values were then used to calculate the gonadosomatic index (GSI). Male albacore testes were not collected for histological study from either site.

Histological processing was done by staff at the Maas Diagnostic Laboratories who followed the

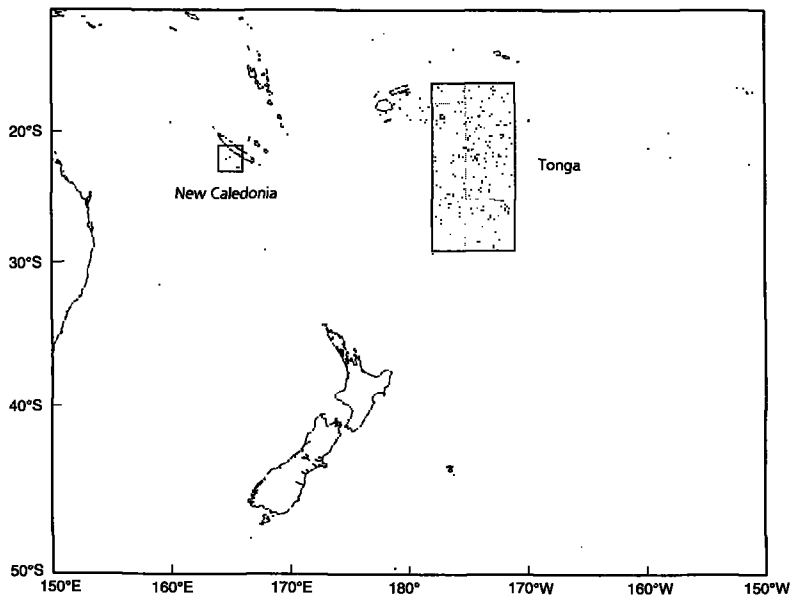

Figure 1

Sampling areas for albacore, *Thunnus alalunga*, in the South Pacific Ocean near New Caledonia and Tonga from 1990 to 1992.

Table 1

Summary of albacore gonads sampled in the South Pacific, January 1990–February 1992. Undeter. = undetermined.

Site	Sampling period	Sex	Number of albacore examined	Number of gonads weighed	Number of ovaries collected
New Caledonia	May 1990–February 1992	Female	108	104	105
		Male	239	0	0
		Undeter.	6	0	0
Tonga	January 1990–February 1992	Female	192	142	45
		Male	560	444	0

methods described in Hunter et al. (1986). A cross section of the ovary was taken from the middle region of the ovary, dehydrated, embedded in paraffin, sectioned at 7 μm, and stained with Harris's hematoxylin followed by eosin counterstain. The slides were examined with a compound microscope to determine the stage of ovarian development (as characterized by the presence or absence of yolk, lipid vesicles, hydrated oocytes, and postovulatory follicles) and were classified as early developing (unyolked), late developing (partially yolked), or advanced (fully yolked) (Schaefer, 1987). A second cross section of ovarian tissue was taken from the outer edge of the ovary to the lumen. This sample was placed in 33% glycerol for 10 to 20 minutes to separate the oocytes from the ovarian connective tissue (Hunter et al., 1986). The separated oocytes were then measured to 0.01 mm to determine the average size of the most developed stage of oocytes in each ovary; this was done by measuring the diameter of 20 oocytes in the sample as described by Schaefer (1987). The mean diameter of the most advanced stage of oocytes was plotted against months to examine the seasonal trend of maturity (Fig. 2). Oocyte diameter and developmental stage of the ovaries were examined to see if differences in weight between the right and left sides of the ovary were associated with differences in the reproductive state.

The histological condition of the samples did not provide the resolution necessary to distinguish

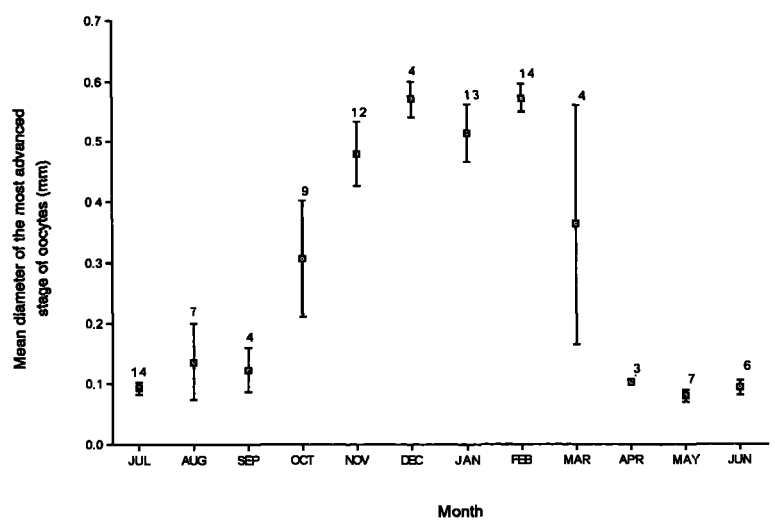

Figure 2

Monthly variation in mean diameter of the most advanced stage of oocytes for albacore, *Thunnus alalunga*, sampled from New Caledonia and Tonga, 1990 to 1992 (±2 standard errors; n=97). Numbers above error bars indicate the sample size for each month.

postovulatory follicles from preservation artifacts. Because of the time between capture and preservation, significant amounts of atresia occurred. The atresia limited the usefulness of the ovary sections because postovulatory follicles could not be distinguished from atretic conditions and histological materials.

Gonadosomatic indices (GSI) were calculated from the ovarian samples collected from New Caledonia and Tonga by using the formula of Kume and Joseph (1969):

$$GSI = 10^4 W / L^3,$$

where W = total gonad weight in grams minus fatbody and L = fork length in centimeters. The GSI was calculated only for those females whose ovaries were collected and processed in the laboratory. The critical GSI value was determined to be 1.7 according to the definition of maturity by Cayré and Farrugio (unpubl. data),[3] the value for which 100% of the females display an advanced mode of oocyte development (>0.3 mm) (Fig. 3).

[3] Cayré, P., and H. Farrugio. 1983. Biologie de la reproduction du listao *Katsuwonus pelamis* de l'Océan Atlantique. Doc. SKJ. Conf./83/12, présenté à la réunion de clôture du Programme International de Recherches sue le listro Atlantique, Teneriffe (Espagne), juin 1983, 62 p.

Results

Length-frequency distributions of sampled albacore

Length and sex data were collected on 1,105 albacore in the South Pacific. Size frequencies differed between males and females in both the New Caledonia and Tonga sites (Fig. 4, A and B). Male albacore had two size modes, 8–91 cm FL and 100–102 cm FL (Fig. 4, A and B). The relative strength of the modes differed at each sampling site. Female albacore from New Caledonia had a single mode, 86–92 cm FL (Fig. 4A), whereas females from Tonga possibly displayed two size modes, 87–89 cm FL and 92–96 cm FL (Fig. 4B). Few females over 100 cm FL were collected in either the New Caledonia or Tonga samples.

Male albacore were encountered more often than female albacore (Fig. 4, A and B). Male albacore accounted for 68.9% of the samples from New Caledonia and for 74.5% of the samples from Tonga (Table 1).

Oocyte development

The most advanced stage of oocytes collected during the austral winter months was the unyolked oocytes

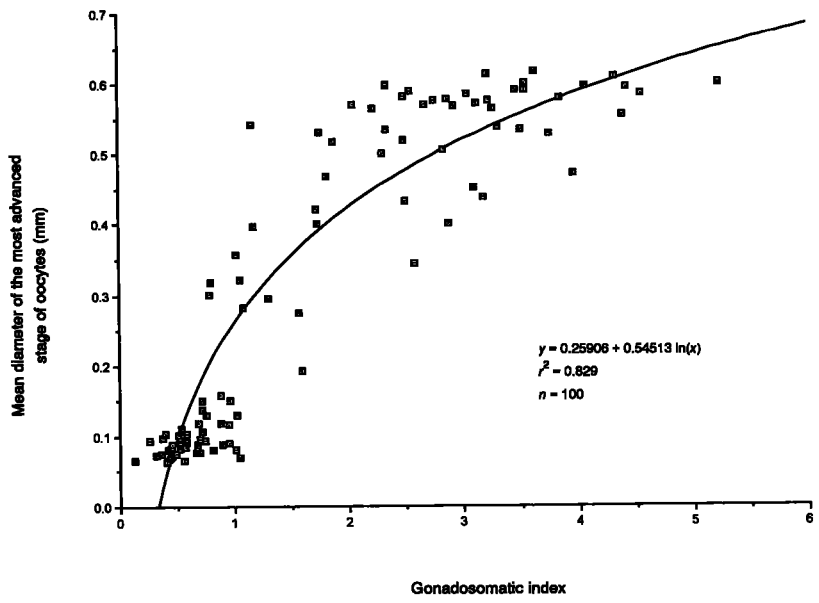

Figure 3

Relationship between the mean diameter of the most advanced stage of oocytes and the gonadosomatic index of female albacore, *Thunnus alalunga*, sampled from New Caledonia and Tonga, 1990 to 1992.

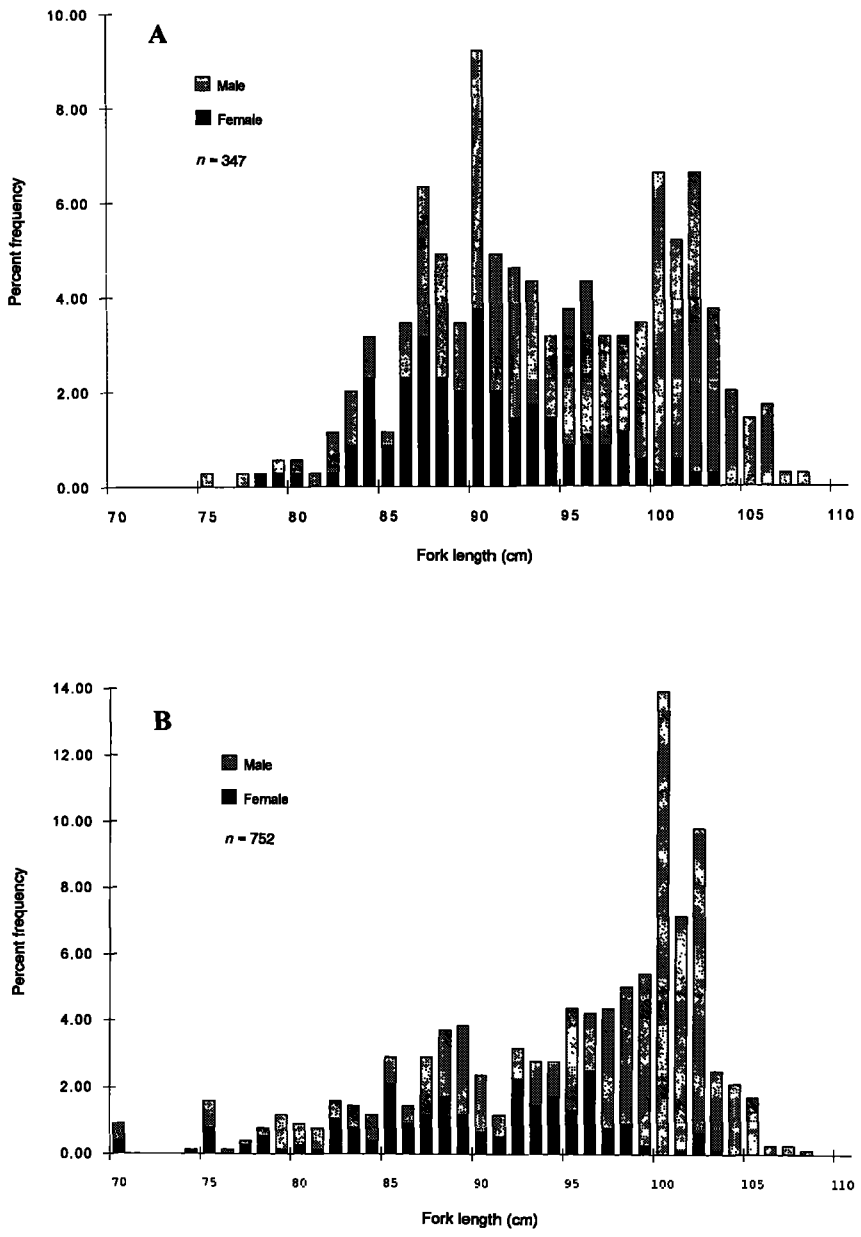

Figure 4

(**A**) Length-frequency distribution of albacore, *Thunnus alalunga*, sampled from New Caledonia, January 1990–February 1990; (**B**) Length-frequency distribution of albacore, *Thunnus alalunga*, sampled from Tonga, January 1990–February 1990.

with a mean diameter near 0.1 mm (Fig. 2). Between September and December, the number of albacore with partially yolked or fully yolked oocytes increased rapidly, and mean monthly oocyte diameters progressed from 0.12 mm to 0.57 mm (Fig. 2). Albacore with fully yolked oocytes were found from the summer months through March. No hydrated ovaries were observed in either the New Caledonia or the Tonga samples. By April, the most advanced-stage oocytes were resting-state oocytes with a mean diameter of 0.1 mm for all samples (Fig. 2).

A correlation exists between the most advanced stage of oocytes and GSI, as indicated by the positive coefficient of determination, $r^2 = 0.829$ (Fig. 3).

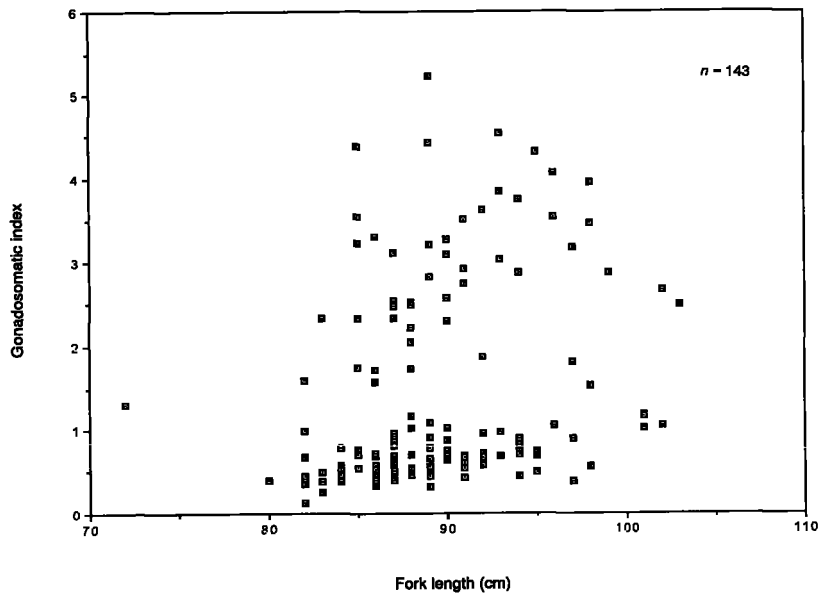

Figure 5

Gonadosomatic index values for female albacore, *Thunnus alalunga*, versus fork length, sampled from New Caledonia and Tonga from 1990 to 1992.

Gonadosomatic index

Because albacore gonads often have a fatbody attached, only those samples processed at the Southwest Fisheries Science Center (SWFSC), with the fatbody removed, were used in calculating GSI. The weight of the fatbody was found to compose an average of 4.4% of ovarian weight, from 0.0% to 31.6% in the samples sent to the SWFSC for processing. Because of the large variability in the weight of the fatbody, we decided not to attempt any corrections for fatbody presence but to use only the weight of ovaries measured in the laboratory. The relationship between GSI and fork length of sampled female albacore is shown in Figure 5.

In this study, a GSI of 1.7 was used as the critical GSI value, delimiting the point at which 100% of the females in our sample displayed an advanced stage of oocyte development (>0.3 mm)(Fig. 3). GSI values of 1.6 (Kikawa, 1959, 1966), 2.0 (Shung, 1973; Koido and Suzuki, 1989), and 2.1 (Kikawa, 1962) have been used to indicate group maturity of different species of female tunas. Female albacore appear to be capable of achieving this level of ovarian maturity and therefore of spawning once they reach 82 cm FL (Fig. 5). Evidence of spawning, as indicated by the presence of residual hyaline oocytes, was found in an 85-cm-FL albacore with a GSI of 2.8 and a mean maximum oocyte diameter of 0.57 mm. The largest GSI measured was 5.2 for a 89-cm female captured in Tonga in November. The weight of its ovary was 368.3 g, and the mean oocyte diameter of its most advanced oocytes was 0.60 mm.

The mean monthly GSI's of females show that peak reproductive development (GSI>1.7) occurs in the austral summer months, November–February (Fig. 6). The first indication of maturation was observed in October, when three of 15 albacore sampled were found to have GSI's greater than 1.7. These three had partially and fully yolked oocytes in the 0.35–0.54 mm size range. The first large increase in mean monthly GSI value occurred in November, when the mean GSI increased to 3.2 (Fig. 6). The largest monthly GSI, a mean of 3.3, occurred in February (Fig. 6). In March, the mean GSI declined to 1.2, although a small number of females still exhibited some spawning activity as indicated by females with high GSI values and late developed ovaries with oocyte diameters greater than 0.3 mm. The mean GSI then dropped to a resting level, close to 0.5, for the austral autumn and winter months.

Gonadal asymmetry

The right gonad was found to be heavier than the left in 80.0% of the females examined, and in 98.6% of the males (Table 2). In terms of collection sites,

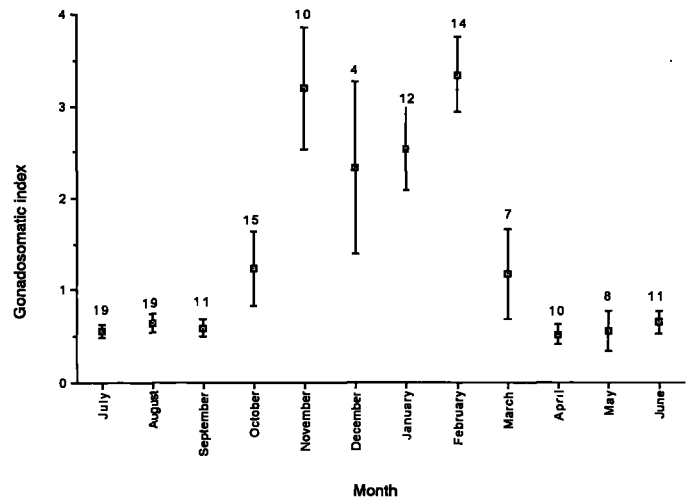

Figure 6

Mean monthly gonadosomatic index values for female albacore, *Thunnus alalunga*, by month, sampled from New Caledonia and Tonga from 1990 to 1992 (±2 standard errors; n=140). Numbers above error bars indicate sample size for each month.

the difference in females was less pronounced in New Caledonia (55.8%) than in Tonga (95.1%).

The left and right ovaries showed no significant difference in oocyte diameters between the left and right ovaries in the paired t-test ($T_{0.05(2),83}$=1.902). Only one of the 150 ovary pairs examined revealed a difference in maturity stages, with the left and smaller ovary being classified as developing and the right and larger as late developing.

Table 2

Asymmetry in gonad weight of albacore sampled from New Caledonia and Tonga, 1990–92.

Gonad weight (g)	New Caledonia female	Tonga female	Tonga male
Right> Left	55.77%	95.10%	98.60%
Right = Left	17.31%	4.90%	1.10%
Right < Left	26.92	0.00%	0.20%
n	104	142	444
$\bar{x}$	9.5	19.3	12.9
SD	41.6	13.7	12.8
Range	−130, +160	0–100	−30, +105

Discussion

Our data indicate that albacore caught near New Caledonia and Tonga are seasonal spawners, spawning mainly during the austral summer months, November–February. This supports the work on albacore reproduction in the South Pacific by Otsu and Hansen (1962). Nishikawa et al. (1985) and Ueyanagi (1969) analyzed larval data and determined that spawning was greatest in spring and early summer (October–December). Few larval surveys, however, were undertaken later in the season, January–March in the spawning area (see Fig. 37 in Nishikawa et al., 1985). It should be noted that albacore larvae are reported to occur south of 10°S in the South Pacific for all months except July–September (Nishikawa et al., 1985), indicating that spawning may be protracted. Leis et al. (1991) found high concentrations of albacore larvae near the islands of French Polynesia (14°–17°S) in January and February, corresponding to the period of peak reproduction period observed in this study.

From the distribution of larval and juvenile albacore, various authors have shown that the spawning area of South Pacific albacore lies between 10° and 25°S (Otsu and Hansen, 1962; Nishikawa et al., 1985; Ishii and Inoue, 1956; Ueyanagi, 1969). In this study, most maturing albacore (i.e. with GSI's above 1.7) were taken between 20° and 23°S.

Both the New Caledonia and the Tonga GSI data support the view that female albacore reach maturity at a minimum length of around 82 cm (Fig. 5). Although, GSI values alone may not present a full

picture of gonadal activity, the similarity in trends of monthly values of GSI's and oocyte diameters (Figs. 2 and 6) suggests that either method can be used to determine spawning season for the samples as a group.

The length frequencies of male and female samples from New Caledonia and Tonga indicate sexually dimorphic size differences. Such dimorphism had previously been reported by Otsu and Sumida (1968). In yellowfin tuna, sexually dimorphic growth has been age verified, and males were found to represent the largest mode in fork lengths (Wild, 1986).

Gonadal asymmetry has been recorded in several fish species (Ovchinnikov, 1971; Sanwal and Khana, 1972) and was documented previously in albacore by Otsu and Uchida (1959) and Ueyanagi (1955). The former compared oocyte diameters from different areas of one pair of ovaries and found that differences existed between anterior and posterior regions of a single ovary but not between the sides. In contrast, Ratty et al. (1990) found that the smaller left testis of males from the temperate troll fishery was consistently more active than the larger right testis. We found no significant difference in the diameters of oocytes in left and right ovaries.

The absence of advanced and fully ripe ovaries in our samples is similar to the state of reproductive development of ovaries in other studies of albacore reproduction in the Pacific that have relied on longline fisheries as the main source of samples (Otsu and Uchida, 1959; Otsu and Hansen, 1962). As these authors have noted, albacore in, or close to, spawning condition are generally unavailable to the fishery, either because they have stopped feeding and will not take hooks or because they have moved beyond the range of gear. In order to capture the latter category of fish, both the New Caledonia longliners and the MV *Lofa* crew set and hauled their gear during daylight hours; it is possible, however, that albacore, like some other tunas, spawn at night (Hunter et al., 1986; Schaefer, 1996). In addition, albacore may pass rapidly through the mature and spawned stages of the cycle, as Hunter et al. (1986) found with skipjack tuna, and McPherson with yellowfin tuna (1991). Thus, there remain a number of key aspects of the reproduction of South Pacific albacore, such as spawning frequency, batch fecundity and length at 50% maturity, that require further investigation.

Acknowledgments

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Immunologic methods for species identification of early life stages of lutjanid fishes from the western central Atlantic. Part I: Characterization of an interspecies protein

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Abstract.—A 66 kDa glycoprotein selected from SDS-PAGE gel profiles of soluble extracts of *Lutjanus griseus* was purified by Fast Protein Liquid Chromatography technology. A polyclonal antiserum produced to the single-chained glycoprotein was tested with 14 other lutjanid extracts in Western blots and produced 3 different patterns: strong reactions with *L. jocu* and *L. apodus;* weak reactions with *L. buccanella, L. synagris, L. analis, L. campechanus, Pristipomoides aquilonaris, Ocyurus chrysurus,* and *Apsilus dentatus;* no reactions with *L. vivanus, L. mahogoni, L. cyanopterus, Etelis oculata,* and the hybrid *L. synagris* × *O. chrysurus.* The anti-66 kDa antiserum also reacted strongly with soluble extracts of oocytes and juveniles of *L. griseus.* Adsorption of the IgG fraction of the antiserum with glutaraldehyde-insolubilized *L. apodus* extract resulted in an antiserum that remained strongly reactive with *L. griseus* extract but that was weakly reactive with *L. apodus* extract and negative with *L. jocu* extract in Western blots. The N-terminal amino acid sequence analyses of the first 10 residues of the purified 66 kDa proteins of *L. griseus* and *L. jocu* were approximately the same, but only 3 of 10 residues were the same with the purified proteins of *L. griseus* and *L. apodus.* Extracts of *L. apodus* contained 3 additional proteins that were not detected in extracts of *L. griseus* as determined by SDS-PAGE. This evidence for both interspecies and species-specific protein determinants is currently being used to produce species-specific polyclonal and monoclonal antisera for identifying species of lutjanid fishes at early life history stages.

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Eighteen species of snappers (Lutjanidae), representing 5 genera, are found in the western Atlantic Ocean (Robins et al., 1991). Species identification of the early life stages of snappers is incomplete because meristic characters are very similar or equivocal within the family. In addition, identification of morphological features requires a great deal of time and experience. Innovative studies are necessary for further species-specific identification of early life stages (eggs, larvae, and early juveniles) because information is available for only a few species and each exhibits a complex recruitment strategy (Richards et al., 1994). Lutjanids constitute one of the major predators of coral-grazing species, but the detrimental impact of overfishing and habitat loss from pollution and development is rapidly leading to an imbalance in the fragile equilibrium of the reef community. Thus, the ability to identify the early life stages of specific lutjanids is an important aspect of conservation measures.

Specific antibodies directed against a minor protein may be useful for species identification at the early life stages (Diano et al., 1992). In our study, starting with the development of biochemical methods to isolate a very pure antigen, we have produced a polyclonal antibody for prototypic studies of previously difficult or unapproachable questions of identification of early life history specimens of snapper. These methods and immunologic reagents have

wide versatility and applicability for current and future studies of early life history forms. The chromatographic purification and characterization of a 66 kDa glycoprotein from soluble extracts of *Lutjanus griseus* (Linnaeus), *L. jocu* (Schneider), and *L. apodus* (Walbaum) and the production of a specific polyclonal antiserum have generated evidence that the glycoprotein has both interspecies and species-specific epitopes. Further characterization of this and other lutjanid proteins, together with the production of both polyclonal and monoclonal antibodies for immunologic assays, may greatly facilitate future identification of lutjanids at any stage of their life history.

Materials and methods

Adult lutjanid specimens were obtained from local fishermen and skin divers, and species identification was carried out according to Robins and Ray (1986) and Robins et al. (1991).

Buffers and the methods for preparing soluble saline fish extracts are described in Schultz and Clarke (1995). In addition to *L. griseus*, the 13 species and one hybrid investigated here were the following: *L. jocu, L. apodus, L. vivanus* (Cuvier), *L. campechanus* (Poey), *L. analis* (Cuvier), *L. synagris* (Linnaeus), *L. mahogoni* (Cuvier), *Ocyurus chrysurus* (Bloch), *L. buccanella* (Cuvier), *Pristipomoides aquilonaris* (Goode and Bean), *Etelis oculata* (Valenciennes), *L. cyanopterus* (Cuvier), *Apsilus dentatus* (Guichenot), and the hybrid *L. synagris* × *O. chrysurus*. Separate extracts were prepared in 300 mL of buffer with approximately 30 g of tissue from gutted legal-size adult fish. The soluble, clear extract was concentrated by ultrafiltration (M_r 10,000 membrane, Amicon Corp., Danvers, MA) at 4°C until the OD_{280} exceeded 10. Also extracted were 1) gutted *L. griseus* juveniles with a total weight of 0.6 g and 2) *L. griseus* female gonads with oocytes, weighing approximately 3.5 g. Juveniles were collected from Biscayne Bay, Florida.

Two different antisera were produced in adult female goats according to the innoculation schedule of Schultz and Clarke (1995). The first was a polyvalent antiserum (anti-GSE) raised against *L. griseus* whole fish extract (14.1 mg protein/mL). The second antiserum (anti-66 kDa) was produced by using the 66 kDa protein (0.32 mg/mL) purified from *L. griseus* saline extracts (see below).

The γ-globulin fraction of anti-GSE and anti-66 kDa sera was isolated by 33% ammonium sulfate (A.S.) precipitation at 25°C (Stelos, 1967) and was further purified as IgG by DEAE-Sephacel (Pharmacia BioTech, Uppsala, Sweden) column chromatography in 10 mM NaPO4/50 mM NaCl, pH 7.4. The IgG-rich fractions were concentrated by ultrafiltration as above.

To eliminate background interference when anti-GSE was used as the primary antiserum in Western blots, it was necessary to biotinylate the IgG fraction (Bayer and Wilchek, 1980). The biotin-conjugated anti-GSE IgG was recovered by Sephadex G-25 (Pharmacia BioTech) gel filtration in 5 mM NaPO4/150 mM NaCl, pH 7.5 (PBS) and the biotin-protein ratio was 56 nmol of biotin per nmol of IgG (Green, 1965).

Soluble extracts of *L. mahogoni, L. apodus,* and *Eucinostomus gula* (silver jenny) were insolubilized with glutaraldehyde according to the method of Avrameus and Ternynck (1969), with 10 mg of glutaraldehyde per mg of soluble fish protein. Insolubilized *E. gula* was used previously to remove cross-reactivity with preimmune and immune goat sera and unrelated fish proteins (Schultz and Clarke, 1995).

The γ-globulin fraction of goat anti-66 kDa serum was adsorbed for 24 to 48 h at 4°C with 60 mg of insolubilized *E. gula* extract per mL γ-globulin, followed by 24 mg of insolubilized *L. mahogoni* extract (the 66 kDa protein was not detected in this species in Western blots). The IgG fraction of the adsorbed anti-66 kDa serum (anti-66 kDa IgG) was isolated by DEAE-Sephacel chromatography (see protocol above). This procedure removed all nonspecific activity.

Another portion of the γ-globulin fraction of anti-66 kDa serum was adsorbed with 100 mg of insolubilized *L. apodus* extract for 24 h per adsorption at 4°C in experiments to distinguish the 66 kDa proteins found in soluble saline extracts of *L. griseus, L. jocu,* and *L. apodus* (see Results section).

The buffers and conditions for ion exchange chromatography with the Fast Protein Liquid Chromatography (FPLC) system (Pharmacia Biotech, Uppsala, Sweden) as described in Schultz and Clarke (1995) were modified to include 10 mM EDTA in the column buffers. The sequence was that of Mono S cation exchanger followed by Mono Q anion exchanger.

Gel filtration on Sephacryl S-300 Superfine (Pharmacia Biotech) in PBS/10 mM EDTA, pH 7.5, was used to separate high molecular weight contaminants from the 66 kDa protein.

During purification procedures, protein concentration was monitored by absorbance at 280 nm. Purified proteins were dialyzed against PBS, pH 7.5, to remove EDTA, and the protein concentration was determined spectrophotometrically as described previously (Arnold et al., in press). Methods for electrophoresis in 10% (w/v) polyacrylamide gels with or without sodium dodecylsulfate (Laemmli, 1970), for Western blots (Towbin et al., 1979), and the molecu-

lar weight standards (Sigma Chemical) are described in Schultz and Clarke (1995).

Glycoproteins were identified on electroblots by using the method of O'Shannessy et al. (1987).

Results

The steps for purification of a 66 kDa protein from a soluble saline extract of *L. griseus* are shown in Table 1. Figure 1 depicts samples of each purification step in SDS-PAGE (gel A) and corresponding Western blots (gels B and C) leading to the highly purified protein. The protein was a trace component of the saline extract (arrow, A1) but was more concentrated with successive purification steps (A, 2–4). The steps of purification included *L. griseus* saline extract in lane 1, the A.S. (0.38 gm/mL extract) supernatant solution of the extract in lane 2, the 0.27 M NaCl eluate from a Mono S cation exchange column after

Table 1

Steps for the purification of *L. griseus* 66 kDa protein. FPLC = Fast protein liquid chromatography.

Procedure	Product
1 Puree fish, separate solid material by centrifugation	Clear extract
2 Solid ammonium sulfate fractionation (0.38 g/mL extract)	Supernatant fluid: elimination of most high molecular weight proteins in precipitate
3 FPLC: Mono S cation exchanger; gradient: 0 to 1.0 M NaCl, pH 5.0	Enriched 66 kDa protein eluted at 0.27 M NaCl
4 FPLC: Mono Q anion exchanger; gradient: 0 to 1.0 M NaCl, pH 7.5	Highly purified 66 kDa protein eluted at 0.32 M NaCl

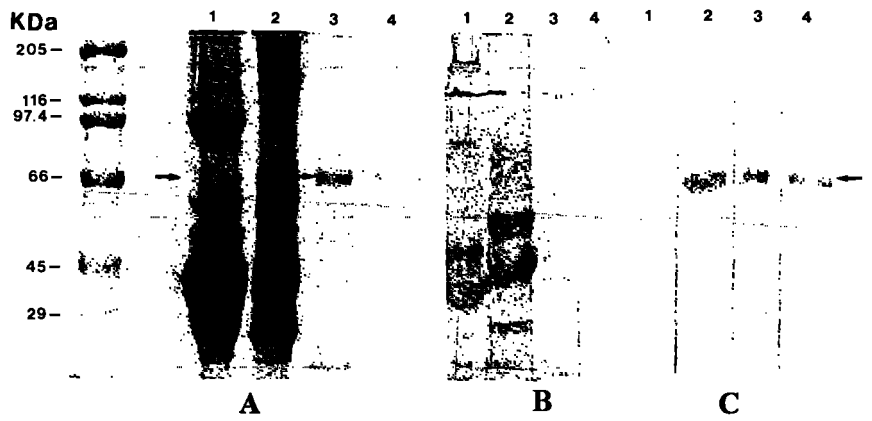

Figure 1

Samples from the purification steps of soluble *L. griseus* extract leading to the highly purified 66 kDa protein in lane 4. Gel (A) shows samples after SDS-PAGE stained with Coomassie brilliant blue. The corresponding Western blots were developed by using biotinylated goat anti-whole *L. griseus* antiserum (B) and goat anti-*L. griseus* 66 kDa protein IgG (C). Reference standard proteins (kDa) are shown in the stained gel. The arrows in gels A and C show the position of the 66 kDa protein. Numbered lanes denote the following: 1) whole *L. griseus* extract (235 μg total protein); 2) ammonium sulfate (0.38 g/mL extract) supernatant solution of *L. griseus* whole extract (228 μg); 3) eluate from Mono S cation exchange column (20 μg) after FPLC; and 4) eluate from Mono Q anion exchange column (0.32 μg) after FPLC. Note that the reaction of biotinylated goat anti-whole *L. griseus* antiserum with the 66 kDa *L. griseus* protein was not detected in B.

FPLC in lane 3, and the 0.32 M NaCl eluate of the highly purified 66 kDa protein from a Mono Q anion exchange column after FPLC in lane 4. Although the biotinylated goat anti-GSE antiserum reacted with many different proteins in the saline extract, it did not contain antibodies that were reactive with the trace 66 kDa protein in the Western blot (B, 1–4). In contrast, where the goat anti-66 kDa IgG was used, the protein was weakly positive with the saline extract (C1), but was strongly positive in the other lutjanid preparations (C, 2–4).

The purification procedure for the 66 kDa protein was repeated 4 times, with an average yield of 119 µg/g of the whole *L. griseus* saline extract. The protein was determined to be a single-chain polypeptide under reducing conditions in SDS-PAGE. The trace glycoprotein was not albumin (Hartmann et al, 1994), and under nonreducing, nondenaturing conditions, the lutjanid glycoprotein migration differed from human or bovine albumin (mol. weight 66 kDa, data not shown).

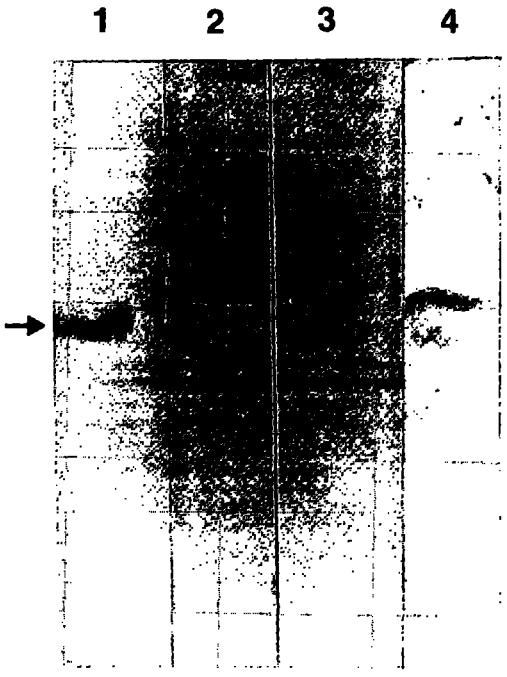

Figure 2

Western blot analysis of *L. griseus* life cycle stages. Samples included are purified 66 kDa protein, 1 µg total protein (lane 1); 50% ammonium sulfate supernatant fluid from a saline extract of female oocytes, 330 µg total protein (lane 2); saline extract of juvenile fish, 118 µg total protein (lane 3); saline extract of a sexually mature fish, 340 µg total protein (lane 4). The blot was developed with goat anti-*L. griseus* 66 kDa protein IgG as the primary antibody and with horseradish peroxidase-conjugated rabbit anti-goat IgG as the secondary antibody. The arrow marks the position of the 66 kDa protein.

After purification of the 66 kDa protein and production of a specific goat antiserum, saline extracts of different life stages of *L. griseus* were tested for the presence of the protein. Western blot analysis (Fig. 2) showed that the protein was present in all stages: oocyte (lane 2), juvenile (lane 3), and adult (lane 4).

Saline extracts of 14 species of adult lujanids and the hybrid (*L. synagris* × *O. chrysurus*) were prepared by the same method (see Materials and Methods section), and each extract was adjusted to 235 µg total protein. After Western blot analyses of the 15 different specimens, each blot was evaluated for the 66 kDa protein by visual inspection as shown in Figure 3, and the species were classified, as shown in Table 2. The species judged strongly positive were *L. griseus, L. jocu,* and *L. apodus* because for these three species the staining intensity of band patterns was approximately equal. Weak reactors were *L. buccanella, O. chrysurus, P. aquilonavis, L. synagris, L. analis, A. dentatus,* and *L. campechanus; L. vivanus, L. mahogoni, L. cyanopterus, E. oculatus,* and the hybrid exhibited no reaction.

Because the staining patterns of the 66 kDa proteins of *L. griseus, L. jocu,* and *L. apodus* were of similar intensity and because seven other species reacted weakly with the anti-66 kDa IgG for Western blots (Table 2; Fig. 3), an important question was raised: Was the protein from the different species identical but present in diminished concentrations, or were dissimilar determinants being detected? To investigate these questions, we selected *L. griseus, L. jocu,* and *L. apodus* because their 66 kDa proteins were strongly reactive with the specific antiserum. In addition, other studies have shown close phylogenetic relationships among these three species through morphological and biochemical data (Rivas, 1966; Vergara, 1980; Chow and Walsh, 1992) and by analysis of mitochondrial DNA sequences (Chow et al., 1993; Sarver et al., in press). Figure 4 shows the results of adsorbing the goat anti-66 kDa IgG with gluteraldehyde-insolubilized *L. apodus* saline extract for 24 h at 4°C. Comparing the Western blot in A (preadsorption) with B (postadsorption), we found that the antiserum reacted equally well with the *L. griseus* marker protein (lane 1, A and B) and the *L. griseus* saline extract (lane 4, A and B). The preadsorption antiserum also reacted with equal potency with *L. jocu* (lane 2A) and *L. apodus* (lane 3A). After adsorption of the antiserum with the insolubilized *L. apodus* saline extract, bands in the Western blots for *L. jocu* (lane 2B) and *L. apodus* (lane 3B) were

greatly reduced in reactivity with the secondary rabbit anti-goat IgG antiserum. The same anti-66 kDa IgG was adsorbed two more times with fresh, insolubilized *L. apodus* saline extract for 24 h at 4°C, and Western blots showed that the reaction of *L. jocu* was completely eliminated, whereas a trace reaction by *L. apodus* was detectable. The marker protein and the *L. griseus* extract reactions were similar to those in Figure 4 (data not shown). Therefore, we conclude that the 66 kDa protein from *L. griseus* must have different and multiple immunodominant regions compared with the 66 kDa proteins of *L. jocu* or *L. apodus*. Otherwise, after the third adsorption of the antiserum with insolubilized *L. apodus*, the immunoblots in B1 and B4 would have been greatly reduced or negative with the extract of *L. griseus*, but they were similar to the preadsorption blots.

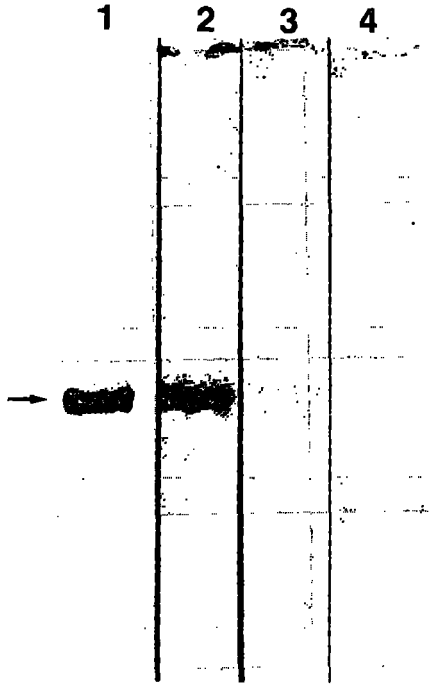

Figure 3

Western blot analysis of the graduated reaction of lutjanid saline extracts to anti-66 kDa protein IgG (primary antibody) followed by horseradish peroxidase rabbit anti-goat IgG (secondary antibody). The samples are as follows: lane 1 = purified *L. griseus* 66 kDa protein, 0.34 µg total protein; lane 2 = *L. griseus* extract, 235 µg total protein, classified as a strong reaction; lane 3 = *O. chrysurus* extract, 235 µg total protein, classified as a weak reaction; and lane 4 = *L. cyanopterus* extract, 235 µg total protein, classified as not detected. The arrow marks the position of the 66 kDa protein. Table 2 shows the reactions of soluble saline extracts of 14 different lutjanid species with the goat anti-*L. griseus* 66 kDa protein IgG.

The 66 kDa protein was purified separately from soluble extracts of the three species as described in Table 1. Figure 5 shows the proteins after SDS-PAGE and Western blots. The only discernible difference was that the 66 kDa protein from *L. griseus* migrated slightly slower than the proteins from *L. jocu* and *L. apodus*, indicating a slightly heavier molecular mass.

Next, it was determined that all three proteins are glycosylated when the method of O'Shannessy et al. (1987) is used. Separately, each of the purified proteins was oxidized with Na periodate. Available carbohydrate moieties were then labeled with biotin-hydrazide. After SDS-PAGE, glycoproteins were detected with peroxidase-labeled streptavidin and 4-chloro-l-naphthol (data not shown).

Finally, N-terminal amino acid sequences of the three proteins were obtained for comparative studies. Table 3 shows that the sequences from *L. griseus* and *L. jocu* for the first ten amino acids were approximately the same (residue no. 4 was not interpretable for *L. griseus*). Comparison of *L. griseus* with *L. apodus* showed that only as many as 3 of 10 amino acids were the same. In addition, only 3 of 10 amino acids of *L. jocu* were the same as *L. apodus*. Thus, as

Table 2

Screening of soluble saline extracts of fourteen different species and one hybrid of family *Lutjanidae* for presence of 66 kDa *L. griseus* protein by Western blot analyses. The basis for the strongly positive, weak, and not detected evaluation is shown in Figure 3. Each individual species was adjusted to 235 µg total protein for the immunoblots.

Species	Western blots for 66 kDa protein
L. griseus	
L. jocu	Strongly positive
L. apodus	
L. buccanella	
O. chrysurus	
P. aquilonaris	
L. synagris	Weak
L. analis	
A. dentatus	
L. campechanus	
L. vivanus	
L. mahogoni	
L. cyanopterus	Not detected
E. oculatus	
O. chrysurus × *(hybrid)*	
L. synagris	

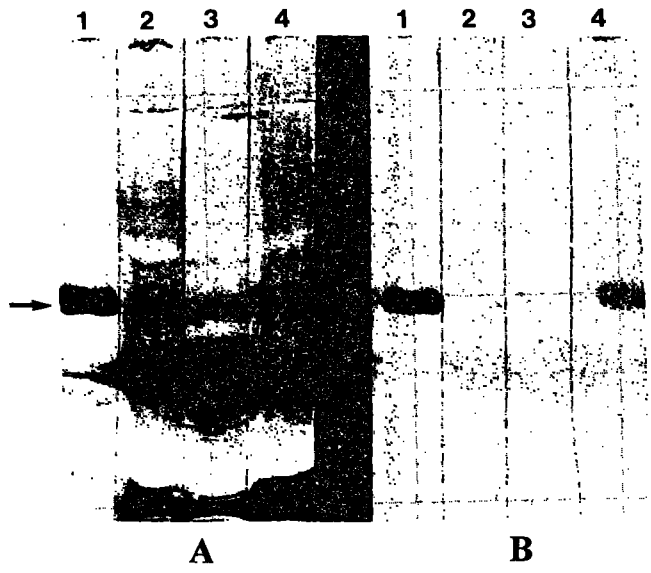

Figure 4

Western blot analysis of saline extracts from three closely related lutjanids, *L. griseus, L. jocu,* and *L. apodus.* The goat anti-*L. griseus* 66 kDa protein IgG was used before (**A**) and after (**B**) adsorption with 100 mg of insolubilized *L. apodus* saline extract for 24 h at 4°C. Lane 1 = purified *L. griseus* 66 kDa marker protein, 1 µg total protein; lane 2 = *L. jocu* extract, 235 µg total protein; lane 3 = *L. apodus* extract, 235 µg total protein; and lane 4 = *L. griseus* extract, 235 µg total protein. The arrow marks the position of the 66 kDa protein.

far as the first ten N-terminal amino acids, the 66 kDa protein of *L. apodus* was different from that of *L. griseus* and *L. jocu.*

Because other studies have shown *L. griseus, L. apodus,* and *L. jocu* to have a close phylogenetic relationship (e.g. Sarver et al., in press), we wanted to determine if there were obvious differences in their respective protein profiles. Fifty percent of A.S. precipitates of saline soluble extracts of each species were prepared at the same time; the precipitates were solubilized and dialyzed with saline, and they were compared in SDS-PAGE. Figure 6 shows that the 66 kDa protein was present in each of the three species (open arrow). However, there are at least three proteins that were present in *L. apodus* that were not detectable in *L. griseus* (closed arrows). Although other lutjanids have not been screened for these proteins, this procedure increases the possibility of isolating species specific proteins for antibody production, and eventually for species identification of early life history forms. Even if one or more of the three proteins of *L. apodus* were present in other lutjanids, some of the determinants on each protein, including different amino acid or glycan substitutions, or both, would probably be structurally different and thus would increase the possibility of producing specific monoclonal antibodies.

Discussion

A trace single-chain 66 kDa glycoprotein was purified to homogeneity by FPLC technology, starting with soluble extracts of adult *L. griseus* (Table 1; Fig. 1). The glycoprotein was not detected in Western blots with the biotinylated goat anti-whole *L. griseus* antiserum, but it was identified in extracts on SDS-PAGE (Fig. 1). This finding is not unusual because trace proteins in human serum frequently are not reactive with an antiserum produced in animals to whole human serum (senior author's unpubl. observations). A polyclonal antiserum was produced to the purified glycoprotein in a goat, and after removal of nonspecific reactivity by adsorption with insolubilized snapper and nonsnapper proteins, Western blots were carried out with the IgG fraction of the antiserum and with soluble extracts of 14 other lutjanid species that were available to us. Because of a comparatively strong reaction in Western blots

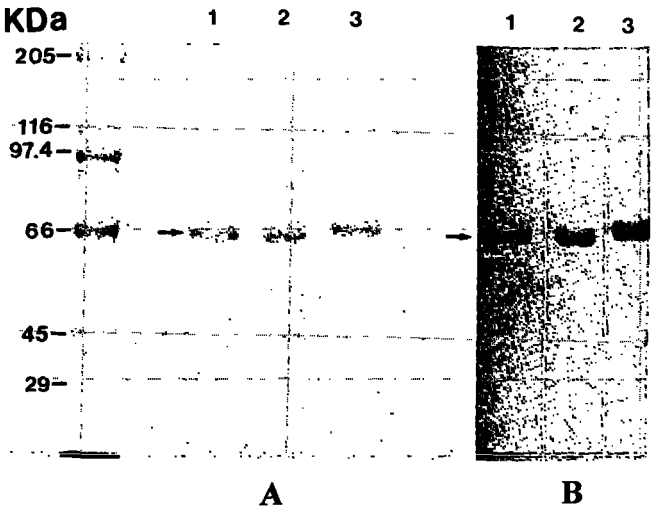

Figure 5

SDS-PAGE (A) and corresponding Western blots (B) of the highly purified 66 kDa proteins from 1) *L. jocu*, 2) *L. apodus*, and 3) *L. griseus*. Total protein added to each lane was 2 µg. The protein of *L. griseus* is slightly heavier compared with the other two species. Comparative N-terminal amino acid sequences of the three proteins are shown in Table 3.

Table 3

The N-terminal amino acid sequence analysis of the 66 kDa glycoproteins purified from *L. griseus*, *L. jocu*, and *L. apodus*.[1]

Snappers	1	2	3	4	5	6	7	8	9	10
L. griseus	Asp/Ala	Glu	Ala	N.I.[2]	Ala	Asp	Ala	Glu	Glu	Val
L. jocu	Asp	Glu	(Ala)[3]	His	Ala	Asp	Ala	Glu	Glu	Val
L. apodus	Asp	Glu/Ala	His	Ala	Asp	Ala	Glu	Glu	Val	Pro

[1] Analyzed at the University of Florida, Dep. of Biochemistry and Molecular Biology (ICBR Protein Chemistry Core Facility), Gainesville, FL.
[2] Not interpretable.
[3] Confidence: ( ) = possible/low.

with the antiserum, we purified to homogeneity similar 66 kDa glycoproteins from *L. jocu* and *L. apodus* (Fig. 5). The antiserum reacted weakly in immunoblots with soluble extracts of seven other species of lutjanid and did not react with extracts of four more lutjanid species and a hybrid of *O. chrysurus* and *L. synagris* (Table 2). The results indicated that the protein had both interspecies and species-specific determinants. In additional experiments, adsorption of the IgG fraction of the anti-66 kDa antiserum with glutaraldehyde-insolubilized *L. apodus* extract resulted in an antiserum that remained strongly reactive with *L. griseus* extracts but that was weakly reactive with *L. apodus*, and negative with *L. jocu* in Western blots (Fig. 4). Although the N-terminal amino acid sequence analyses of the first ten residues of *L. griseus* and *L. jocu* were approximately the same, only three of the ten residues were the same from *L. apodus*. These analyses did not take into account the possibility that the interspecies 66 kDa proteins may have different carbohydrate moieties that influence the antigenicity of the respective epitopes. For example, the 66 kDa protein of *L. griseus* was slightly heavier compared with the proteins of *L. jocu* and *L. apodus* in SDS-PAGE (Fig. 5) and thus could account for, but not prove, differences in glycan-dependent epitopes.

This approach was used as a model for distinguishing the different species of lutjanids. The eventual goal of these studies is to produce species-specific

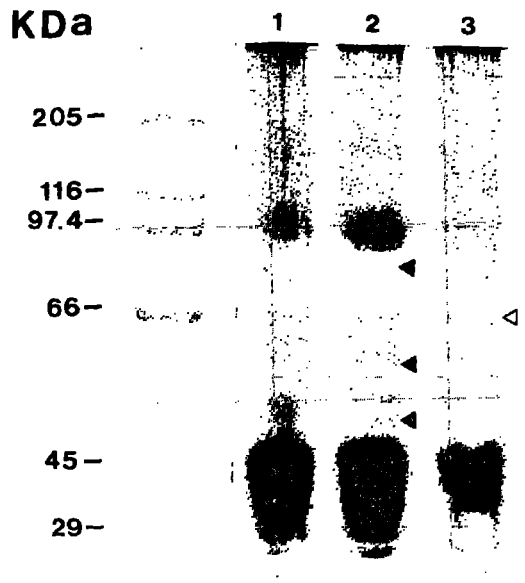

Figure 6

SDS-PAGE of the dissolved precipitates from the ammonium sulfate fractionation (0.38 mg/mL) of soluble extracts of 1) *L. jocu*; 2) *L. apodus*; and 3) *L. griseus*. Total protein added to each lane was 235 µg. The open triangle (◁) shows the position of the 66 kDa protein; the closed triangle (◀) marks bands not seen in *L. griseus* (lane 3). The gel was stained with Coomassie brilliant blue.

polyclonal and monoclonal antisera for identifying specimens at an early life stage. Animals will be immunized with highly purified proteins to enhance possibilities of producing antibodies to minor structural protein differences. The use of highly purified protein is especially important for monoclonal antibody production because immunization with complex mixtures of antigens generally results in monoclonal antibodies being produced to immunodominant epitopes (Barclay and Smith, 1986; Matthew and Sandrock, 1987). Immunization with a highly purified protein increases possibilities of producing monoclonal antibodies with a fine degree of specificity for each species of lutjanid. It remains for future experiments to determine if these specific antisera will also be species specific for life history specimens, such as eggs, larvae, and early juveniles. Although the anti-66 kDa IgG used in these studies also reacted with the early life history specimens of *L. griseus* (Fig. 2), future experiments with monoclonal antibodies generated to the 66 kDa protein and other lutjanid proteins (Fig. 6) will determine their usefulness as specific reagents.

In other studies, the use of a very pure antigen was successful for predator-prey studies with *Sciaenops ocellatus* (red drum) (Schultz and Clarke, 1995; Arnold et al., in press), in which a specific polyclonal antiserum was prepared by immunizing a goat with a highly purified 80 kDa glycoprotein.

Monoclonal antibodies were used successfully to detect epitopes in a number of marine and fresh water species. For example, An et al. (1990) used a low molecular weight eluate from SDS-PAGE slab gels of a protein extract from rock shrimp to produce highly specific murine monoclonal antibodies. A monoclonal antibody to partially purified mature egg proteins reacted with eggs, embryos and larvae of *Asterina pectinifera* but not with other species belonging to the same genus or in mixtures of biological specimens of marine origin (Ikegami et al., 1991). Murine monoclonal antibodies were employed by Miller et al. (1991) to distinguish three barnacle species of similar size, and Beck et al. (1992) investigated surface antigens of rainbow trout sperm with monoclonal antibodies.

Immunological detection methods with monoclonal antibodies have also been valuable for many aspects of seafood science. Recently, Huang et al. (1995) were able to distinguish the commercially valued red snapper, *L. campechanus,* from less valuable substitutes by using ELISA with two monoclonal antibodies raised to a red snapper protein.

It is now evident that identification of species of the western Atlantic snapper at early life history stages by examining external features alone is insufficient and that new methods are necessary to increase our knowledge. The use of highly purified lutjanid proteins, together with the production of polyclonal and monoclonal antibodies for a variety of immunoassays, has wide versatility and applicability for future studies.

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Forecasting the fishery for pink shrimp, *Penaeus duorarum*, on the Tortugas Grounds, Florida

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Abstract.—In this report I review the biology of and fishery for pink shrimp, *Penaeus duorarum*, harvested from the Tortugas Grounds off southwest Florida, and present models used to forecast annual pink shrimp landings in this area. Pink shrimp spawn all year, and larvae recruit to nurseries in the seagrass-mangrove ecosystem surrounding Everglades National Park and Florida Bay. Juveniles move out of the nurseries all year, but catch per unit of effort for smallest size classes generally exhibits March and September peaks. Total landings usually rise sharply in November and taper off after April. The fishery was relatively stable during 1960–85, averaging 4,350 metric tons annually, but it has shown a singular decline and potential recovery since 1985. In 1987, I began forecasting annual landings by using multiple regression analyses of fishery catch statistics and environmental factors that could affect survival, growth, and recruitment. Potential predictor variables from May through October were investigated in order to release a timely annual forecast by November. Each year, the updated data set from 1966 onwards was examined to derive the "best" forecast models. Important predictor variables included indices of fishing activity during the waning months of the fishery (May–July) and surface and ground water levels within Everglades National Park during June-September. Forecasts were within ±20% of actual landings for five of eight years, whereas forecast direction (increase or decrease over the prior year) was usually correct. Cause-effect relationships between predictor variables and pink shrimp recruitment to the fishery remain to be determined.

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Fishery Bulletin 94:743–755 (1996).

The pink shrimp, *Penaeus duorarum*, fishery over the Tortugas Grounds, southwest of Florida, averaged 4,525 metric tons (t) of shrimp tails per year during 1960–80 (Nance and Patella, 1989). Landings began to decline in the mid-1980's, collapsed to 2,000 t during 1988–91 for no apparent reason, and rebounded to over 4,000 t in 1994.[1,2] Coincident with this unprecedented decline, the Gulf of Mexico Fishery Management Council (GMFMC) requested that the National Marine Fisheries Service (NMFS) evaluate the possibility of forecasting annual landings for the Tortugas pink shrimp fishery. The Gulf of Mexico Fishery Management Council and NMFS expected that such a model could aid in the planning and evaluation of management actions and could assist shrimp fishermen in preparing for the upcoming fishing season. NMFS has been forecasting annual brown shrimp, *P. aztecus*, landings for Texas since 1962 (Berry and Baxter, 1969; Baxter and Sullivan, 1986) and for Louisiana since 1985.[2] Annual forecasts are released to the fishing industry in newsletters and direct mailings. Forecasting models for the Tortugas pink shrimp fishery have been proposed previously (Yokel et al., 1969; Browder, 1985). However, Yokel et al. never implemented their model, and Browder's annual models provided relatively poor forecasts for the three years beyond her base data set (estimated from Fig. 9 in Browder [1985] to be –24%, +53%, and +56% of actual 1981, 1982, and 1983 landings, respectively).

In this report I review both the biology of and the fishery for pink shrimp in southern Florida. I then present empirical models used by NMFS since 1987 to forecast annual Tortugas pink shrimp landings. These models are based on environmental conditions in the primary pink shrimp nurseries of Florida Bay, Everglades National Park, and adjoining coastal waters. Pink shrimp production is likely linked to survival and growth of juveniles in these habitats. For example, high water levels in Everglades National Park during October–December and January–March were associated with subsequent high pink shrimp catches in January–March and April–June, respectively (Browder, 1985). A disruption in nursery habitat functions, such as those resulting from seagrass mortality (Robblee et al., 1991) or freshwater diversion (Light and Dineen, 1994), may have been causes of previously noted fluctuations in pink shrimp harvest.

[1] Nance, J. M. 1994. A biological review of the Tortugas pink shrimp fishery through December 1993. Unpublished report to the Gulf of Mexico Fishery Management Council, National Marine Fisheries Service, 4700 Avenue U, Galveston, TX 77551, 11 p.

[2] National Marine Fisheries Service. 1985–1994. 4700 Avenue U, Galveston, TX 77551. Unpubl. data.

The predictive model(s) was intended to provide an estimate of a future 12-month total pink shrimp catch with a forecast issued in advance of the main shrimping season. For the Tortugas fishery, monthly catches generally rise sharply in November and taper off after April (Nance and Patella, 1989). Ideally, the forecast should be released to the industry no later than October. In practice, however, there are time delays between data collection for a given month and availability of final data. My goal was to release a forecast by October $_{Yr.t}$ for the November $_{Yr.t}$ through October $_{Yr.t+1}$ "fishing year."

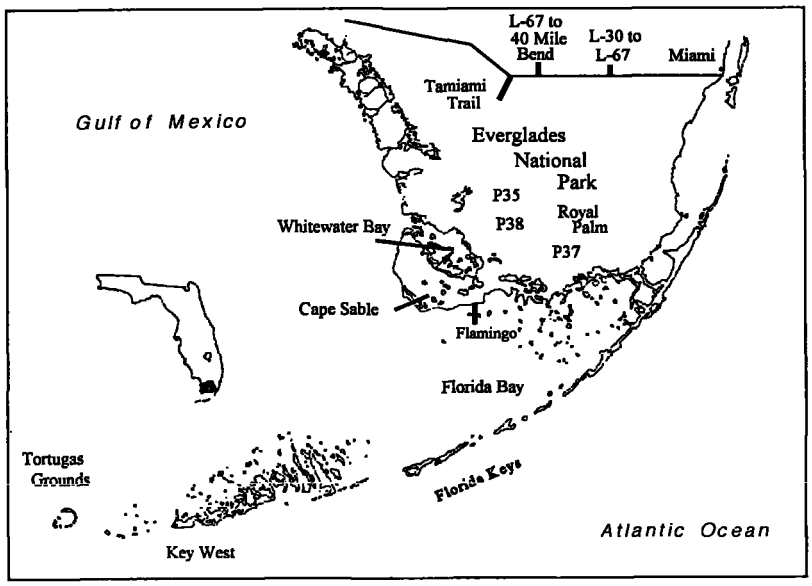

Figure 1

Location of the Tortugas pink shrimp grounds in relation to the southern Florida environmental data sources. P35, P37, and P38 are wells in Everglades National Park. Rain gauges are located at Flamingo, Royal Palm, and Tamiami Trail. Surface water discharge gates are located at L-67 to 40-Mile Bend and at L-30 to L-67.

Since the fishery's inception in 1949, researchers have postulated that landings from the Tortugas Grounds were dependent on survival and growth of postlarval and juvenile pink shrimp in primary nursery habitats of Florida Bay and Whitewater Bay (Fig. 1). Female shrimp in spawning condition were found all year on the Tortugas Grounds west of Key West, with the highest frequency of ripe females occurring April through July (Ingle et al., 1959; Cummings, 1961). Larval stages were found all year in waters west and south of Florida Bay but were generally most abundant in the same months as ripe females (Munro et al., 1968; Jones et al., 1970). Postlarval stages also were found all year, but late postlarval stages were found primarily near the coast and in Florida Bay and Whitewater Bay (Tabb et al., 1962; Jones et al., 1970; Roessler and Rehrer, 1971; Allen et al., 1980). Larval and postlarval stages were first thought to migrate into Florida Bay by riding surface waters on the eastward tidal excursion and by dropping to the bottom either during westward tidal movement (Koczy et al., 1960) or after detecting lower salinities (Hughes, 1969). Alternatively, currents were hypothesized to sweep larvae south and east of the spawning grounds and along the south side of the Florida Keys until larvae entered Florida Bay through passes between the keys (Rehrer et al., 1967; Munro et al., 1968). Recent research on larval shrimp distributions in relation to currents has indicated that both immigration methods may be effective (Criales and Lee, 1995).

Postlarvae reaching coastal seagrass and mangrove nurseries encounter several distinctive environments: Florida Bay seagrass beds are frequently hypersaline, the Whitewater Bay ecosystem is estuarine, and the Florida Keys are oceanic (Tabb et al., 1962; McIvor et al., 1994). Catches of postlarval and juvenile pink shrimp were highest in seagrasses of western Florida Bay and the middle Florida Keys, moderate in central Florida Bay and the lower Keys, and low to absent in eastern Florida Bay (Costello et al., 1986; Holmquist et al., 1989). Pink shrimp also recruit to the mangrove-lined Whitewater Bay system and were found to be more abundant in submerged aquatic vegetation than in nonvegetated areas during trawl surveys (Idyll and Yokel, 1970). Higher densities of pink shrimp are associated with seagrass (*Thalassia testudinum* and *Halodule wrightii*) habitats than with algal, red mangrove (*Rhizophora mangle*) prop root, or nonvegetated habitats (Sheridan, 1992; Sheridan et al.[3]). Widespread mortality of seagrasses (Robblee et al., 1991) thus might be expected to reduce subsequent pink shrimp harvests.

Juvenile pink shrimp exhibit early spring and late summer peaks in abundance in western Florida Bay (although only a single summer peak has been observed for the last decade[4]) and move out of coastal habitats on ebb tides, at night, during full and new moons (Tabb et al., 1962; Hughes, 1968; Yokel et al.,

[3] Sheridan, P., G. McMahan, G. Conley, A. Williams, and G. Thayer. 1996. Response of macrofaunal communities to seagrass mortality in Florida Bay (Florida, USA). I. Shallow bank-top habitats. In review.

[4] Robblee, M. 1995. National Biological Service, Southeastern Research Program, Florida International University, Miami, Fl 33199. Unpubl. data.

1969). Rapid salinity changes, as might be experienced during rainy season floods, may also force shrimp out of nearshore habitats (Hughes, 1969). Emigration of juvenile pink shrimp from nurseries in summer and fall has been postulated to form the fall and winter landings of new recruits by the fishery (Higman et al., 1972). Juvenile and subadult pink shrimp marked and released in southwest Florida coastal habitats were primarily recaptured on the Tortugas fishing grounds (Costello and Allen, 1966; Gitschlag, 1986). Apparent pink shrimp movement speeds were 1–2 km/day (Costello and Allen, 1966); thus pink shrimp could reach the fishing grounds 100 km southwest of Cape Sable (Fig. 1) in 50–100 days, as postulated by Higman et al. (1972).

Environmental determinants of pink shrimp growth and survival have not been examined extensively. Most available information consists of pink shrimp abundance and size by season or habitat, with coincident measurements of temperature and salinity. Pink shrimp have wide tolerances for salinity and temperature (0–65‰ and 11–40°C; Costello and Allen, 1970; Costello et al., 1986). Maximum growth of postlarval pink shrimp (7.8–10.1 mm total length [TL]) was found at 30–35°C under constant salinity (28–32‰, Teinsongrusmee, 1965). The only experimental analyses of pink shrimp survival versus combined temperature and salinity variations was conducted by Williams (1960). Survival of juveniles (35–100 mm TL) was highest (77–100%) at 15–30‰ and 8.8–28.4°C but was significantly lower (62–67%) at 10‰ and 8.8–28.4°C due to impaired osmoregulation. Higman et al. (1972) conducted enclosure experiments to determine pink shrimp growth in the field but felt that poor water quality conditions confounded their results. Neither Williams (1960) nor Teinsongrusmee (1965) addressed the hypersaline conditions often experienced in Florida Bay (up to 70‰; McIvor et al., 1994).

The Tortugas fishery began in 1949, and since 1956 monthly catch and effort data have been collected by NMFS personnel using standard methods (Nance and Patella, 1989). The fishery has landed an average of 4,350 metric tons (t) annually during 1960–85 (NMFS[2]) and was relatively stable (coefficient of variation=17%; Nance and Patella, 1989). Since that time, however, the fishery has shown a singular, and as yet unexplained, decline and apparent recovery (Fig. 2). In conjunction, the bimodal trend in monthly catch per unit of effort (CPUE) of the smallest pink shrimp size class (≥68 tails to the pound, or "68-count") has changed (Fig. 3). The fall peak in recruitment of 68-count pink shrimp that dominated in early years (1960–69) has shifted in favor of a spring peak. This shift may have been the result of management measures enacted during 1961–81 to restrict the catch of small shrimp (Caillouet and Koi, 1981; Gulf of Mexico Fishery Management Council, 1981).

Materials and methods

Fishery yield forecasts often depend upon indices of larval or juvenile abundance as indicators of recruitment into a fishery. Forecasting brown shrimp yield off Texas depends upon landings of juveniles by the Galveston Bay bait shrimp industry immediately prior to their emigration from the bay (Berry and Baxter, 1969; Baxter and Sullivan, 1986). Forecasting western rock lobster, *Panulirus cygnus*, yield is based on seasonal settlement of the final planktonic stage (puerulus) on collectors at a single site, Seven Mile Beach, Western Australia (Phillips, 1986). In Florida, however, there are no long-term fishery-independent data sets describing larval or juvenile pink shrimp abundance in coastal habitats. Thus, my models are based on fishery-dependent catch statistics and on environmental variables that could affect the survival, growth, and recruitment of pink shrimp, even though causal mechanisms may be

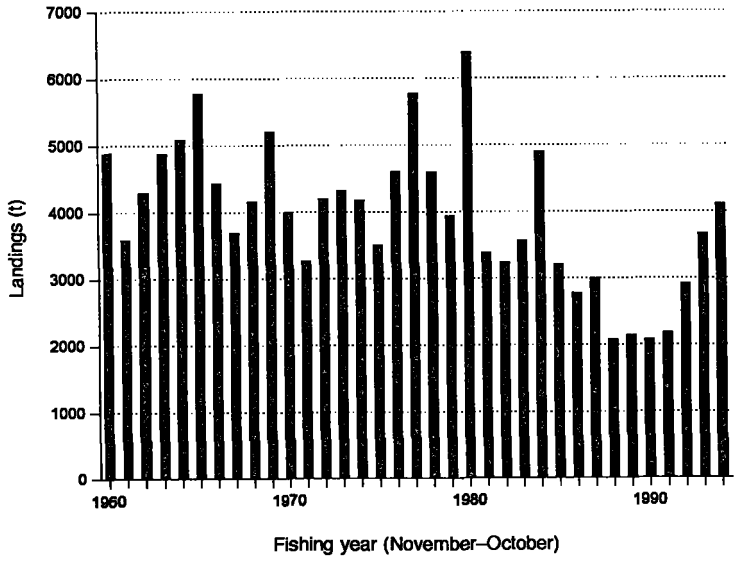

Figure 2

Annual landings by the Tortugas pink shrimp fishery (NMFS, Footnote 2 in the text).

unknown. The above review of the literature indicated that factors affecting larval and juvenile pink shrimp abundance and survival during the months of May–October were most likely to affect recruitment to the next fishing year.

Data sources

Development of forecasting models requires sets of long-term data collected in a consistent manner. There are no long-term environmental or biological data sets from within Florida Bay per se (Schmidt and Davis, 1978), with the exception of an historical salinity data set that has been compiled by the National Biological Service.[4] Thus, the primary sources of long-term data used in my models were those with physical or biological factors for May–October in locations near Florida Bay. These sources were the U.S. Department of Commerce (National Weather Service [NWS]; National Ocean Service [NOS]; and NMFS) and the U.S. Department of the Interior (Everglades National Park [ENP]).

National Weather Service stations in Key West and Miami, Florida, bracket Florida Bay and Everglades National Park (Fig. 1). The NWS collects data that provide hourly, daily, and monthly maxima, minima, means, and totals for climatic factors.[5] Monthly values at each site were compiled for the following variables: mean air temperature; total heating and cooling degree days (on any given date, one degree day accrues for each °F that the mean temperature falls below or above 65°F [18.3°C], respectively); total days with air temperatures ≤55°F (13°C) and ≥90°F (32°C) to examine effects of temperature extremes; mean wind speed; mean cloud cover; and total rainfall.

NOS records monthly sea level data at Miami Beach and Key West, Florida. I compiled monthly mean sea level data for Key West (station number 8724580), the tide gauge used by NOS to develop tide tables for Florida Bay.[6]

ENP maintains a series of ground water wells, surface water discharge gates, and rain gauges to monitor hydrology within the park.[7] I compiled the following data: mean monthly water level at three wells closest to the coast (P35 and P38 in Shark River Slough flowing into Whitewater Bay and the Gulf of Mexico, and P37 in Taylor Slough flowing into central Florida Bay); monthly total surface water discharge into northern ENP via two sets of water control structures (Canal L-67 to 40-Mile Bend and Canal L-30 to Canal L-67, later referred to as L-67 and L-30) along the Tamiami Trail, U.S. Highway 41; and total monthly rainfall at three gauges within the park (from south to north: Flamingo, Royal Palm, and Tamiami Trail; Fig. 1). In 1987, a correlation analysis of the ENP, Key West, and Miami monthly rain data was conducted for the period 1963–86. Although all five gauges were significantly correlated (r=0.514–0.792, P<0.05), the Royal Palm gauge had the highest correlations with gauges other than Key West (r=0.773–0.792). Lowest correlations were found between Key West and other gauges (r=0.514–0.609). For these reasons, Royal Palm was selected as the primary rainfall indicator (Miami was substituted directly in 1993 because of disruptions in ENP data availability caused by Hurricane Andrew).

Finally, NMFS collects monthly catch and effort data (and thus catch per unit of effort, CPUE) by various size classes for shrimp fisheries in the Gulf of Mexico.[8]

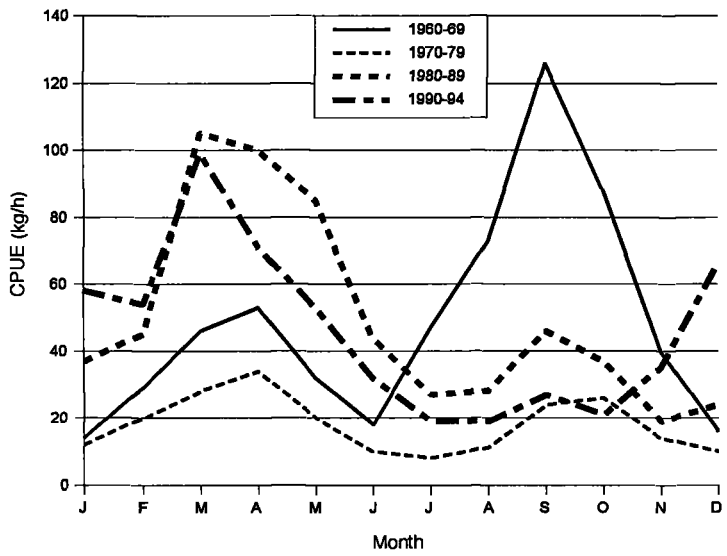

Figure 3

Decadal average monthly catch per unit of effort (CPUE) of 68-count pink shrimp (NMFS, Footnote 2 in the text).

[5] National Weather Service. 1963–1994. Local climatological data, monthly summaries for Miami and Key West, Florida. NOAA, National Climatic Data Center, Asheville, NC 28801.

[6] National Ocean Service. 1963–1994. Tides, high and low waters. NOAA, National Ocean Service, Tidal Analysis Branch, Silver Spring, MD 20910.

[7] Sikkema, D., and G. Schardt. 1987–1994. Hydrological Section, South Florida Research Center, Everglades National Park, Homestead, FL 33034. Unpubl. data.

[8] National Marine Fisheries Service, Statistics Operation Team. 1960–1994. 75 Virginia Beach Drive, Miami, FL 33149. Unpubl. data.

I compiled monthly pink shrimp catch, effort, and CPUE for all sizes combined and for the smallest size category (≥68 tails to the pound or "68-count") in NMFS statistical subareas 1–3 off southwestern Florida.

In addition to monthly values for these 29 variables, two quarterly means or totals for each variable (May–July and August–October) were created. These data resulted in a suite of 232 variables (29 variables × 6 months plus 29 variables × 2 quarters) as potential predictors. All data were received and analyzed in American system units (e.g. shrimp in pounds, rainfall in inches). Actual and predicted landings are presented in metric equivalents. Analyses began with the year 1966 because it was the approximate completion date for the system of major water control structures that influence ENP and Florida Bay (Light and Dineen, 1994).

Statistical analyses

The statistical relationships of annual pink shrimp catches in NMFS statistical subareas 1–3 with environmental and biological variables were examined by multiple linear regression. The tentatively entertained models were of the form

$$C = b_0 + b_1x_1 + b_2x_2 + \dots b_kx_k,$$

where C = total November$_{Yr.\ t}$–October$_{Yr.\ t+1}$ pink shrimp catch;
x_k = variables measured during May–October;
b_k = regression coefficients; and
k = number of variables in the model.

For the first forecast (released in November 1987), environmental and biological data for May–October 1966–86 were used to develop descriptive ("hindcast") models, whereas data for May–October 1987 were reserved for the forecast. Initial regression analyses employed the "R-square" option of the SAS regression procedure (SAS Institute Inc., 1985) to capitalize on the power of Mallow's test statistic C_p. This option produces regression equations and multiple R^2 values for all possible subsets of p variables, allowing the investigator to choose the "best" linear model(s) based on R^2. Mallow's C_p statistic detects a "best" set of explanatory variables that minimizes both error due to too few variables and variance of predictions due to too many variables (Daniel et al., 1971). Regression equations with $C_p > p$, where p = number of variables in the equation, have increased bias whereas equations with $C_p < p$ have increased error. Regression equations including more than one form of a variable, such as those with a quarterly variable plus one or more of its component months, were not allowed. For models with $C_p \approx p$, stepwise regression (F-to-enter=0.25 and F-to-stay=0.25) was used to determine all partial and full statistics. The Durbin-Watson statistic was used to assure that autocorrelation in the selected models was minimal (i.e. that errors in regression were independent; Draper and Smith, 1981). The relationship between residuals and fitted values was examined to assure constant variance. Residuals were checked against Cook's statistic to assure that outliers did not unduly influence model coefficients (Draper and Smith, 1981). Models passing all these tests were employed for the annual forecast. Model performance was assessed by examining the direction of the forecast (whether landings increased or decreased over the prior year) and the accuracy of the forecast (expressed as percent above or below actual landings). Forecasts in the same direction and with accuracies of actual landings ±20% were termed successful.

After 1987, data sets were updated regularly and the regression procedures were repeated each year for the annual forecast, beginning with development of new descriptive models.

Results

Of the 232 possible predictors, only 30 monthly variables and two quarterly variables have ever appeared in the 26 forecast models generated since 1987 (Table 1). Only a few of these variables have occurred on a regular basis, including in decreasing frequency: 1) days fished during July; 2) ENP L–67 discharge during September and June; 3) ENP groundwater level in wells P38 during August and P37 during September; 4) CPUE of 68-count pink shrimp during May, and 5) Key West wind speed in September. Relationships of these variables to subsequent fishing year landings are illustrated in Figures 4–7. Five- and six-variable models incorporating four or more of these variables provided the most accurate forecasts.

Single forecast models were used in 1987 and 1988, whereas all other forecasts employed 2–4 models (Table 2). In multiple-model years, models usually differed by a single variable, and tests for selecting those models (Mallow's C_p and R^2) gave little reason for favoring one model over another. One exception occurred in 1989 when two sets of models with different independent variables were developed (models 3 and 4 versus models 5 and 6 in Table 2). Forecasts released to the industry stated whether landings were expected to improve or decline and gave high and low landing estimates from the models. A set of revised models for 1993 (forecasts were not

Table 1

Variables included in at least one regression generated for 1987–95 Tortugas pink shrimp landings forecasts. Variables are monthly means or totals (month 5=May) except RRain57 and MRain57 which are summed over months 5–7. NMFS = National Marine Fisheries Service; ENP = Everglades National Park; NWS = National Weather Service; NOS = National Ocean Service. Data are received from sources in American system units (in parentheses). Abbreviations are used in Table 2. ac-ft = acre feet.

			Frequency of occurrence by month					
Source	Variable	Abbreviation	5	6	7	8	9	10
NMFS	Total pink shrimp catch (lb)	Pink		8				1
	Total fishing effort (days)	Days	1	1	20		2	
	Catch per unit of effort of 68-count pink shrimp (lb/day)	CPUE68	11	1		1	3	
ENP	Mean water level in well P35 (ft)	P35	1			3	4	
	Mean water level in well P37 (ft)	P37				1	9	
	Mean water level in well P38 (ft)	P38		1	1	15	1	5
	Total rainfall, Royal Palm (in)	RRain		1				
	Total rainfall during May–July, Royal Palm (in)	RRain57	3					
	Total surface water discharge, L-67 to 40-Mile Bend (ac-ft)	L67		14		2	19	2
NWS	Total rainfall during May–July, Miami (in)	MRain57	1					
	Mean air temperature, Key West (°F)	KAir						4
	Mean wind speed, Key West (mi/h)	KWind	3		2		9	
NOS	Mean sea level, Key West (ft)	Sea	1					

released to the industry) is included as well (Table 2) because Hurricane Andrew impacted south Florida in August 1992 and disrupted ENP data collection through the remainder of 1992 and into 1993. All data were held until ENP had verified that recording instruments had not been disturbed by the hurricane or that instruments had been resurveyed and appropriate corrections had been applied to data sets.[7] These revised forecasts are presented in Table 2 because ENP data figured prominently in every other model.

All models derived in 1987, 1990, 1991, 1992, and 1994 produced forecasts that were within ±20% of actual landings (Table 2). All 1990 and 1991 models (models 7–12) contained the same first five variables. Models 13 and 14 (1992) and models 22 and 23 (1994) contained similar independent variables as did successful 1990–91 models. Forecast models for 1989 included two relatively successful ones (models 3 and 4, –10% and +18% of actual landings) and two poor ones (models 5 and 6, +45% and +44% of actual landings). None of the 1989 models approached the Mallow's test criterion of $C_p = p$, but models 3 and 4 had relatively high R^2 values compared with those of models 5 and 6. Model 2 (1988) and models 15–17 (1993) produced unsuccessful forecasts. Model 2 was the only forecast equation that had no variable directly associated with the Tortugas fishery, although all other unsuccessful models did have such variables. Models 15–17 were derived without access to ENP data which had been incorporated in all other models, successful or otherwise. Had ENP data been available, models 18–21 would have been generated with all but model 19 producing successful forecasts. Models generally forecasted increases or decreases in future landings correctly, with exceptions in 1989, 1991, and 1993. In both 1989 and 1993, three of four models correctly forecasted increased landings, whereas in 1991 only one of three models correctly forecasted decreased landings. Finally, the forecast models for 1995 (for which actual landings will not be available until late 1996) are presented for comparison with previous models and as documentation of the wide range in forecasts (2,858–4,581 t) seen previously only in 1989.

Every model contained at least one independent variable measured in September, and some models included October measurements. These data were usually unavailable until November, thus my goal of releasing each forecast in October was never achieved.

The fact that several variables consistently entered forecast models that were generated annually argues for selecting a single model with fixed variables. This strategy was assessed by applying monthly data, collected in years after generating each model, to those models in order to determine accuracy, if a given

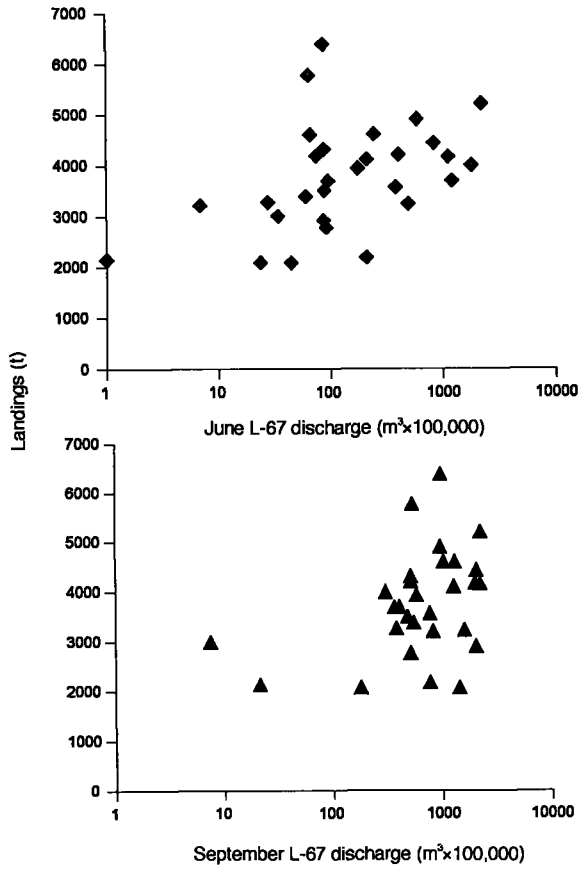

Figure 4

Scatterplots of surface water variables against subsequent fishing year landings, 1966–94.

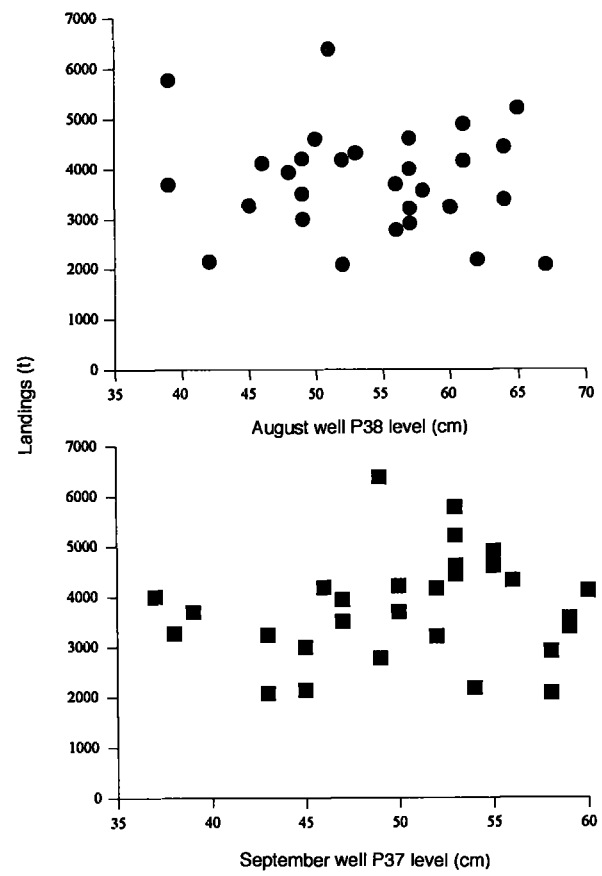

Figure 5

Scatterplots of well water levels against subsequent fishing year landings, 1966–94.

year's model had become "the" forecast model (Table 3). The results indicate that a model that successfully forecasts for the year it was developed does not always function well in succeeding years (e.g. models 1, 3, and 9) and that initially poor models can later become successful (e.g. models 5 and 6). Generating new forecast models each year from updated databases appears to be more accurate than using a fixed forecast model.

Discussion

These models were quite accurate at forecasting whether landings would increase or decrease and only moderately accurate at forecasting amounts landed, but they did not address cause-effect relationships between environmental variables and pink shrimp recruitment. The regular selection of only a few variables in the regression models, however, implies that determining the mechanisms behind selected variables describing Florida Bay and adjacent waters could provide the requisite data for more accurate forecasting of pink shrimp landings. Two classes of data regularly occurred as forecast variables: 1) measurements of upland freshwater supply during the rainy season, and 2) fishing activity on the Tortugas grounds during the waning months of a given fishing year.

Correlation between penaeid shrimp production and freshwater inputs have been recorded worldwide, even though the exact relationship between landings and freshwater may be site- or species-specific. In a previous study of the Tortugas pink shrimp fishery, quarterly landings were found to be either positively or negatively correlated with ENP ground water levels (Browder, 1985). Elsewhere, correlations between penaeid shrimp landings and rainfall, river discharge, or well-water levels have been positive (Hildebrand and Gunter, 1953; Gunter and Edwards,

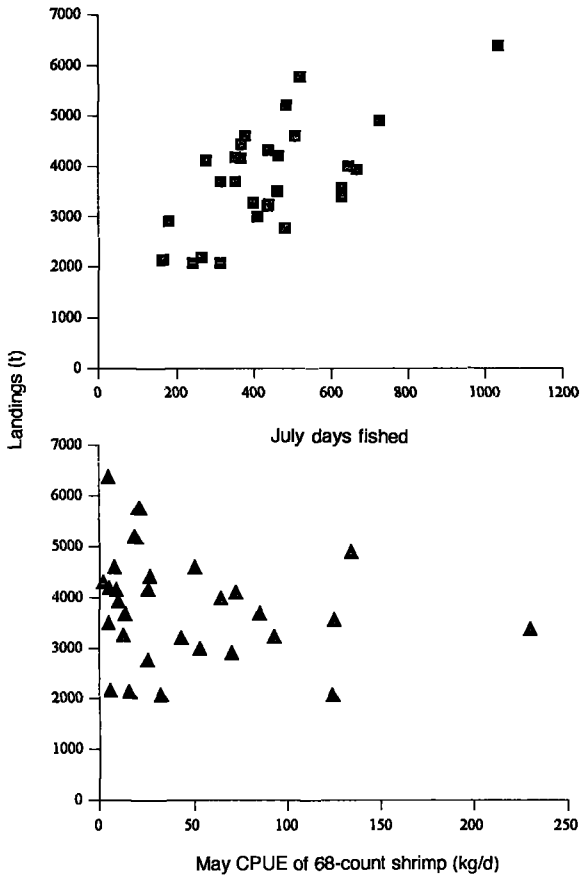

Figure 6

Scatterplots of fishery variables against subsequent fishing year landings, 1966–94.

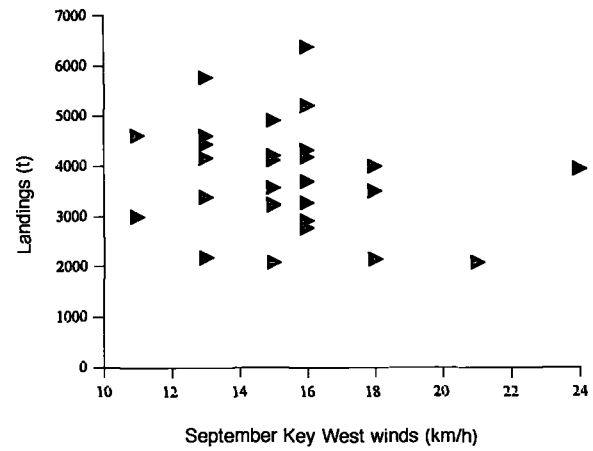

Figure 7

Scatterplot of September Key West winds against subsequent fishing year landings, 1966–94.

1969; Ruello, 1973; Edward, 1978; Glaister, 1978; annual model of Browder, 1985; Vance et al., 1985; Gracia, 1989), negative (Barrett and Gillespie, 1973, 1975; Barrett and Ralph, 1977), or absent (Glaister, 1978; Hettler and Chester, 1982).

In this analysis, freshwater indices exhibited both positive and negative influences on pink shrimp forecasts. Coefficients for L-67 surface water discharge into ENP were always positive, although the nature of the relationship is not as clear for September as it is for June (Fig. 4). The two years with highest landings (1980 and 1977) both occurred when there was moderate L-67 water discharge. Lowest pink shrimp production was associated with extremely low L-67 discharges during the drought of 1989–90. Coefficients for groundwater at well P37 (flowing toward Florida Bay) were always positive whereas those for well P38 (flowing toward Whitewater Bay) were always negative, but again the relationships to landings are not clear (Fig. 5). In most cases, including the present one, the mechanisms behind any relationship between freshwater and penaeid shrimp landings have not been determined experimentally. It has been postulated that excessive freshwater may prevent habitat utilization by postlarval penaeids (Barrett and Gillespie, 1973, 1975) or may initiate early movement of juvenile penaeids out of estuaries (Vance et al., 1985). Hypersalinity is a more frequent condition in Florida Bay (McIvor et al., 1994). Although the direct effects of hypersalinity on pink shrimp are unknown, low surface water discharges are associated with low landings. Examples of the linkage of freshwater inputs to other marine organisms include positive correlation with sea nettle, *Chrysaora quinquecirrha*, abundance in Chesapeake Bay (Cargo and King, 1990) and positive or negative correlation with production by several commercial fisheries in Maryland (Ulanowicz et al., 1982).

Another class of variables typically included in penaeid shrimp forecast models are indices of fishing activity or standing crop prior to the forecast period. The Texas brown shrimp forecast covers the July–June period and is based on average weekly CPUE by the Galveston Bay live bait shrimp fishery during April–June, just prior to emigration of the shrimp into the offshore fishery (Baxter and Sullivan, 1986). The Louisiana brown shrimp forecast also covers July–June, but it is based on inshore and offshore landings from the western half of the state during May.[2] Descriptive models for Tortugas pink shrimp (Browder, 1985) included indices for fishing effort and CPUE that were usually positive in nature and appeared to influence landings up to four

Table 2

Regression models and forecast versus actual Tortugas pink shrimp landings during fishing years 1987–95. See Table 1 for definitions of abbreviations of variables (V1–V6), listed with signs and in order of inclusion by stepwise regression. n = number of variables; Cp = Mallow's test; % = accuracy = 100 (forecast-actual)/actual.

		Variables in regression						Statistics			Landings (t)		
Year	Model	V1	V2	V3	V4	V5	V6	n	Cp	Mult. R^2	Forecast	Actual	%
1987	1	–KAir10	+P379	–CPUE688	+P386	+RRain6	—	5	5.20	0.849	3454	3000	15
1988	2	+RRain57	–L678	+P389	–P388	+L679	+P387	6	6.36	0.775	2857	2075	38
1989	3	–CPUE685	+Pink6	+L6710	+P379	+L676	—	5	6.53	0.883	1917	2141	–10
	4	–CPUE685	+Pink6	+L6710	+P379	+L676	–P3810	6	5.77	0.911	2516	2141	18
	5	+Days7	+RRain57	–P388	+L679	–KWind7	—	5	6.21	0.746	3100	2141	45
	6	+Days7	+RRain57	–P388	+L679	–KWind7	+P359	6	5.22	0.792	3081	2141	44
1990	7	+Days7	+L679	–P388	+L676	+P379	—	5	5.28	0.809	1904	2078	–8
	8	+Days7	+L679	–P388	+L676	+P379	+Pink6	6	6.31	0.819	1786	2078	–14
	9	+Days7	+L679	–P388	–P359	+P379	+L676	6	6.36	0.811	1911	2078	–8
1991	10	+Days7	+L679	–P388	+L676	+P379	—	5	5.16	0.810	2153	2179	–1
	11	+Days7	+L679	–P388	+L676	+P379	–P355	6	6.25	0.830	1993	2179	–9
	12	+Days7	+L679	–P388	+L676	+P379	–L678	6	6.02	0.822	2006	2179	–8
1992	13	+Pink6	–Cpue685	+P359	+Days9	–P3810	—	5	5.37	0.873	2830	2914	–3
	14	+Pink6	–Cpue685	+P359	+Days9	–P3810	+L679	6	6.02	0.897	3066	2914	5
1993	15	+Days7	–KAir10	–CPUE685	–KWind5	–CPUE689	+MRain57	6	6.16	0.880	1982	3696	–46
	16	+Days7	–KAir10	–CPUE685	–KWind5	–CPUE689	–Days6	6	6.01	0.861	1574	3696	–57
	17	+Days7	–KAir10	–CPUE685	–KWind5	–CPUE689	+Sea5	6	6.03	0.858	2106	3696	–43
1993	18	+Days7	+L679	–P388	–KWind9	+L676	+P378	6	6.20	0.898	3237	3696	–12
Revised	19	+Days7	+L679	–P388	–KWind9	+L676	–P3810	6	6.04	0.884	2531	3696	–32
	20	+Days7	+L679	–P388	+L676	–KWind9	+Days5	6	6.37	0.884	3738	3696	1
	21	+Days7	+L679	–P358	+L676	–KWind9	+Pink10	6	6.02	0.878	3483	3696	–6
1994	22	+Days7	+L679	–P388	–KWind9	+Pink6	–CPUE685	6	6.08	0.867	4517	4127	9
	23	+Days7	+L679	–CPUE685	+Pink6	–KWind9	–P3810	6	6.27	0.866	3709	4127	–10
1995	24	+Days7	–KWind9	–P358	+L676	+L679	–CPUE685	6	6.03	0.863	2858	—	—
	25	+Days7	–KWind9	–P358	+L676	+L679	–P388	6	6.00	0.861	3266	—	—
	26	+Days7	–KWind9	–P388	+Pink6	+L679	–CPUE685	6	6.16	0.861	4581	—	—

quarters (12 months) in advance of a given fishing year, thus covering new recruits and spawning stocks. In my models, fishing activity on the Tortugas Grounds during the waning months of a given fishing year (May–July) may be related to the status of the spawning stock and its future production of larvae during the summer and fall months. Catch and effort variables in these models had positive effects on forecasted landings, although CPUE variables had negative coefficients. These indices may be related to prerecruits or to potential parent spawning stocks, although there are no statistically significant parent stock-recruitment relationships for Gulf of Mexico *Penaeus* (Nance, 1993).

In a descriptive model for the North Carolina pink shrimp fishery (Hettler and Chester, 1982; Hettler, 1992), landings during February–July were positively correlated with water temperatures during the coldest two weeks of the preceding winter. Severe cold temperatures were postulated to have reduced landings by killing postlarvae and juveniles overwintering in estuaries (Hettler and Chester, 1982). The model successfully described landings within ±20% of actual landings in five of 10 years (Hettler, 1992). The opposite effect was seen in Florida (Browder, 1985), where mean January–March air temperature,

Table 3

Accuracy (% above or below actual landings) of Tortugas pink shrimp forecasts if forecast equations had become fixed in the year generated. Model = model number from Table 2. Boldface values are ±20% of actual landings.

		Accuracy (%)							
Year	Model	1987	1988	1989	1990	1991	1992	1993	1994
1987	1	**15**	153	55	72	109	87	**3**	**–17**
1988	2		38	56	56	58	119	**–1**	55
1989	3			**–10**	–29	39	–29	53	22
	4			**18**	**–13**	57	**14**	71	46
	5			45	25	31	**4**	**–20**	–32
	6			44	**17**	42	**18**	**–18**	–26
1990	7				**–8**	**–1**	29	**–14**	**–13**
	8				**–14**	**–12**	26	–23	**–15**
	9				**–8**	**–14**	22	–38	–25
1991	10					**–1**	29	**–13**	**13**
	11					**–9**	25	**–18**	–26
	12					**–8**	35	**–11**	**–4**
1992	13						**–3**	23	23
	14						**5**	22	28
1993	15							–46	–63
	16							–57	–73
	17							–43	–40
1993	18							**–12**	–28
Revised	19							–32	–33
	20							**1**	**–9**
	21							**–6**	**–17**
1994	22								**9**
	23								**–10**

as a proxy for water temperature, was negatively correlated with Tortugas pink shrimp landings during the following July–September. The present analyses for the Tortugas fishery rarely included air temperature as a predictor variable, perhaps because predictors were limited to the warmest months of May–October. Costello and Allen (1970) listed no known negative impacts of high summer temperatures on pink shrimp. Air and water temperature have been found to be potential predictors in a variety of other fisheries (Fogarty, 1989).

One final type of data consistently entered my models, i.e. September wind speed at Key West. Wind speed and direction were postulated by Vance et al. (1985) to affect recruitment and settlement of postlarval *Penaeus merguiensis* and thus subsequent harvest. Off Florida, high winds in September, associated with passage of tropical storms, could break up advective processes that deliver planktonic pink shrimp to the nursery areas during the summer. However, concurrent studies of oceanographic features and larval pink shrimp abundance remain to be conducted during this period (Criales and Lee, 1995). It is also possible that high winds in September reduce fishing effort and thus subsequent harvest, but high winds occur during the low point of the fishing year.

My forecasting method involves generating new prediction equations each year, rather than employing a single fixed equation, because 1) the models do not describe cause and effect relationships, 2) causal relationships between most variables and subsequent recruitment to the fishery are not well known (leading to the "hazards of correlative studies" noted by

Hannah (1993), and references cited therein), and 3) changes occur in the database used to make predictions. In time, new environmental, biological, or fishery conditions are encountered. For example, the database for the Tortugas pink shrimp fishery now reflects (directly or indirectly) results of massive seagrass mortality in Florida Bay which began in 1987, a prolonged drought in south Florida during 1989–91, and the four worst fishing years on record. None of these factors would have influenced the first forecast model derived in 1987, and assessment of that model indicated it would have been a failure if used in most future years. Even the durable Texas brown shrimp forecast, first released to the public in 1962 and accurate within ±20% of actual landings for 22 of its first 29 forecasts, was modified in 1994 to reflect the changing nature of the Galveston Bay live bait shrimp fishery after 1980.[2]

Incorrect fishery forecasts can have negative economic impacts on fishermen and processors (Bocking and Peterman, 1988; Walters, 1989), especially if the fishery in question is actively regulated on a short-term basis like the salmonid fisheries of the northeastern Pacific. The penaeid shrimp fisheries of the U.S. Gulf of Mexico are managed to prevent the harvest of undersized shrimp (Gulf of Mexico Fishery Management Council, 1981; Klima et al., 1986). Shrimp management strategies are assessed annually and are accomplished by seasonal closure of Federal and state waters off Texas and by areal closure of shallow Federal waters off southwest Florida. Flexible, in-season adjustments are possible but rare, and to date shrimp management has not been altered in response to forecasts of high or low harvests. As yet, no assessment of the utility and economic effects of either pink shrimp or brown shrimp forecasts have been made among members of the fishing community.

This study indicates that landings of Tortugas pink shrimp might be forecast reliably with some advance knowledge of environmental conditions and abundance of juvenile pink shrimp in nursery areas. Cause-effect relationships are not yet known, and mechanisms describing pink shrimp responses to predictor variables need to be determined through experimental analyses.

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Energetics of larval red drum, *Sciaenops ocellatus*. Part I: Oxygen consumption, specific dynamic action, and nitrogen excretion

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Abstract.—Oxygen consumption and nitrogen excretion rates were determined by direct measurement in fed and starved red drum, *Sciaenops ocellatus*, larvae between the ages of two and eighteen days. Oxygen consumption rates (Y, μL O_2/ind./h) scaled isometrically with mass (X, mg) according to the equation $Y = 4.58X^{1.04}$ (r^2=0.80) in larvae fed 5 prey/mL, resulting in a dry mass-specific oxygen consumption (QO_2) of 4.18 μL O_2/mg DM/h at a mass of 100 μg. In contrast, oxygen consumption of starved larvae scaled with mass according to the relationship $Y = 1.00X^{0.697}$ (r^2=0.50), resulting in a QO_2 of 2.01 μL O_2/mg DM/h at 100 μg. The 50% drop in QO_2 between fed and starved larvae over the mass range addressed in the study was assumed to represent the metabolic cost of growth (specific dynamic action).

Nitrogen was excreted in the form of ammonia and urea. Ammonia excretion (Y, μg NH_3/ind./h) varied with mass (X, mg) in fed individuals according to the relationship $Y = 0.277X^{0.728}$ (r^2=0.58), resulting in a dry mass-specific ammonia excretion rate of 0.52 μg NH_3/mg DM/h at a mass of 100 μg. Like oxygen consumption, nitrogen excretion in starved individuals dropped to 50% of that in fed animals, suggesting a general metabolic slowdown during starvation. Urea production as a percentage of total N-excretion was inversely related to ammonia production in starved individuals and increased with time of starvation; it may be an indicator of starvation in very young fish.

The isometric scaling of metabolism with mass in young larvae suggests that physiological vulnerability, i.e. susceptibility to starvation, does not decline rapidly with increasing size in young fish larvae. Larger larvae are nearly as vulnerable to starvation as smaller ones though their ecological position has improved, i.e. their predator spectrum has declined and their prey spectrum has increased.

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Energy utilization during a fish's early life history reflects its strategy for survival. Ingested energy must be apportioned between metabolic requirements and the need for growth in size; the remainder is lost as fecal and nitrogenous waste. The need for rapid growth in very young larvae is particularly critical: increasing size rapidly decreases the spectrum of potential predators even as it increases the spectrum of items available for forage (Weatherly and Gill, 1987). The two factors that most profoundly influence the amount of ingested energy available for growth are the energy lost to respiration and excretion (Brett and Groves, 1979; Houde, 1989).

Respiration in eggs and larvae is believed to occur through cutaneous diffusion (de Silva, 1974). At hatching, most species of fish lack respiratory pigments and are almost transparent. The blood of these larvae becomes pink weeks or months later upon transformation, which marks the time of blood pigment development and advanced gill filament formation (Weihs, 1981; Blaxter, 1986). Energy demands of respiration in fish larvae are temperature-dependent, ranging from 48% of the gross ingested food energy at 10°C to 31% at 30°C (Houde, 1989).

A portion of the food energy ingested by an individual is indigestible and lost as feces (up to 20% in older fish; Brett and Groves, 1979). In larval fishes, feces are small, difficult to collect, and, as a consequence, are rarely measured. The fraction of ingested energy lost to fecal excretion is therefore usually computed by the difference between the sum of the energy devoted to growth and metabolism and that ingested. Of the remaining food energy that is digestible, a portion is lost as nonfecal nitrogen, mainly as ammonia and urea. Brett and Groves (1979) have stated that energy lost through nonfecal excretion ranges from 3% to 10% of total ingested calories in adults. However, data describing nitrogen excretion in young fish larvae are very scanty. Available figures suggest that total excretion ranges from 23% to 40% of the gross ingested energy (Houde, 1989).

Data collected simultaneously on oxygen consumption and ammonia excretion can be used to determine the biological substrate that is combusted as fuel by using the atomic ratio of oxygen consumed to nitrogen produced (O:N ratio) (Davenport et al., 1983). The O:N ratios of 8 or less indicate that pure protein

is being combusted. Values higher than 20 suggest that lipids are the primary source of energy (Bayne, 1973). Larvae depleting their yolk-sac lipid reserves should thus exhibit high O:N values, whereas fast-growing larvae actively synthesizing protein with little or no lipid deposition or combustion should have low O:N values.

The aims of this study were to determine the respiratory costs of red drum larvae in their first 2 weeks of life, to determine the amount of energy lost as nitrogenous waste in the form of ammonia and urea, to determine the effects of starvation on both nitrogen excretion and respiration, and to determine, by using O:N ratios, the main biological fuel being combusted for energy.

Methods and materials

Maintenance of specimens

Fertilized eggs were obtained from the Florida Department of Environmental Protection (FDEP) hatchery in Port Manatee, Florida. Broodstock was maintained at a temperature of 25°C and a salinity of 30‰. Eggs were obtained from six spawnings over the course of six months to complete the respiration and excretion experiments described below.

Eggs were transported to the University of South Florida Marine Science Laboratory in St. Petersburg, and 2,500–3,000 individuals were placed into each 26-L experimental aquarium. The high mortality associated with first-feeding (cf. Roberts et al., 1978) resulted in a concentration of 250–300 individuals per aquarium after the first 3 days of life. Aquaria were kept in a photoperiod- and temperature-controlled incubator; water was maintained at 25°C and 30‰. A 13-hour light and 11-hour dark photoperiod was used throughout all experiments. Larvae were fed rotifers (*Brachionus plicatilis*) starting at day 3 after hatching until transformation (approximately day 14), when experiments were terminated. Aquaria were aerated and 10% of the water in each was changed daily.

Rotifers were cultured by using the procedure of Hoff and Snell (1987). Seawater for culturing was obtained from offshore in the Gulf of Mexico. The seawater was coarse-filtered, treated with bleach (sodium hypochorite, 5.25%) to remove any additional plankton, and neutralized with sodium thiosulfate. Salinity was adjusted with distilled water and Tropic Marine Seasalt to achieve a final salinity of 30‰.

Rotifers were provided at 5.0 per mL from first feeding (day 3) through day 14. Prey concentrations were monitored twice daily by removing a 25-mL sample from each aquarium, counting the number of prey in 0.5-mL aliquots, and taking the average. Concentrations were adjusted to maintain prey concentrations as necessary.

Oxygen consumption rate

Oxygen consumption was measured in red drum larvae ranging in age from 3 to 18 d. Individuals used in respiratory determinations were of two types: those fed ad libitum and those that had been starved for 24 h. Oxygen partial pressure was monitored in respiratory chambers with both "micro" and "needle" polarographic oxygen electrodes (Mickel et al., 1983; Revsbech and Ward, 1983) as individuals or groups of individuals reduced the oxygen levels to low (0–40 mm Hg) partial pressures. Cathode diameters on both the micro- and needle electrodes were sufficiently small to preclude the need for stirring; both types were manufactured in our laboratory. Starved individuals were monitored with the needle electrodes and fed larvae were monitored by both micro and needle electrodes. Electrodes were calibrated before and after each experimental run with air- and nitrogen-saturated seawater.

Respiratory chambers were manufactured from plastic 1-mL and 10-mL syringes. Each chamber was filled with seawater filtered through a 0.45 μm millipore filter and capped with an electrode fitted with an O-ring. The respiratory chamber within the syringe barrel was thus defined at one end by the syringe plunger and at the other end by the oxygen electrode. Single individuals were run by using a 1-mL syringe and the needle electrode set-up. Groups of 2 to 4 individuals were run in 10-mL syringes with a micro-electrode. Chambers were kept at 24 (±1.0)°C.

Data were continuously recorded throughout each run with either a computer-controlled data logging system (micro-electrodes) or a chart recorder (needle electrodes) (Donnelly and Torres, 1988). For data acquired with the chart recorder, the oxygen consumption rates were computed directly from the slope of the recorded data. Rates were calculated from the data-logger by noting the oxygen depletion over 10-min intervals. Typically, the first 30 min of a run were characterized by a high rate because of excitement associated with introduction into the respirometer. Thus, in all cases, data acquired during the first 30 min of the run were discarded. A mean respiratory rate for each run was determined by taking a mean of all the 10-minute rates comprising the run after the first 30 min. The lowest and highest 10-min rates for each run were designated the minimum and maximum rates.

After each run, individuals were rinsed with distilled water and dried at 60°C for 24 h, then weighed

with a Cahn Electrobalance for dry mass measurements. It should be noted that the number of replicate experiments for larvae starved for 24 h was lower than that for fed individuals because many of the larvae that survived the period of starvation were not hardy enough to be good experimental subjects.

Oxygen consumption as μL O_2 was converted to calories (cal) by using the oxycalorific equivalent of 0.00463 cal/μL O_2 (Brett and Groves, 1979). Calories were then converted to joules (J) by multiplying by 4.1868 J/cal (Pennycuick, 1988).

Nitrogen excretion

Nitrogen excretion rates were determined for larvae of the same ages and feeding states as those used in the oxygen consumption experiments. Larvae aged 3 to 14 d were split into 2 feeding groups: those fed to satiation and those starved for 24 h. Five sets of 10 larvae were removed from each feeding group and each set was placed in a 10-mL screw-top centrifuge tube filled with seawater that had been filtered through activated charcoal. To measure any ammonia addition caused by transfer of the larvae, an additional tube was filled with charcoal-filtered seawater, and a volume of water from the incubation bowl equivalent to that associated with transfer of the larvae was added. A second additional tube was filled with 10 mL of charcoal-filtered seawater to serve as a blank.

All tubes were sealed and incubated for 4 h at 25°C. Larvae were subsequently filtered from the tubes with 50-μm mesh netting, dried at 60°C for 24 h, and weighed. The remaining sample water was split into 10-mL aliquots and immediately capped and frozen for later analysis. Concentrations of ammonia and urea for each sample were determined colorimetrically with an Alpkem autoanalyzer (Price and Harrison, 1987).

O:N ratios

O:N ratios (mol/mol) were calculated by using mass-specific oxygen consumption rates and our data for mass-specific total nitrogen excretion (ammonia and urea). Rates of mass-specific ammonia excretion were used to obtain O:NH_3 ratios.

Results

Oxygen consumption rates

Absolute oxygen consumption rates for individuals (ind.) fed 5.0 rotifers/mL increased with increasing dry mass and, as a consequence, with the age of the larvae as well (Table 1: Fig. 1). Rates ranged between 0.05 (day 3) and 0.14 μL O_2/ind./h (day 7) for the first week of growth. During the second week of growth, values increased sharply from 0.14 to 0.34 μL O_2/ind./h at day 14, reaching 0.77 μL O_2/ind./h at 18 d after hatching. The slope (b) of the oxygen consumption versus mass curve was 1.04 ±0.08 ($\bar{x}$ ±SE), indicating that metabolism was directly proportional to mass (isometric scaling) for the first two weeks of life. Mass-specific oxygen consumption (QO_2) varied between 2 and 6 μL O_2/mg DM/h with a mean of 4.23 ±0.17 μL O_2/mg DM/h ($\bar{x}$ ±SE). The slope (b) of the regression line for oxygen consumption versus age was 1.28 ±0.12.

Individuals starved for 24 h also had absolute oxygen consumption rates that increased with mass and age, but with lower b values (Fig. 2). Slope (b) for the oxygen consumption vs. mass curve dropped to 0.697 ±0.230 ($\bar{x}$ ±SE); that for oxygen consumption vs. age dropped to 0.975 ±0.400 ($\bar{x}$ ±SE). Absolute and mass-specific oxygen consumption and, as a consequence, energy utilization of starved larvae was one-half or less that of fed larvae at all ages up to day 17 (Table 2).

Table 1

Oxygen consumption of red drum, *Sciaenops ocellatus*, larvae fed at 5.0 prey/mL. n = number of sample runs; MDM = mean dry mass in μg; QO_2 = mass-specific oxygen consumption in μL O_2/mg DM/h; and ( ) = standard deviation.

Day	n	MDM	μL/ind./h	Mean QO_2	Min QO_2	Max QO_2
3	6	17.0	0.0473	2.78 (0.93)	1.15 (0.43)	4.56 (0.65)
4	4	24.1	0.1128	4.68 (1.02)	2.54 (1.38)	7.48 (1.71)
7	2	31.5	0.1402	4.45 (2.59)	1.53 (1.35)	11.70 (3.30)
8	4	34.1	0.1238	3.63 (1.73)	1.35 (1.17)	8.28 (2.79)
9	8	46.1	0.2466	5.35 (1.47)	2.01 (1.13)	11.10 (6.27)
10	5	52.0	0.2844	5.47 (0.83)	3.22 (1.46)	8.91 (3.85)
12	6	68.6	0.2593	3.78 (1.94)	1.24 (0.33)	10.80 (2.79)
14	6	109.0	0.3412	3.13 (1.56)	1.20 (0.54)	8.08 (3.18)
17	2	155.0	0.7316	4.72 (2.63)	1.46 (0.05)	12.40 (7.61)

Nitrogen excretion rate

Absolute ammonia excretion rates (Y, µg/ind./h) increased with increasing mass (X, mg) in larvae fed to satiation according to the relationship $Y = 0.277X^{0.728}$ (r^2=0.58) (Fig. 3). The slope of the excretion vs. mass curve in fed larvae (0.728) indicates that mass-specific ammonia excretion declines with increasing mass.

The relation between ammonia excretion and mass was substantially changed with a 24-h period of starvation, such that $Y = 0.058X^{0.328}$ (r^2=0.40) (Fig. 4). The change indicates that absolute ammonia excretion in starved individuals is roughly 50% that of fed individuals. In addition, the decline in mass-specific ammonia excretion with increasing mass is more pronounced as is indicated by the lower slope (0.328).

The increasing mass of growing larvae fed to satiation resulted in an increase in absolute ammonia excretion with age (Fig. 3). Starvation resulted in about a 50% decline in the slope of the relationship between excretion and age, similar to that observed in excretion vs. mass.

The percent contribution of ammonia and urea to total excretion differed; urea dominated in starved individuals. Urea in starved larvae (as total N excreted) was twice that of fed larvae (Table 3).

O:N ratios

The low O:N ratios based on both ammonia-N (O:NH_3) and total nitrogen (ammonia-N and urea-N) excretion rates indicated that protein was the combusted fuel (Table 4). O:NH_3 ratios ranged between 4 and 12 for all ages. O:N values based on combined ammonia-N and urea-N excretion were lower, ranging between 1 and 9. Larvae starved for 24 h

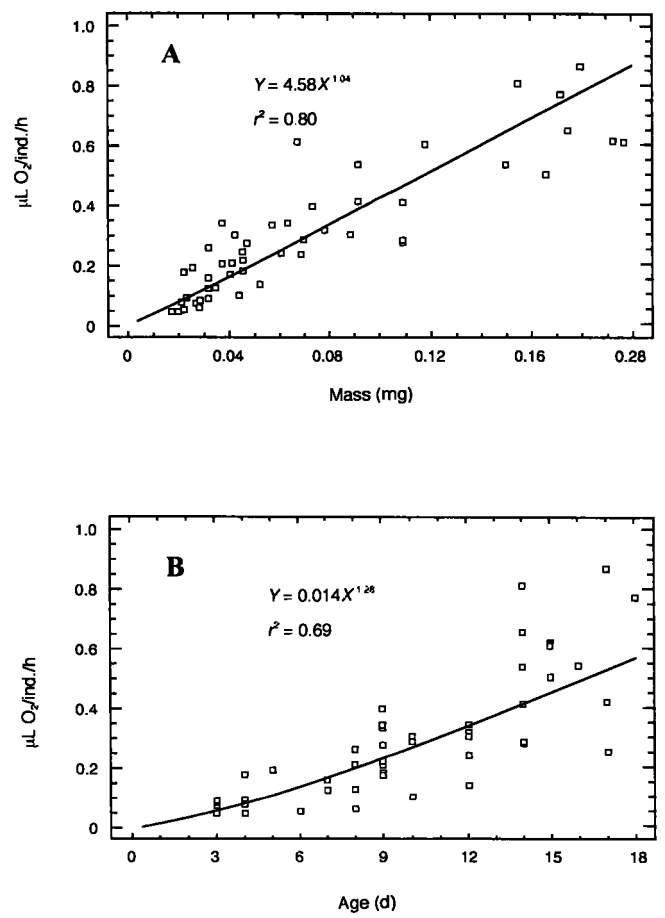

Figure 1

Absolute oxygen consumption (µL O_2/ind./h) in red drum, *Sciaenops ocellatus*, larvae fed to satiation as a function of (**A**) dry mass (mg) and (**B**) age (d).

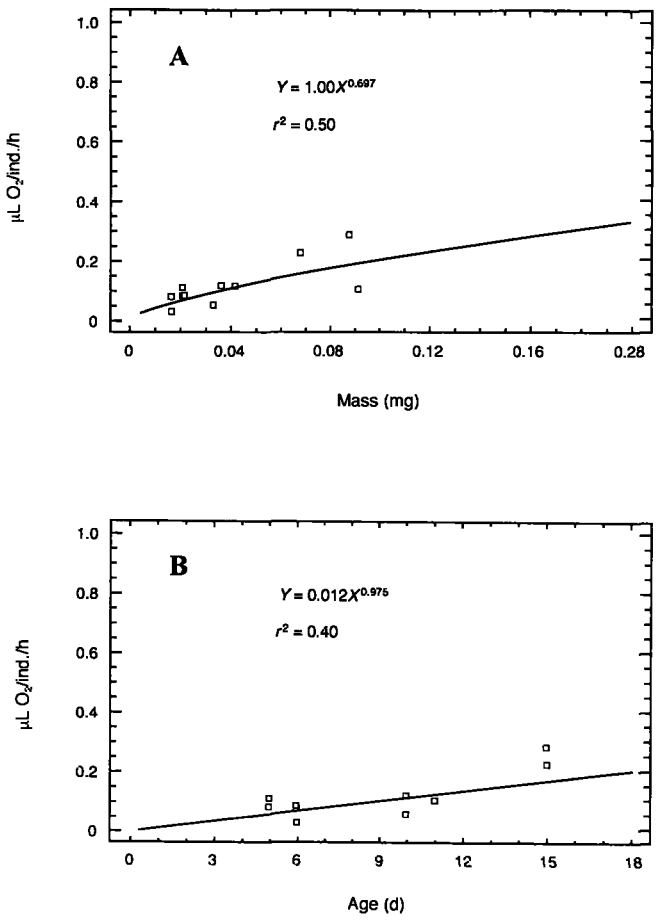

Figure 2

Absolute oxygen consumption (µL O_2/ind./h) in red drum larvae starved for 24 hours as a function of (**A**) dry mass (mg) and (**B**) age (d).

had lower O:N ratios than fed larvae on days 6 and 10. Starved larvae had O:NH_3 ratios between 4.3 and 12.0 and O:N ratios between 1.7 and 9.0.

Discussion

Oxygen consumption rates

Absolute oxygen consumption of red drum larvae was similar to that reported for other larval fishes. Fyhn and Serigstag (1987) found absolute oxygen consumption rates of 0.05–0.100 µL O_2/ind./h in cod larvae for the first 5 d of life at 5°C, which, despite the differences in species and temperature, were similar to our results for red drum. A comparison with other subtropical species is offered by the data of Houde (1983) who reported rates of 0.08 to 0.14 µL O_2/ind./h for 25.5 µg-sized sea bream, *Archosargus rhomboidalis*, reared at 26°C, increasing to 0.44–0.62 µL O_2/ind./h in 41–66 µg individuals. Values for red drum

Table 2

Energy allocated to feeding metabolism of red drum larvae during the first two weeks of life. J = joule.

Age (d)	Fed rate (J/ind./h)	Starved rate (J/ind./h)	% reduction
3	0.0015	0.0008	46.7
4	0.0017	0.0010	41.2
6	0.0024	0.0013	45.9
10	0.0044	0.0021	52.2
14	0.0083	0.0033	60.2

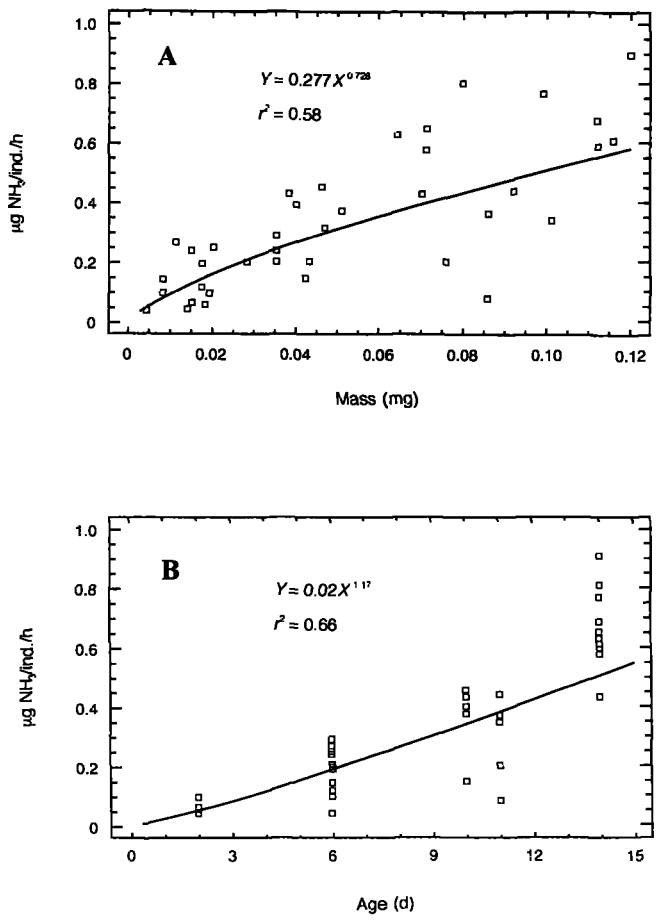

Figure 3

Absolute ammonia excretion (µg NH_3/ind./h) in red drum larvae fed to satiation as a function of (**A**) dry mass (mg) and (**B**) age (d).

larvae were lower at 0.05–0.14 µL/ind./h for 21–31 µg fish and 0.26–0.28 µL/ind./h for 52–68 µg larvae.

The regression of absolute oxygen consumption versus mass in larval red drum conformed to the equation $Y = aM^b$ (Fig. 1) and had a slope or "*b* value" of 1.04 (±0.08), which is greater than the most widely used figure of 0.75 (Schmidt-Nielsen, 1983), and the slope of 0.80 commonly cited for adult fish (Brett and Groves, 1979; Houde, 1983; Prasad, 1986). The slope of 1.04 (±0.08) exhibited by red drum larvae indicates that oxygen consumption scaled directly with body mass (1.0) rather than with surface area (0.67). It is becoming increasingly apparent that metabolism scales isometrically with mass in larval fishes (see review by Giguere et al., 1988); thus, a *b* value of 1.0 is the norm rather than the exception for larval fishes and most likely for larval forms in general (Manahan, 1990).

Feeding metabolism

Oxygen consumption rates for two-week-old red drum starved for 24 h declined to about 50% of those for fed individuals (Table 2), which is within the range reported in larval starvation studies with several other species (Holliday et al., 1964; Giguere et al., 1988; Tucker, 1989). The reduction of oxygen consumption in starved versus fed individuals reflects the decrease in energy expenditure associated with feeding metabolism, otherwise known as specific dynamic action (SDA) (Kleiber, 1961; Kiørboe et al., 1985; 1987; Kiørboe, 1989). Jobling (1981a, 1983) suggested that SDA represents the energy expenditure associated with growth. His arguments may be summarized as follows. Biosynthesis is an energy-requiring process (Lehninger, 1985). As a consequence, some fraction of the adenosine triphosphate

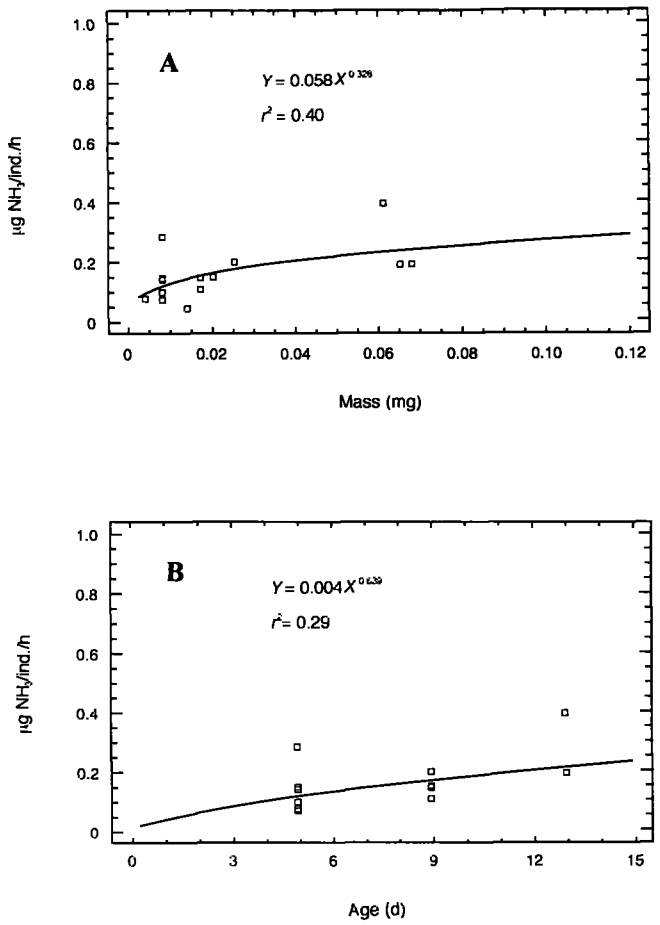

Figure 4

Absolute ammonia excretion in red drum larvae starved for 24 hours as a function of (**A**) dry mass (mg) and (**B**) age (d).

(ATP) generated by aerobic metabolism must be used for growth in a normal, developing individual. The fraction of aerobic metabolism that generates the ATP for biosynthesis is the increase in metabolism following feeding variously known as specific dynamic action (SDA) (Kleiber, 1961), specific dynamic effect (Kleiber, 1967), or heat increment (Brett and Groves, 1979). Thus, diets that promote high growth induce high energy use as SDA. Jobling's view conflicts with the more traditional idea that growth and SDA are in direct competition for ingested energy.

The 40% to 60% reduction in metabolic rates of starved individuals indicates that feeding metabolism (SDA) is a substantial fraction of the daily metabolic costs above maintenance in fed larvae. Because SDA is specifically related to growth, and individuals growing slowly demonstrate little change in metabolic rate following feeding (Jobling, 1985), it follows that the large reduction in metabolic rate of starved red drum is indicative of a rapidly growing fish.

Nitrogen excretion

Our data on nitrogen excretion are the first reported for larval red drum; they add significantly to the very limited information describing excretion in fish larvae. Absolute ammonia excretion rates of red drum larvae (Table 3; Fig. 3) were similar to those reported by Klumpp and von Westernhagen (1986) for similar size *Pleuronectes platessa* (0.025–0.050 µg NH_3/ind./h at 100 µg and 11 d) and *Blennius pavo* (0.05–0.10 µg NH_3/ind./h at 100 µg and 5 d).

The 50% drop in absolute and mass-specific ammonia excretion with starvation (Table 3; Figs 3 and 4) mirrors the drop observed in oxygen consumption rate, indicating a general slow-down in metabolic

Table 3

Mean ammonia and urea excretion in red drum larvae fed to satiation and starved for 24 h. *n* = the number of samples (10 fish per sample); * = 24 h starved; ( ) = standard deviation.

Age (d)	*n*	Ammonia μg/ind./h	Ammonia μm/ind./h (× 10^{-3})	Urea μm/ind./h (× 10^{-3})	Excretion % urea
2	5	0.006 (0.001)	0.325 (0.20)	0.0793 (0.08)	32.8
6	10	0.023 (0.007)	1.333 (0.38)	0.2058 (0.03)	23.6
6*	10	0.016 (0.008)	0.660 (0.20)	0.4648 (0.11)	58.5
10	10	0.038 (0.012)	2.215 (0.40)	0.3038 (0.03)	21.5
10*	5	0.015 (0.004)	0.883 (0.23)	0.6678 (0.85)	60.2
14	10	0.067 (0.013)	3.918 (0.78)	0.4205 (0.04)	17.7
14*	5	0.039 (0.001)	2.265 (0.07)	0.4160 (0.25)	32.7

Table 4

Molar oxygen:nitrogen ratios for red drum larvae fed to satiation, and those starved for 24 and 48 h. ( ) = Standard deviation; * = starved 24 hours.

Age (d)	Oxygen (μm/mg/h)	Ammonia (μm/mg/h)	Urea (μm/mg/h)	O:NH_3	O:N
2	0.244 (0.021)	0.024 (0.005)	0.006 (0.005)	10.16 (2.44)	6.78 (1.49)
6	0.367 (0.183)	0.084 (0.039)	0.013 (0.002)	4.37 (3.12)	3.37 (3.02)
6*	0.401 (0.087)	0.089 (0.039)	0.063 (0.014)	4.51 (1.74)	1.86 (0.63)
10	0.598 (0.183)	0.050 (0.018)	0.006 (0.001)	11.96 (2.07)	9.65 (1.70)
10*	0.189 (0.062)	0.044 (0.006)	0.033 (0.004)	4.30 (0.58)	1.72 (0.26)
14	0.321 (0.091)	0.049 (0.008)	0.005 (0.001)	6.55 (1.64)	5.44 (1.37)
14*	0.288 (0.005)	0.024 (0.012)	0.004 (0.003)	12.00 (0.18)	9.00 (0.12)

processes with starvation. As was demonstrated by the O:N ratios (see below), the normally fast-growing young larvae apparently combust their own tissues to fuel their metabolic needs.

Values obtained in the present study for the percentage of nitrogenous waste in the form of urea agree well with previously reported values. Jobling (1981b) found that 15% to 25% of nitrogenous waste in plaice larvae occurred in the form of urea: his values agree well with our values of 18% to 33%. Ammonia as a percent of the total nitrogen excretion increased with age in red drum larvae fed to satiation.

Production of urea may play a role in survival of young larvae. Griffin (1991) proposed that urea synthesis was a mechanism for detoxifying ammonia during early embryogenesis, particularly before hatching, and several investigators have reported the presence of urea-cycle enzymes in larval fish (Rice and Stokes, 1974; Dépêche et al., 1979; Anderson, 1995). Urea costs more energy to produce than ammonia, but it is less toxic. It is used extensively in osmoregulation by elasmobranchs (Anderson, 1995), as an excretory product to prevent poisoning during estivation by African lungfish (Janssens, 1964), and in response to elevated external ammonia levels or to stress in toadfish (Walsh et al., 1990). It is possible that production and retention of urea in young red drum larvae could be used to increase blood osmolarity, in a manner similar to that of elasmobrachs, to aid in osmoregulation. Alternatively, it may be a response to the stress of starvation.

The percent increase in urea production with starvation has been observed in other fishes under hatchery conditions (Brett and Zala, 1975). The constant mass-specific nitrogen excretion in starved fish, despite the changes in relative contributions of ammonia and urea, is indicative of continued protein catabolism. However, the protein catabolized in starved individuals was the protein contained within the larva's own tissues.

Urea normally contributes less than 50% of the total nitrogen excreted and is often overlooked, but the results here suggest urea is an excellent indicator of starvation in larval fishes. The decrease in

percentage of urea excreted by larger red drum larvae could indicate a metabolic shift away from urea production in larvae approaching transformation or in the secondary loss of the ability to produce it (cf. Anderson, 1995).

O:N ratios

Nitrogen excretion data for larval red drum suggest that protein was the major catabolic substrate, with little, if any, energy being stored in, or produced from, lipid reserves. Low O:N ratios in well-fed red drum larvae as well as in those starved for 24 h indicated a protein fuel source in all cases. Ingested rotifers were protein-rich (Brightman, 1993) which almost certainly contributed to the low O:N ratios of fed individuals. The slightly lower O:N ratios for starved larvae suggest an even stronger dependence on protein for metabolic fuel, combusted at the expense of tissue protein.

Conclusions

An interesting outgrowth of the present study is not only the amplitude of change in metabolism with starvation, but the change in the scaling coefficient as well. The drop in "*b*" from 1.04 to 0.697 as a result of starvation suggests that the larger larvae have sustained a proportionately greater drop in metabolism than the smaller ones, which, in turn, underscores a metabolic "catch-22" situation in young larvae. Rapid growth of a larva decreases the number of its potential predators, thereby giving the larva the ecological refuge of increased size. In addition, it simultaneously increases the size range of its potential prey. However, the fact that metabolism scales directly with mass means that larger larvae will also be combusting more metabolic fuel in an absolute sense than will smaller individuals. Because energy storage in red drum larvae is almost nonexistent (Brightman, 1993), the absolute metabolic costs of being larger could prove to be rapidly debilitating during times of starvation (cf. Giguere, 1988). In juvenile and adult fishes, "*b*" values typically are close to 0.80 (Giguere, 1988) and weight-specific oxygen consumption declines with increasing size. Thus, in adult fish, larger size gives a metabolic refugium as well as an ecological one. Because larger adults have a proportionately lower metabolism than smaller adults, starvation will be proportionately less debilitating for the larger fish. Thus, the "catch-22" of isometric scaling (b=1.0) in the very early life history of fish is that it is almost certainly part of the metabolic underpinnings of rapid growth, but it also makes larger larvae nearly as vulnerable to starvation as smaller ones. Rapid growth gives an ecological refuge but it comes at the expense of physiological vulnerability.

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Nearshore assemblages of larval rockfishes and their physical environment off central California during an extended El Niño event, 1991–1993

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Abstract.—Rockfish are among the most prevalent members of nearshore ichthyoplankton assemblages off central California, yet their abundance varies greatly from year to year. Warm events, like El Niño, can have pronounced effects on the success of a year class. We evaluate distribution, abundance, and species composition of rockfish larvae on small spatial and temporal scales in the upwelling center north of Monterey Bay during an extended El Niño (December 1991 through June 1993) relative to regional hydrography.

Anomalously warm, low-salinity water to depths greater than 50 m during much of our study was indicative of an onshore displacement of the California Current. Upwelling was reduced and delayed relative to other years. The two years differed, however, in the intensity, duration, frequency, and direction of wind events. Larval rockfish abundance was similar in both years of the El Niño, peaking in early February, and was among the highest when compared with estimates from CalCOFI surveys off central California (1951–84). Using larval ages, we determined that median birthdates of shortbelly rockfish were in early- to mid-February both years. Growth rates of larval shortbelly rockfish did not differ among months or between years. Relative to 1993, rockfish larvae were more abundant, and sizes of larval shortbelly were significantly greater at onshore stations in 1992. This coincided with onshore advection of water during the onset of the El Niño, suggesting retention of larvae nearshore. Initiation of upwelling in March and April 1993 and fewer larvae at onshore stations are indicative of greater offshore transport during the second year.

Juvenile rockfishes were extremely rare in summer of 1992; in 1993 they were twenty times more abundant and larger. Surviving juvenile shortbelly rockfish were born late during both years; upwelling occurred coincidentally during this period in 1993 but not in 1992. We suggest that substantially higher survival and recruitment of juvenile rockfishes in 1993 was due to increased offshore transport and perhaps lower predation during the larval stages.

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Ocean conditions off central California are influenced seasonally by a variety of factors and processes that operate on a local scale (e.g. wind, upwelling, freshwater input, and bathymetry) and larger spatial scales (e.g. the California Current System and El Niño events). Prevailing winds from the northwest produce relatively intense upwelling, particularly near capes and headlands, typically during March through September (Kelly, 1985; Breaker and Broenkow, 1994; Rosenfeld et al., 1994a). An abrupt decrease in sea-surface temperature, occurring sometime between February and May, defines the spring transition to coastal upwelling, which is associated with increased nutrient concentration, primary production, and offshore transport of surface water. Because the coastal ocean environment can respond rapidly to changes in local wind speed, direction, and duration, onshore transport of water off central California can occur during periods of reduced equatorward winds and subsequent cessation of upwelling (Broenkow and Smethie, 1978; Rosenfeld et al., 1994a). This transport is manifested nearshore by the occurrence of warm, relatively low salinity water representative of the offshore core of the California Current.

Point Año Nuevo (37.1°N, 122.3°W), to the north of Monterey Bay, has been identified as a distinct center of upwelling, associated with bifurcated plumes of cool, saline, nutrient-rich surface water that are advected both seaward and southward across Monterey Bay (Tracy, 1990; Schwing et al., 1991; Rosenfeld et al., 1994a). According to satellite and in situ data, these recurrent upwelling plumes can extend 10–100 km offshore and persist from days to weeks. As it flows equatorward, some of this upwelled water is advected into the bay.

Rockfishes (*Sebastes* spp.) are tremendously diverse, dominate coastal benthic fish assemblages and support heavily exploited recreational and commercial fisheries in California (Lea, 1992). Although rockfish larvae are among the most prevalent members of nearshore ichthyo-

plankton assemblages, especially off central California, annual abundance varies widely (Moser and Boehlert, 1991; Moser et al., 1993). Factors affecting survival of young fishes, including hydrographic conditions and associated transport processes, density of prey and predators, and spawning seasonality are potentially critical determinants of rockfish recruitment.

Rockfishes are viviparous, with larval release (parturition) occurring mainly from January to April for many of the species off central California (Wyllie Echeverria, 1987), just before and during the onset of upwelling. Duration of the pelagic larval and juvenile stages of many species is typically several months (Anderson, 1983; Woodbury and Ralston, 1991) but may be up to one year (Boehlert, 1977). The arrival and subsequent settlement of pelagic juvenile rockfishes in subtidal areas off central California may be associated with upwelling events and onshore transport during periods of wind relaxation (VenTresca et al., 1990; Larson et al., 1994). The recurring bifurcated plumes of upwelled water off Pt. Año Nuevo, a relatively unfished area that could serve as a source of larvae, interspersed with occasional periods of wind relaxation and onshore transport, may be important vehicles for transport of young rockfishes from upwelling centers into nearshore areas of Monterey Bay and farther south.

Warm events, often indicative of an El Niño, occur along the coast of California every 2–10 years (Norton et al., 1985) and persist for 1–3 years (Chelton et al., 1982). Strong events occurred coastwide in 1926, 1941, 1958, and 1983 (Ware, 1995). El Niño-like conditions can include 1) increased sea-surface temperature (SST) and depth of thermocline; 2) positive sea-level anomalies (Chelton and Davis, 1982); 3) reduced upwelling, nutrients, and primary and secondary production (Fiedler, 1984; McGowan, 1985; Miller et al., 1985); and 4) increased poleward and onshore flow of coastal water (Simpson, 1984; Hayward et al., 1994; Lynn et al., 1995). Significant increases in SST were noted off central California during winters of 1972, 1976, 1979, and 1983, which corresponded with El Niño episodes (Breaker et al., 1983).

Warm events like, but not restricted to, El Niño can have disastrous effects on year-class strength of rockfishes, a group with arctic to temperate affinities and distribution (Karpov et al., 1995; Lenarz et al., 1995; Ralston and Howard, 1995). Anomalously warm water and suppression of upwelling have been associated with large-scale reductions in the primary prey (e.g. euphausiids and smaller zooplankton) of juvenile and adult rockfishes (Mullin and Conversi, 1989). Reduced prey abundance may negatively affect the somatic and reproductive condition of adult rockfish (Lenarz and Wyllie Echeverria, 1986; VenTresca et al., 1995), potentially disrupting the timing, location, and net output of reproduction. Changes in distribution and dispersal patterns of pelagic larvae, and altered production of their prey and predators, are expected during anomalous warm events (Bailey and Incze, 1985; Brodeur et al., 1985).

In this paper we evaluate distribution, abundance, and species composition of rockfish larvae and associated hydrography on small spatial (<20 km) and short temporal (biweekly to monthly) scales in an upwelling center north of Monterey Bay during an extended El Niño event (1991–93). From size, age, and estimated growth models, we compare birthdate distributions of early larvae and surviving pelagic juveniles of the most common species. We discuss potential larval transport and subsequent strength and timing of juvenile recruitment to nearshore areas along the central California coast.

Methods

Sampling

Ichthyoplankton surveys were conducted during daytime aboard the RV *Ricketts* (ca. 11 m long) at five stations along a northeast–southwest transect off Davenport, California (37°N, 122°10'W; Fig. 1). Sta-

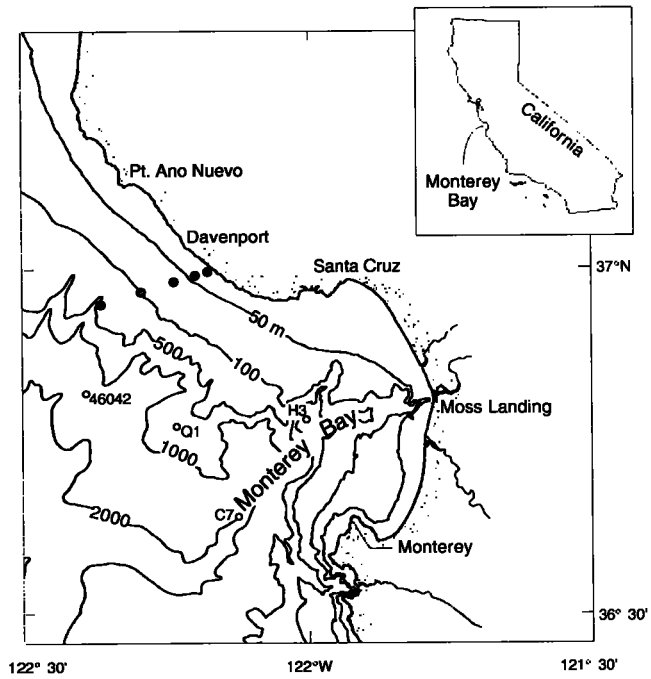

Figure 1

Monterey Bay study area and five stations (solid dots) sampled for larval fish off Davenport. Sites of wind measurements (46042) and 1989–91 CTD casts (H3, C7, and Q1) are indicated.

tions were located across the shelf at 1 km (15 m water depth), 3 km (30 m water depth), 7 km (60 m water depth), 13 km (100 m water depth), and 19 km (180–713 m water depth) from shore. During 1991–92, samples were collected at approximately two-week intervals from early December to April; less frequent sampling extended through June because of the absence of expected upwelling events during spring. Sampling between January and April 1993 was limited to monthly intervals by frequent storms and rough seas.

Larvae were sampled with two 70-cm (mouth diameter) open nets of 0.505-mm mesh, black Nitex fitted onto a bongo frame. Volume of water filtered (30–465 m^3 per net) was estimated from calibrated mechanical flowmeters positioned in the mouth of each net. Tows were made parallel to bathymetry at 1–3 k for 2–20 min (depending on depth) obliquely from near the bottom to the surface at nearshore stations and from 200 m to the surface at the offshore station. Three replicate tows were conducted at most stations (Table 1). Oceanographic data were collected from near bottom to the surface at each station with a calibrated CTD (conductivity, temperature, and depth) profiler (model SBE 19 SEACAT, Sea-Bird Electronics). Daily wind speed and direction during the survey period in each year were calculated from daily averages of east and north wind components measured at the National Data Buoy Center moored buoy 46042 (Fig. 1).

Table 1

Dates of collection and number of replicate oblique bongo net tows conducted along an onshore–offshore transect off Davenport, California, during winter–spring months of 1991–93. Stations are defined by bottom depth (m) and distance from shore (km). "—" indicates no samples were taken.

	Station depth (m)				
Date	15 (1 km)	30 (3 km)	60 (7 km)	100 (13 km)	200 (19 km)
1991–92					
02 December	3	3	2	3	3
18 December	3	3	3	3	3
09 January	3	3	3	3	3
23 January	3	3	3	3	3
06 February	3	3	3	3	3
21 February	3	3	3	3	3
12 March	3	3	3	3	3
02 April	3	3	3	3	3
04 May	—	—	—	1	1
16 June	—	3	3	3	—
Subtotal	24	27	26	28	25
1993					
29 January	3	3	3	3	3
12 February	—	—	3	3	3
07 March	—	3	—	—	3
06 April	—	3	—	3	3
Subtotal	3	9	6	9	12
Total	27	36	32	37	37

Plankton samples were preserved at sea, one sample from each bongo pair in 5% buffered formalin and the other in 80% buffered ethanol. Rockfish larvae were sorted under a dissecting microscope from each paired sample for all replicates per station. Formalin-preserved rockfish from all replicates were enumerated for abundance estimates. Only one ethanol-preserved replicate per station was processed for species identification. Standard length (or notochord length for preflexion larvae) was measured to the nearest 0.1 mm for shortbelly rockfish, *Sebastes jordani*, and blue rockfish, *S. mystinus*, preserved in ethanol. Otoliths were removed for age determination from a subsample of these two dominant species; larval ageing methods (i.e. counting daily growth increments in otoliths) followed Yoklavich and Bailey (1990). Within the otolith microstructure of larval shortbelly rockfish, a well-defined increment is formed at parturition, which has been adequately resolved with optical microscopy at 1250× magnification (Ralston et al., 1996). Daily formation of increments in otoliths has been demonstrated in juvenile black rockfish (*S. melanops*; Yoklavich and Boehlert, 1987) and in shortbelly and brown rockfish (*S. auriculatus*; Laidig et al., 1991).

Birthdates of larval shortbelly and blue rockfishes were calculated by using a linear growth model (e.g. fitted from the aged subsample) to estimate age from length and by subtracting age from date of capture. Birthdate distribution estimated from larvae was compared with that estimated from older pelagic young-of-the-year shortbelly rockfishes collected from May to July, 1992 and 1993, near Monterey Bay (see Loeb et al.[1] for details of surveys). Ages of these pelagic juveniles were estimated from length by using linear growth models developed for this species and size range collected from central California during May and June 1992 and 1993 (Woodbury[2]). Birthdate distributions were corrected for age-specific mortality across all daily cohorts with rates modified from

[1] Loeb, V. J., M. M. Yoklavich, and G. M. Cailliet. 1994. The importance of transport processes in recruitment of rockfishes (Genus *Sebastes*) to nearshore areas of Monterey Bay, California. Final Report, NOAA, California Sea Grant College, Project R/F-142, 25 p.

[2] Woodbury, D. 1996. Natl. Mar. Fish. Serv., NOAA, 3150 Paradise Dr., Tiburon, CA 94920. Unpubl. data.

Ralston and Howard (1995): 0.1165, 0.10, 0.08, 0.06, 0.04, and 0.03/d for fish of age <15, 15–27, 28–42, 43–70, 71–100, and >100 d, respectively.

Larval identification

Preflexion and flexion rockfish larvae were identified primarily from melanistic pigment patterns, including: length of ventral midline series, occurrence of dorsal midline pigmentation, and occurrence of pectoral fin pigmentation. Distinctions among larvae with shared primary pigment patterns were based on secondary pigment characters (e.g. external dorsal midline pigment configuration, lower lip pigment, and pectoral fin size and pigment pattern), and on reproductive seasonality of adults (Wyllie Echeverria, 1987; Love et al., 1990).

Preextrusion, yolk-sac, and preflexion stages have been illustrated or described in some detail for 49 of the 52 species of rockfishes off central California (see Kendall [1991] for a general review). More advanced larval stages have been described for relatively few species of rockfish. We used serial descriptions of larvae from preflexion through flexion to identify shortbelly (Moser et al., 1977), blue (Moreno, 1993), cowcod (*S. levis*; Moser et al., 1977), bocaccio (*S. paucispinis*; Moser, 1967), and stripetail rockfish (*S. saxicola*; Laidig et al., 1996). All postflexion larvae with dorsal, anal, and pectoral fin rays were identified to species.

Squarespot rockfish, *S. hopkinsi,* were abundant as preflexion larvae and were identified cautiously from a description of their preextrusion stage (Moser et al., 1977). Two groups of species also were identified on the basis of shared pigment patterns. The "copper complex" informally is synonymous with the subgenus *Pteropodus* (Jordan et al., 1930; Kendall, 1991), and comprises copper (*S. caurinus*), gopher (*S. carnatus*), black-and-yellow (*S. chrysomelas*), grass (*S. rastrelliger*), china (*S. nebulosus*), and quillback (*S. maliger*) rockfishes. We include brown (*S. auriculatus*) and kelp (*S. atrovirens*) rockfishes in a "copper complex +" because their pigmentation is indistinguishable from members of *Pteropodus*. A "*Sebastosomus* +" group includes black, olive (*S. serranoides*), yellowtail (*S. flavidus*), widow (*S. entomelas*), and bank (*S. rufus*) rockfishes. Identification of this group is limited because yolk-sac and early preflexion larvae are indistinguishable from many other species, including most in the subgenus *Sebastomus*.

Data analysis

Larval abundance was calculated for each replicate at each station by multiplying the number of larvae by depth of tow and by dividing by the volume of water filtered per sample. Abundance was expressed as number of larvae per 10 m^2. Abundance data were examined for normality and were log-transformed where appropriate. Among-station and among-time differences in total abundance of larval rockfishes were tested for significance by using a 2-factor analysis of variance (ANOVA), including only those samples collected during the first eight periods in 1991–92 (i.e. those with three replicates per station and five stations per time period). Between-year comparisons of abundance were made with 2-factor ANOVA (i.e. factors were year and time) by using only those time periods and stations equally represented in both years. Specific time periods and stations that contributed to significant factors in the models were identified by using post-hoc pairwise multiple comparisons of cell means with Bonferroni-adjusted probabilities. Differences in mean size and growth rate of the two dominant species of larval rockfish among stations, collection times, and years were similarly analyzed.

Results

The physical environment

Our 1991–93 study period off central California was characterized by a prolonged El Niño event. Anomalously warm, low-salinity water in nearshore areas during much of our study indicated an onshore displacement of the California Current, similar to that reported by Lynn et al. (1995) for this time period and by Simpson (1984) for the 1982–83 El Niño event. Upwelling was reduced and delayed relative to other years, and distinct persistent upwelling plumes were not evident within the survey area during the sampling periods. The two years differed, however, in the intensity, duration, frequency, and direction of wind events that affected transport processes.

Coastal winds off Monterey prior to the 1991–93 El Niño event were primarily from the northwest during December to April (Fig. 2A), as estimated from daily wind components measured at buoy 46042 (Fig. 1) and averaged from 1988 to 1991. Associated with this prevailing wind pattern was a steady shoaling of cold, high salinity water, indicative of upwelling, in the upper 200 m of the water column in the outer part of Monterey Bay, as measured by a total of 37 CTD casts from stations H3, C7, and Q1 (Fig. 1) during April 1989, December 1989–April 1990, and December 1990–March 1991 (Fig. 2, B and C; raw data from Rosenfeld et al., 1994b).

During winter 1991–92, daily wind speeds were largely greater than the average calculated during

the same period from 1988 to 1991, but wind direction reversed in late December and the greater part of February and March 1992, blowing predominantly from the southeast for 2–12 d at a time (Fig. 3A). Coincidentally, water in the upper 80 m was warmer and fresher following these periods of southeast winds (Fig. 3, B and C); water of 15°C and 33.2‰ occurred near the surface by 2 April. Contoured vertical sections of temperature during the spring ichthyoplankton surveys off Davenport in 1992 indicated an increasingly stratified and warm water column at least to 19 km offshore (Fig. 4A); isohalines were similarly stratified. There was no evidence of upwelling (i.e. no shoaling of isotherms and isohalines near the coast) during winter–spring 1992. For comparison with the following year, note that the 10°C isotherm remained below 100 m during the 1992 sampling season.

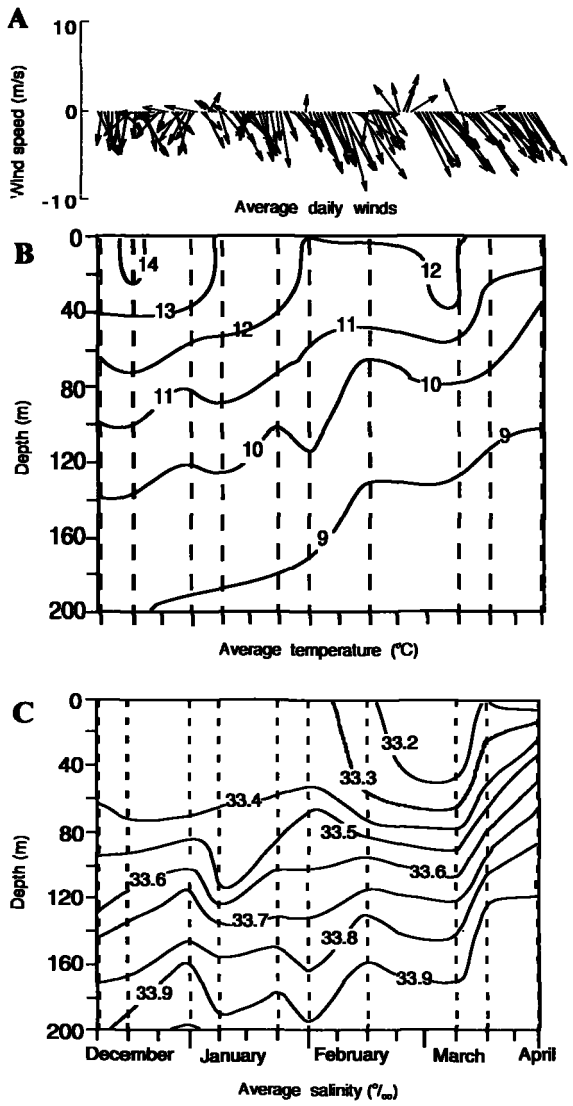

Figure 2

Wind, temperature, and salinity profiles for offshore Monterey Bay, California. (**A**) Wind vectors from December to April, as estimated from daily wind components measured at buoy 46042 and averaged from 1988 to 1991 (arrows point in the direction to which wind was blowing [north is toward top of page]); (**B**) weekly average temperature (°C); and (**C**) salinity (‰) in upper 200 m in the outer part of Monterey Bay during December to April, 1989–91. Weeks of CTD sampling are indicated with dashes. (Raw data from Rosenfeld et al., 1994b.)

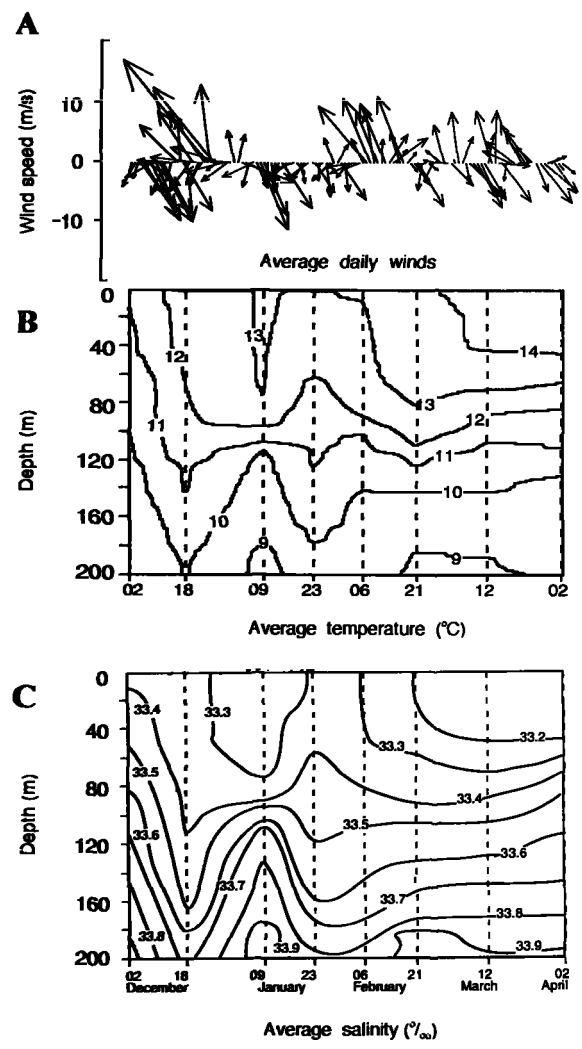

Figure 3

Wind, temperature, and salinity profiles for offshore Davenport, California. (**A**) Daily averaged wind vectors measured at buoy 46042 in Monterey Bay (arrows point in direction to which wind was blowing [north is toward top of page]); (**B**) temperature (°C); and (**C**) salinity (‰) in upper 200 m at an offshore station (19 km) during ichthyoplankton surveys 2 December 1991–2 April 1992. CTD sampling dates are indicated with dashes.

During winter 1993, a lens of warm surface water deepened from late January to mid-February, with 13.5°C water at 60 m along the transect line (Fig. 4B). Winds were variable, with no distinct periods of reversal. Unlike 1992, however, persistent wind from the northwest (favorable to upwelling) commenced in early March 1993 (Fig. 5A) and resulted in cooler water temperatures in the upper 80 m off Davenport by early April (Fig. 5B). This was the first evidence of upwelling during either year of the ichthyoplankton surveys, as indicated by the 10°C isotherm sloping up toward the coast from 19 km offshore in the 6 April 1993 CTD profile series (Fig. 4B).

Ichthyoplankton surveys

Patterns of distribution and abundance The 130 bongo-net tows made during ten ichthyoplankton surveys in 1991–92 (Table 1) contained 9,389 rockfish larvae; 39 tows made during four surveys in 1993 included 3,492 rockfish larvae. Rockfish larvae were collected during all surveys, occurring in 78.7% of all tows and in 100% of the tows made at the three stations 7–19 km from shore. Forty-seven percent of the rockfish larvae collected in 1992 and 66% in 1993 were identified as eight species or species-groups (Table 2). Shortbelly rockfish were numerically dominant both years, representing 46% of the total catch in 1993 and 29% in 1992. Shortbelly rockfish larvae occurred from late December to early May, largely in the offshore samples (13 and 19 km). Although much less numerous than shortbelly rockfish, blue, stripetail, and squarespot rockfish larvae also were relatively abundant each year (3–6% of the total). Although members of the "copper complex +" represented only 1–2% of the total catch and generally occurred in greater numbers offshore, they were the most abundant rockfish taxon identified at inshore stations (1 and 3 km).

Abundance of rockfish larvae varied among sampling dates and locations in 1991–92, with significant interaction between the two factors (ANOVA, $P<0.001$; Fig. 6A). Larvae were relatively abundant from January to April. Pairwise comparisons indicated that the large catches in early February 1992 at all stations were unique among all other time periods and that abundances across all stations early in the season (December and early January) were not significantly different from those that followed later (late-February, March, and April). Pairwise comparison of interstation abundance indicated two groups, one of stations closest to shore (1, 3, and 7 km) and another of the two offshore stations (13 and 19 km). The offshore stations had significantly greater abundance through time than did those inshore and, while abundance at most stations generally declined from a peak in early February, numbers of larvae remained relatively high through April at stations farthest from shore (13 and 19 km).

As with the 1991–92 collections, larval rockfish abundance varied significantly among sampling dates in 1993, with greatest abundances in February (Fig. 6B). Average abundances of larval rockfishes estimated at comparable stations and times from January through April were not significantly different between years (mean=602 larvae/10 m^2, SE=161 in 1992; mean=376 larvae/10 m^2, SE=179 in 1993; t-test, $P>0.383$), but distribution patterns differed. In contrast to the previous year, large catches of rockfish larvae occurred only at the two offshore stations in 1993. Significantly greater numbers of larvae occurred at the three stations closest to shore (1, 3, and 7 km) during January and February 1992, compared with the same months in 1993 (Kolmogorov-Smirnov tests, $P<0.05$).

Size, age, and birthdate distributions Size of larval shortbelly rockfishes collected on the same days in 1992 varied significantly among the 7, 13, and 19 km stations (ANOVA, $P<0.001$). Virtually all shortbelly rockfish larvae collected at the 7 km station were greater than 5 mm SL and significantly larger than those at the two offshore stations (Table 3). Shortbelly rockfish larvae were collected at the 7 km station only from early January to mid-March, and size composition remained similar throughout this period (overall mean=6.5 mm SL, SE=0.1). Size composition of shortbelly rockfishes did not differ significantly between the two offshore stations (overall mean=5.3 mm SL, SE=0.04), and the smallest larvae (<5 mm SL) were relatively abundant in all samples through early April.

Fewer samples and larvae collected at onshore stations in 1993 precluded among-station comparisons, although size composition of shortbelly rockfishes at the two offshore stations differed significantly (e.g. smaller larvae at the 13 km station compared with the 19 km station). The smallest larvae (<5 mm SL) were most abundant at the 13 km station in February and at the 19 km station in early April (Table 3).

Ages of 302 larval shortbelly rockfish collected in January–May 1992 and February–April 1993 were 1–28 d (Table 4). A least-squares linear model, $Length = a + b\,(Age)$, was fitted to separate sets of age-length data for each month in both years. Because no significant differences in growth rate were found among months (ANCOVA, $P>0.64$ [1992]; $P>0.73$ [1993]), age-length data were combined for each year. Moreover, there was no interannual difference in growth rate (ANCOVA, $P>0.90$). A least-squares linear model

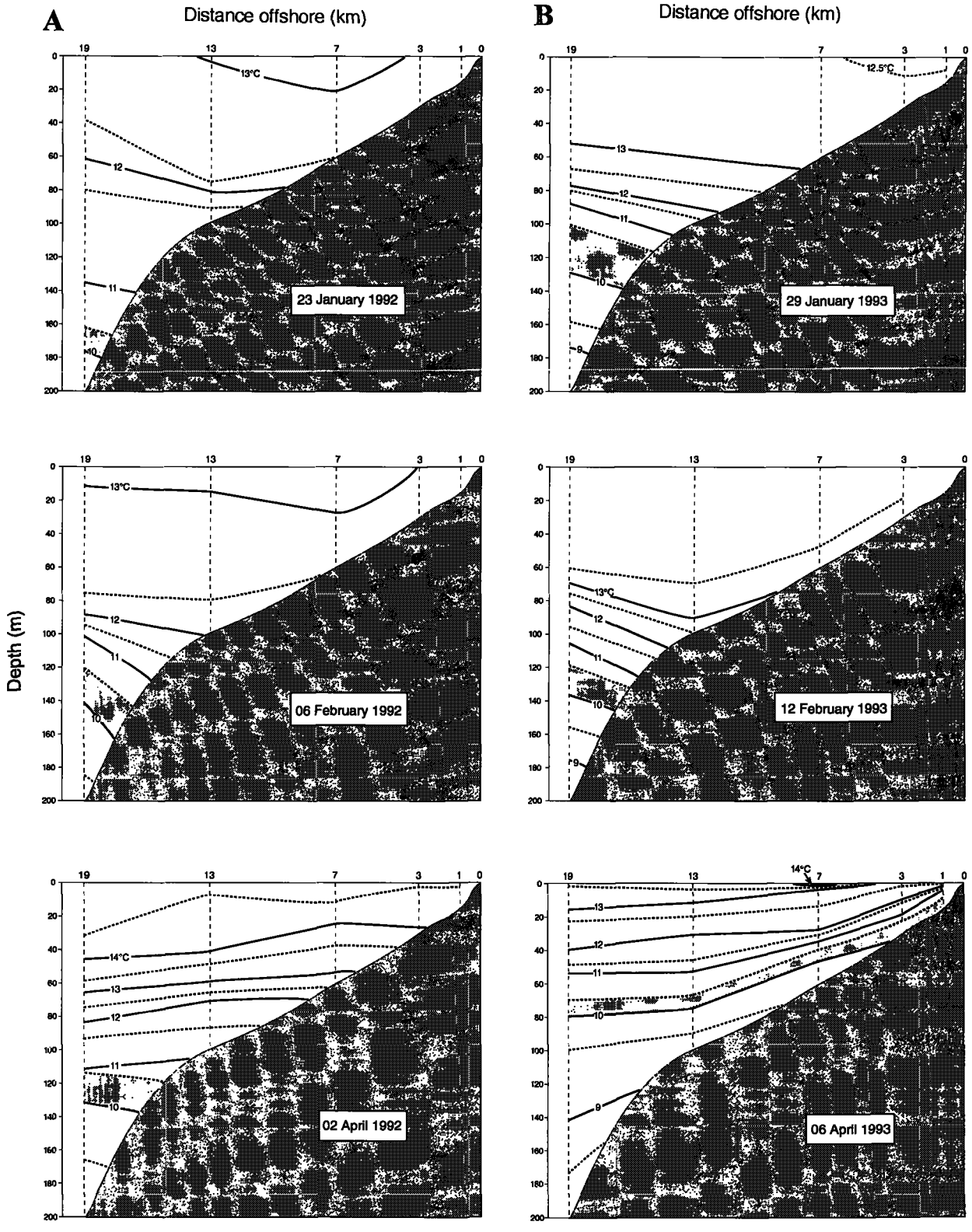

Figure 4

Vertical temperature profiles along the ichthyoplankton sampling transect off Davenport, California, during January, February, April, (**A**) 1992 and (**B**) 1993. The five CTD stations are indicated by distance offshore. Temperatures from 10.0 to 10.5°C are shaded for comparative purposes.

was computed for pooled age-length data because of the narrow age range (i.e. *Length*=4.63 + 0.20 [*Age*]; r^2=0.83; n=288). As an aside, the larval length at time of extrusion estimated by this model was 4.63 mm, which closely approximates the mean size of full-term shortbelly rockfish larvae collected from females off central California (4.7 mm SL; Laidig et al., 1991).

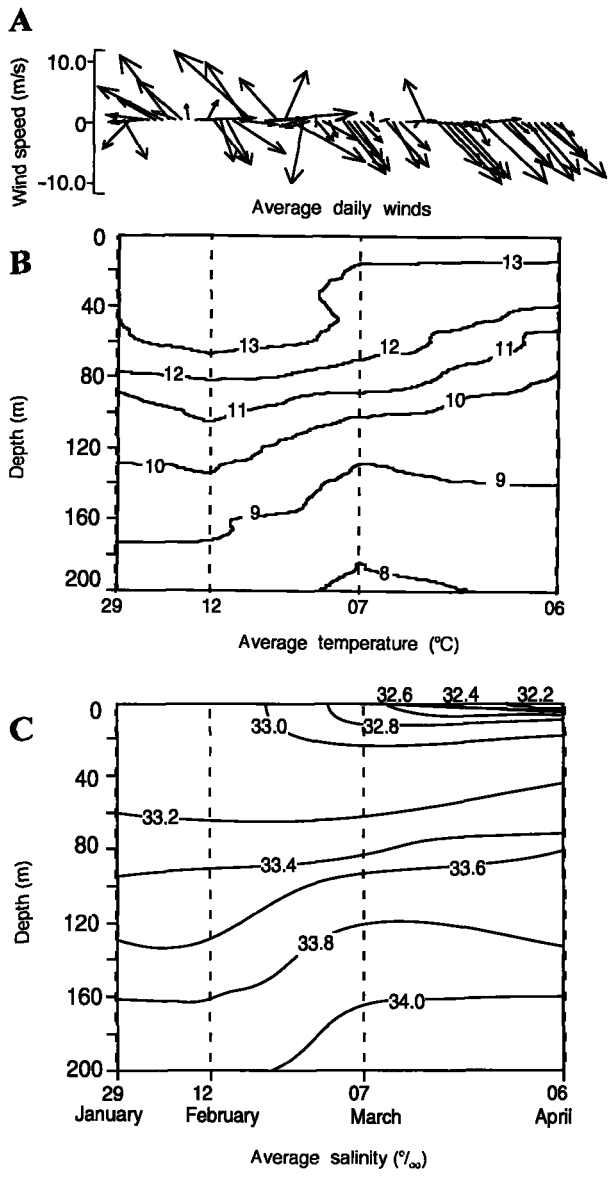

Figure 5

Wind, temperature, and salinity profiles for offshore Davenport, California. (**A**) Daily averaged wind vectors measured at buoy 46042 in Monterey Bay (arrows point in direction to which wind was blowing [north is toward top of page]); (**B**) temperature (°C); and (**C**) salinity (‰) in upper 200 m at the most offshore station (19 km) during ichthyoplankton surveys 29 January–6 April 1993. CTD sampling dates are indicated with dashes.

Birthdate distributions were compared between shortbelly rockfish larvae collected early in the season and pelagic juveniles collected from May to July. According to larval ages and collection dates, birthdates of shortbelly rockfishes extended from December to early May (median=5 February) 1992, and January to early April (median=12 February) 1993 (Fig. 7). Birthdates estimated from juvenile shortbelly rockfishes occurred much later in both years (Fig. 7). The relatively few pelagic juveniles (2.3 fish/trawl, n=56 midwater trawls; see Loeb et al.[1] for survey results) collected in May–July 1992 had an extremely narrow range of birthdates from 8 April to 2 May (median=21 April). Greater numbers of surviving juvenile shortbelly rockfishes during May–July 1993 (75.1 fish/trawl, n=64 midwater trawls; see Loeb et al.[1] for survey results) had a broader range of birthdates from 24 January to 7 June (median=15 March).

Larval blue rockfish, the second most abundant of the identified species, had a much narrower range of lengths (2.8–6.9 mm SL) and, unlike shortbelly rockfish, were abundant only from late January to early February in both years (Table 3). Size of larval blue rockfishes, collected on the same days in 1992, varied significantly among the 7, 13, and 19 km stations (ANOVA, P<0.001), with larger larvae occurring at the innermost station (mean size=5.0 mm SL, SE=0.1; Table 3). As with shortbelly rockfish larvae, size composition of blue rockfishes was not significantly different between the two offshore stations (overall mean=4.5 mm SL, SE=0.1). Although 1993 collections were limited and comparisons not statistically significant, there was a continued trend of smaller blue rockfish larvae farther offshore.

Ages of 96 larval blue rockfish collected in January–February of 1992 and 1993 ranged from 2 to 21 d (Table 4); only 7 of these specimens were from 1993 because of problems with preservation. Because growth rates estimated over similar age ranges were not significantly different in January and February 1992 (ANCOVA, P>0.78), age-length data were combined and a least-squares linear model was calculated (i.e. *Length*=3.98 + 0.14 [*Age*]; r^2= 0.63; n=96). Birthdates were estimated for all blue rockfish larvae collected in 1992 and 1993 by using fish length and this growth model. Birthdate distribution was narrow in both years, ranging from 31 December 1991 to 21 February 1992 and from 12 January to 12 February 1993; the median birthdate was 27 January in both years. Birthdates could not be compared with those of pelagic juvenile blue rockfishes because no juveniles were collected in 56 midwater trawl

Table 2

Standardized abundance (number per 10 m²) of larval rockfishes in bongo-net tows collected off Davenport, California, December 1991–June 1992 and January–April 1993. "—" indicates that zero larvae were collected.

	2 Dec					18 Dec					9 Jan					23 Jan					6 Feb				
	1	3	7	13	19	1	3	7	13	19	1	3	7	13	19	1	3	7	13	19	1	3	7	13	19
1991–1992																									
S. jordani	—	—	—	—	—	—	—	—	4	8	—	—	34	29	186	4	—	144	269	21	—	—	152	656	166
S. mystinus	—	—	—	—	—	—	3	—	—	—	—	7	15	—	38	2	4	85	21	109	—	—	109	180	90
S. hopkinsi (?)	—	—	—	—	—	—	3	12	12	—	—	—	49	4	34	—	—	25	25	11	—	—	67	46	54
S. saxicola	—	—	—	—	—	—	—	—	—	4	—	—	4	—	17	—	—	11	17	189	—	—	4	8	54
Copper complex +	—	—	—	—	—	—	—	4	—	—	—	—	—	—	—	—	—	7	—	4	3	4	38	17	27
S. paucispinis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	21	—	—	21	64	32	—	—	4	8	18
Sebastosomus +	—	—	—	—	—	—	—	8	—	—	—	—	4	—	—	—	—	—	—	4	—	—	42	—	36
S. levis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	4	—
Unidentified	—	3	—	13	37	4	8	19	56	62	—	3	42	69	169	8	4	113	191	186	3	61	160	3,127	714
Damaged	—	—	—	3	—	—	—	4	—	—	—	—	4	—	47	—	—	18	7	21	—	4	29	75	81
All *Sebastes* spp.	—	3	—	16	37	4	14	47	71	74	—	10	151	101	512	14	8	423	593	575	6	69	610	4,122	1,239

	21 Feb					12 Mar					2 Apr					4 May		16 Jun			Stand. abun.	Overall % abun.	Count (N)
	1	3	7	13	19	1	3	7	13	19	1	3	7	13	19	13	19	3	7	13			
1992 (cont'd)																							
S. jordani	—	—	43	131	—	—	4	41	380	823	—	—	—	—	372	49	3	—	—	—	3,520	29	836
S. mystinus	—	—	9	26	22	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	719	6	183
S. hopkinsi (?)	—	—	43	33	18	—	—	4	23	14	—	—	—	—	4	4	3	—	—	—	487	4	121
S. saxicola	—	4	—	23	4	—	—	—	14	29	—	—	—	19	—	—	—	—	—	—	401	3	104
Copper complex +	—	—	17	3	4	8	4	8	—	—	6	7	4	27	—	—	—	—	10	4	207	2	52
S. paucispinis	—	—	—	3	13	—	—	—	5	—	—	—	—	—	—	—	—	—	—	—	189	2	50
Sebastosomus +	—	—	—	3	4	—	—	—	—	—	—	—	—	—	4	—	—	—	—	4	109	1	26
S. levis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3	—	—	—	12	0.1	3
Unidentified	—	12	72	311	88	—	—	4	135	91	—	—	4	22	29	185	128	—	—	4	6,137	50	1,526
Damaged	—	—	26	7	9	—	—	4	28	29	—	—	—	—	—	—	—	—	—	—	394	3	94
All *Sebastes* spp.	—	16	208	540	162	8	8	62	585	987	6	7	7	68	410	238	138	—	10	12	12,175	100	2,995

	29 Jan					12 Feb			7 Mar		6 Apr			Stand. abun.	Overall % abun.	Count (N)
	1	3	7	13	19	7	13	19	3	19	3	13	19			
1993																
S. jordani	—	—	21	153	189	2	1,274	92	—	274	—	44	199	2,248	46	534
S. saxicola	—	—	—	32	76	—	91	70	—	9	—	—	4	282	6	62
S. mystinus	—	—	5	90	167	—	25	15	—	—	—	—	—	302	6	58
S. hopkinsi (?)	—	—	11	11	—	—	147	44	11	—	—	—	—	224	5	49
Sebastosomus +	—	—	—	48	11	—	45	19	—	7	—	—	—	130	3	28
Copper complex +	—	—	5	—	—	—	35	15	—	2	—	—	—	57	1	13
S. paucispinis	—	—	—	11	5	—	—	11	—	—	—	—	4	31	1	7
S. levis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Unidentified	—	8	53	99	156	25	395	282	—	126	—	39	188	1,371	28	343
Damaged	—	—	11	37	—	—	243	—	—	—	—	—	—	291	6	57
All *Sebastes* spp.	—	8	106	480	604	27	2,255	549	11	418	—	83	393	4,936	100	1,151

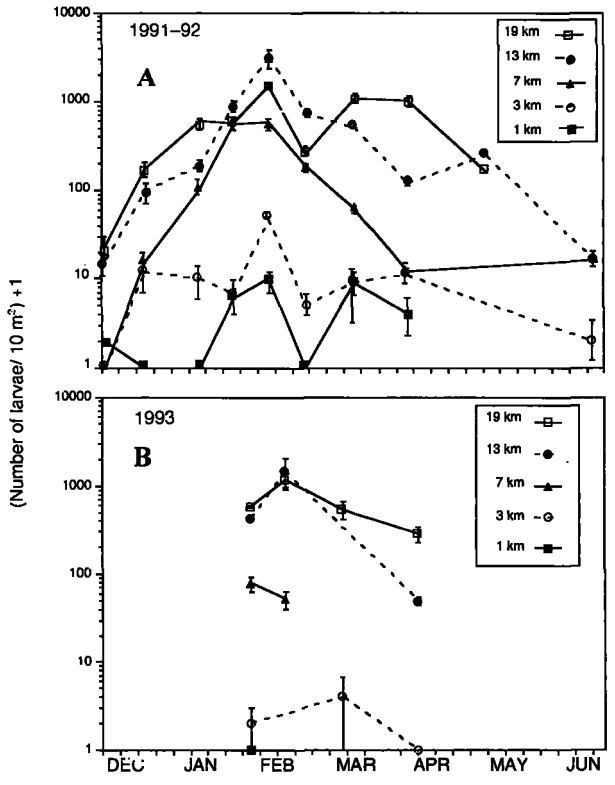

Figure 6

Larval rockfish abundance (per 10 m^2) at five stations along an onshore–offshore transect, Davenport, California. Each point is the average of 3 replicates, except for 2 tows made at the 7 km station on 2 December 1991 and single tows made at two offshore stations in May 1992; error bars = 1 SE. (**A**) 2 December 1991–16 June 1992; (**B**) 29 January–6 April 1993.

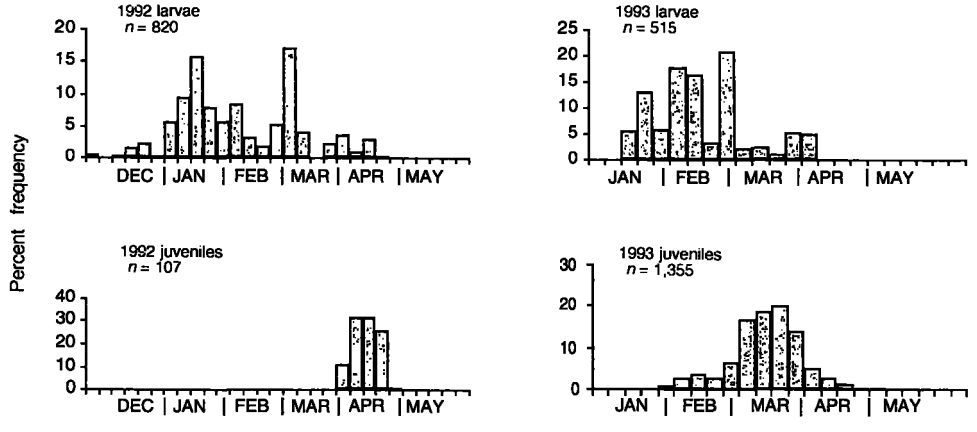

Figure 7

Hatch date distributions for shortbelly rockfish, *Sebastes jordani*, estimated from age of larvae collected January–April 1992 and 1993 and from age of juveniles collected June 1992 and May–July 1993.

Table 3

Size (mean, SE, and *n*) of larval shortbelly and blue rockfish collected by standard oblique bongo-net tows at stations 7, 13, and 19 km off Davenport, California, December 1991–April 1993.

	1991–92									1993				
	18 Dec	9 Jan	23 Jan	6 Feb	21 Feb	12 Mar	2 Apr	4 May	Overall	29 Jan	12 Feb	7 Mar	6 Apr	Overall
Shortbelly rockfish														
7 km mean (mm)	—	6.6	6.3	6.7	6.2	6.1	—	—	6.5	4.8	6.3	—	—	5.1
SE	—	0.2	0.1	0.2	0.4	0.2	—	—	0.1	0.1	—	—	—	0.3
n	0	9	41	36	10	10	0	—	106	4	1	—	—	5
13 km mean (mm)	6.1	4.8	6.0	4.8	5.2	6.0	—	7.5	5.4	5.1	4.9	—	6.2	4.9
SE	—	0.1	0.1	0.1	0.1	0.1	—	0.4	0.1	0.1	0.1	—	0.4	0.1
n	1	8	77	155	39	82	0	11	373	31	233	—	9	273
19 km mean (mm)	7.0	5.6	5.5	5.0	—	5.0	4.7	6.5	5.0	5.6	6.3	5.8	5.3	5.7
SE	1.3	0.1	0.3	0.2	—	0.1	0.1	—	0.1	0.1	0.3	0.1	0.1	0.1
n	2	44	6	35	0	166	84	1	338	37	24	121	55	237
Blue rockfish														
7 km mean (mm)	5.8	5.0	4.8	5.3	5.4	—	—	—	5.0	4.1	—	—	—	4.1
SE	—	0.2	0.1	0.1	0.5	—	—	—	0.1	—	—	—	—	—
n	1	4	24	25	2	0	0	0	56	1	0	0	0	1
13 km mean (mm)	—	—	4.0	4.4	4.5	—	—	—	4.4	4.4	4.6	—	—	4.4
SE	—	—	0.2	0.1	0.1	—	—	—	0.1	0.1	0.2	—	—	0.1
n	0	0	6	43	7	0	0	0	56	19	5	0	0	24
19 km mean (mm)	—	4.7	4.4	4.9	4.3	—	—	—	4.6	4.2	4.4	—	—	4.2
SE	—	0.2	0.1	0.2	0.3	—	—	—	0.1	0.1	0.2	—	—	0.1
n	0	9	31	20	5	0	0	0	65	33	4	0	0	37

samples from May to July 1992 and only 29 individuals (0.5% of total catch) occurred in 65 midwater trawl samples from May to July 1993 (Loeb et al.[1]).

Discussion

Larval rockfish are a dominant group in the ichthyoplankton along the west coast of the United States, with relatively high abundances occurring seasonally in surveys off southern and central California (Barnett et al., 1984, Moser and Boehlert, 1991) and off northern California, Oregon, and Washington (Richardson and Pearcy, 1977; Richardson et al., 1980; Boehlert et al., 1985; Doyle et al., 1993). During our study, mean overall abundance of larval rockfish ranked second only to that of the northern anchovy (*Engraulis mordax*; 749 larvae/10 m^2) in 1992 and Pacific hake (*Merluccius productus*; 1,520 larvae/10 m^2) in 1993 (B. Daly, unpubl. data). Larval rockfishes are generally characterized as members of offshore assemblages; their abundance increased with distance from shore in our study as well as in the surveys cited above. Distribution of at least the youngest larvae is defined by the location of spawning adults, which for many rockfish species is principally over rock bottom along the edge of the continental shelf and submarine canyons. This is supported by the significantly greater numbers of small shortbelly rockfish larvae in samples collected at our most offshore station, located over Año Nuevo submarine canyon.

Declines in somatic and reproductive condition (VenTresca et al., 1995) and decreased fat storage (Lenarz and Wyllie Echeverria, 1986) in adult rockfish collected off central California during El Niño years likely are responses to reduction in primary prey biomass. Mullin and Conversi (1989) documented large-scale reductions in abundance of euphausiids and smaller zooplankton (e.g. the pri-

Table 4

Size, age, and number of larval shortbelly, *Sebastes jordani*, and blue, *S. mystinus*, rockfish included in age and growth estimates in 1992 and 1993.

	1992						1993				
	Jan	Feb	Mar	Apr	May	Overall	Jan	Feb	Mar	Apr	Overall
Shortbelly rockfish											
No. aged	54	60	34	15	12	175		47	36	44	127
Mean age (d)	8.4	8.2	6.3	2.6	11.6	7.6		6.7	7.2	4.5	6.1
SE	0.8	0.9	0.7	0.7	1.3	0.5		0.8	0.7	0.7	0.4
Range (d)	1–28	1–28	1–20	1–11	4–18	1–28		1–21	2–22	1–21	1–22
Mean SL (mm)	6.3	6.2	5.9	5.2	7.4	6.2		5.8	6.1	5.8	5.9
SE	0.2	0.2	0.2	0.2	0.4	0.1		0.2	0.2	0.2	0.1
Range (mm)	4.0–10.8	3.9–9.8	4.2–8.8	4.3–6.3	5.0–9.7	3.9–10.8		4.3–9.0	4.8–9.0	4.2–9.2	4.2–9.2
Blue rockfish											
No. aged	43	46				89	3	4			7
Mean age (d)	4.3	6.3				5.3	8.0	6.0			6.9
SE	0.3	0.7				0.4	4.0	1.6			1.8
Range (d)	2–14	2–21				2–21	4–16	2–10			2–16
Mean SL (mm)	4.7	4.8				4.8	5.1	4.5			4.8
SE	0.1	0.1				0.1	0.4	0.2			0.2
Range (mm)	3.4–6.1	2.8–6.9				2.8–6.9	4.4–5.9	4.0–5.0			4.0–5.9

mary prey of juvenile and adult rockfishes) during the 1958 El Niño. Poor condition of adult rockfishes could influence larval production and reproductive timing. Abundance of rockfish larvae in our study, however, was not significantly different between the two years of the extended El Niño event along the central California coast and was much greater than estimates from earlier ichthyoplankton surveys coastwide. Greatest mean abundance of rockfish off Oregon was 350 larvae/10 m^2 in May 1971 (Richardson and Pearcy, 1977), 199/10 m^2 in March 1972, and 176/10 m^2 in March 1973 (Richardson et al., 1980). Peak abundance of rockfish sampled during CalCOFI surveys in February 1951–81 averaged about 200 larvae/10 m^2 off northern and central California and 90 larvae/10 m^2 off southern California (Moser and Boehlert, 1991). Average larval rockfish abundance estimated from those CalCOFI lines (i.e. 63, 67, 70) and stations (i.e. 49–57) closest to our sampling sites was 486 larvae/10 m^2 in February, 1960–84. We estimated a mean abundance of 990 rockfish larvae/10 m^2 at the three offshore stations in February during our 2-year survey. This figure demonstrates that overall larval abundance was not negatively affected by an El Niño event and that the area north of Monterey Bay is a significant production ground for larval rockfishes. This finding is substantiated by the results of pelagic juvenile rockfish surveys along California, which indicate a center of distribution in this area (Larson et al., 1994).

Further, the El Niño event of 1991–93 did not seem to have caused a significant shift in overall timing of parturition, at least for the two species that dominated our ichthyoplankton surveys. Median hatch dates of shortbelly rockfish larvae collected during late winter and early spring of 1991–92 and 1993 were similar to each other (first and second week in February, respectively), and to the primary month of parturition (i.e. February) according to reproductive stages of this species off central California from 1977 to 1984 (Wyllie Echeverria, 1987). Release of blue rockfish larvae during our study likewise was as expected (i.e. January; Wyllie Echeverria, 1987). Absence of sampling in late December 1992 could have masked an unlikely peak of parturition earlier in the 1993 season.

Although reproductive timing and production seemingly were not influenced by the prolonged El Niño event, occurrence of juvenile rockfishes in trawl samples collected in late spring and summer was dramatically different between years. Extremely low numbers of pelagic juvenile rockfish were encountered during midwater trawl surveys (n=56 trawls) conducted from 4 May to 10 July 1992 north and south of Monterey Bay (Loeb et al.[1]). In contrast, pelagic juvenile rockfishes collected during the same time period in 1993 (n=65 trawls) were 20 times more abundant, comprised twice as many taxa, and were substantially larger than juveniles collected in 1992 (Loeb et al.[1]). Shortbelly, copper-complex, and kelp rockfishes dominated the relatively low numbers of

rockfish juveniles in 1992. The 1993 pelagic juveniles were dominated by shortbelly, squarespot, halfbanded (*S. semicinctus*), and chilipepper (*S. goodei*) rockfishes, in that order. All of these species can produce larvae relatively late in the season.

Among the dominant species, only those shortbelly rockfish larvae released late in the season (March and April) were represented in the birthdate distributions of juveniles collected in the summer of both years of the El Niño. The few pelagic juvenile shortbelly rockfishes collected in May–June during the 1983 El Niño event also had late birthdates (Woodbury and Ralston, 1991). It is clear that the largest proportion of larval shortbelly rockfish production, >65% occurring prior to March during both years of the 1991–93 El Niño event, did not survive until the juvenile surveys conducted during the summers of 1992 and 1993. Blue rockfishes, largely produced in January and February and ranked second (1992) and third (1993) in larval catches, were not collected at all during pelagic juvenile surveys in May–July 1992 (56 midwater trawls; Loeb et al.[1]), and represented 0.5% (n=29 individuals) of the total catch of pelagic juveniles in May–July 1993 (65 midwater trawls; Loeb et al.[1]). Stripetail rockfish, another species whose parturition period is restricted to early in the year off central California (i.e. November–March with a peak in January [Wyllie Echeverria, 1987]), was relatively abundant in the plankton both years but rare in the pelagic juvenile collections (<0.1 and 0.5 fish per trawl).

In accordance with the results of the surveys by Loeb et al.,[1] subtidal observations along the central coast made by California's Department of Fish and Game Sportfish Project biologists indicated that few juveniles of nearshore rockfish species recruited to rocky and kelp canopy areas off the Monterey Peninsula during May–August 1992 (VenTresca[3]). Low abundance of pelagic juvenile rockfishes off central California also was noted during May–June 1992 surveys conducted by scientists of the NMFS Tiburon Laboratory (Lenarz et al., 1995; Ralston and Howard, 1995) and during previous El Niño events of 1983 and 1986 (Wyllie Echeverria et al., 1990). In contrast, overall abundance of pelagic juvenile rockfishes in 1993 was fourth greatest among the past eight years of NMFS-Tiburon surveys (Lenarz et al., 1995), and relatively high numbers, dominated by blue rockfishes, settled off Monterey during June–September 1993 (VenTresca[3]). Substantially greater abundance and larger sizes of pelagic juvenile rockfishes during May–July 1993 indicated that recruitment was likely related to the timing of optimal environmental conditions during larval development. This is consistent with the dome-shaped relationship described by Ralston and Howard (1995) between interannual variability in winter SST's and estimates of year-class strength for blue and yellowtail rockfishes off central California collected from 1983 to 1992 (e.g. juvenile abundance was lowest when SST's were either exceptionally low or high during winter months of larval production).

Mortality of fishes during the larval stage has been attributed to starvation and predation; debate continues as to which factor is more significant for successful recruitment (Hunter, 1981; Bailey and Houde, 1989). There was no evidence from our ichthyoplankton samples that suggested that young rockfishes were starving in either year of the El Niño event. Growth of young shortbelly rockfishes was similar throughout the parturition period, no differences were detected between the two years, and growth in 1992–93 was similar to that estimated for this species from the central California during non-El Niño years (i.e. in 1989 [Laidig et al., 1991] and in 1991 [Ralston et al., 1996]). Moreover, blue rockfish, although relatively common in the ichthyoplankton, abruptly disappeared at young ages (i.e. when many were still dependent on yolk reserves) from samples collected in late January and early February and had very poor recruitment to the pelagic juvenile stage in 1992. This finding suggests acute mortality, perhaps coincident with onshore transport and increased encounter rates with predators.

Time of release of rockfish larvae can contribute to variation in year-class abundance by influencing the spatial and temporal coincidence of larvae, prey availability, predator abundance, and favorable environmental conditions, such as temperature, upwelling, and transport (Parrish et al., 1981; Methot, 1983; Checkley et al., 1988; Nyman and Conover, 1988). Rockfish larvae were more abundant and the dominant species (shortbelly rockfish) was significantly larger at onshore stations in 1992 than in 1993, indicating retention of larvae nearshore during the first year of the El Niño event. These occurrences coincided with onshore advection of water, as characterized by reversals in wind direction and by warmer, less saline water that occurred during peak larval rockfish abundance in February 1992.

Larval retention in nearshore areas could be responsible for heavy mortality, possibly through increased predation. Significant changes in zooplankton assemblages associated with wind relaxation and subsequent onshore transport have been noted along central California (Farrell et al., 1991), and abun-

[3] VenTresca, D. 1995. California Department of Fish and Game, 20 Lower Ragsdale Dr., No. 100, Monterey, CA 93940. Unpubl. data.

dance of several potential larval fish predators can increase nearshore during these events. During the 1958 El Niño event, the California Current moved shoreward, and abundance of potential larval fish predators (siphonophores and chaetognaths) increased in inshore coastal waters (Smith, 1985). Mean zooplankton biomass, dominated by copepods, euphausiids, and chaetognaths, was significantly greater in nearshore than in offshore areas of Monterey Bay during the first year of the 1991–93 El Niño event (Baduini, 1995); this trend reversed after upwelling commenced in early April 1993. Limited information on chaetognaths (largely *Sagitta bipunctata*) collected in our ichthyoplankton samples (Bridges[4]) indicated extremely high numbers (e.g. up to 20,000 individuals/10 m^2 at 3 km from shore, which represented five times the greatest larval rockfish abundance) in early February 1992, coincident with the wind reversal, onshore transport of water, and peak abundance of larval rockfish. At least 20% of these animals were >11 mm in length, a size at which chaetognaths are capable of ingesting a larval fish (senior author, unpubl. data). The lack of upwelling and associated offshore transport during subsequent months could prolong nearshore retention and further reduce recruitment success.

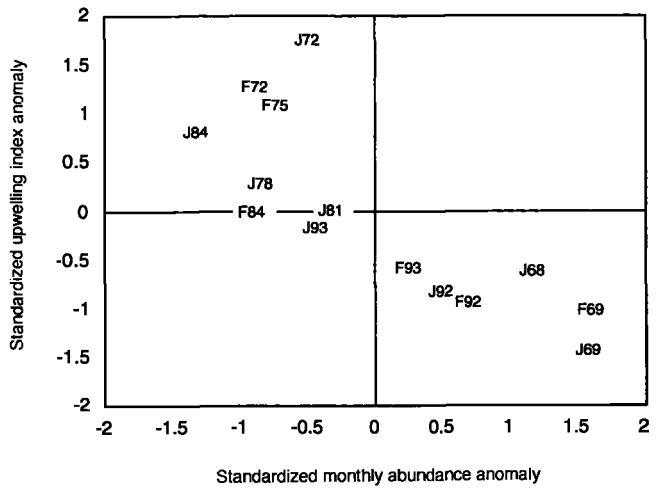

Figure 8

Comparison of mean monthly standardized anomalies of larval rockfish abundance in January (J) and February (F) of various years (indicated by last two digits of each year), with those of upwelling indices estimated at 36° and 39°N and averaged over a 4-day period prior to and including day of ichthyoplankton sampling. Estimates of larval abundance prior to our study are from CalCOFI ichthyoplankton surveys conducted inshore of station 60 along lines 63, 67, and 70 (Moser et al., 1993). Standardized anomalies were calculated by using data from our study and the CalCOFI surveys.

Although predation on fish eggs and larvae has been generally characterized as a density-independent control on fish populations (Bailey and Houde, 1989), exceptions include co-occurrence of predators and prey concentrated in small areas (e.g. high density of herring larvae and scyphomedusae [Moller, 1984]) and prey-switching when preferred diet is not available (Pepin, 1987). Although small copepods are the preferred prey of larval fish and many of their invertebrate predators, reduction in this food source during El Niños (McGowan, 1985; Miller et al., 1985) could increase the likelihood of predation on small fish larvae. Several species of chaetognaths prey secondarily on young fish larvae (Kuhlmann, 1977), and an inverse relationship between larval fish abundance and chaetognath densities has been described from CalCOFI samples collected during the 1958 El Niño off California (Alvariño, 1980).

In contrast, increased upwelling intensity and offshore transport during March and April 1993 may have facilitated survival of larval stages for those species with broad periods of parturition by advecting them from nearshore areas. Although there is a significantly negative relationship (r^2=0.63; P<0.001) between larval rockfish abundance and offshore Ekman transport (i.e. positive upwelling indices) during peak production in January and February (Fig. 8), dispersal mechanisms like upwelling seem to be important in determining recruitment to the juvenile stage (Ralston and Howard, 1995). Breaker (1983) characterized the spring transition from winter ocean conditions to the onset of upwelling and offshore Ekman transport as an abrupt decrease in SST (e.g. 0.38–0.59°C per day) off central California (36°26'N); dramatic spring transitions occurred in six of the twelve years (1971–83), with suppression of transition during El Niño events. According to examinations of daily SST's from the same station during the 1991–93 El Niño event (Schwing[5]), a spring transition did not occur at all in 1992 and a modest transition (0.34°C per day) was initiated in early April 1993, coinciding with the birthdate distribution of the surviving cohort of shortbelly rockfish juveniles.

In conclusion, the extended El Niño event of 1991–93 provided a unique opportunity to assess abundance and distribution of larval rockfishes during a

[4] Bridges, J. 1994. Department of Biology, University of California, Santa Cruz, CA 95064. Unpubl. data.

[5] Schwing, F. 1995. Pacific Fisheries Environmental Group, Natl. Mar. Fish. Serv., Pacific Grove, CA. Unpubl. data.

significant environmental perturbation, an opportunity that yielded some insight into the recruitment process. Characterizing the link between larval rockfish distribution and the hydrographically dynamic environment of the central California coast required finer-scale spatial and temporal sampling than has been achieved previously. Rockfish larvae were more abundant and larger at onshore stations in 1992, coinciding with onshore advection of water during the onset of the El Niño event and suggesting retention of larvae nearshore; abundance of juvenile rockfishes in nearshore areas later in that year was extremely low. Initiation of upwelling in March and April of 1993 and the occurrence of fewer rockfish larvae at onshore stations suggest greater offshore transport during the second year; juvenile rockfish abundance was greater than the previous summer. From these data, we suggest that substantially higher survival and recruitment of juvenile rockfishes in 1993 likely are due to increased offshore transport and dispersal, and possibly lower predation, during the larval stages.

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Do herring grow faster than orange roughy?

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In growth studies it is common to find the statement "P grows faster than Q". However, it is much less common to find a clear definition of what the author means by that statement. What is it about two sets of growth parameters, or two growth curves, that should make us conclude that "P grows faster than Q"? In this note I will show that this is not as simple a question as it may seem. There are several plausible ways of answering it and these have very different consequences. Thus, the statement "P grows faster than Q" is ambiguous and it is important for authors to be specific about what they mean by it. I will also give reasons for preferring one of the possible meanings.

In what follows it will sometimes be convenient to refer to the two entities being compared as "species P" and "species Q." However, my conclusions are the same whether the growth comparison is made within species (e.g. males vs. females [Horn, 1993; Hostetter and Munroe, 1993; Kitagawa et al., 1994; Collins et al., 1995], one time period vs. another [Raspopov, 1993; Collins et al., 1995], or one area vs. another [Horn, 1993; Savard et al., 1994]), or between species (Arkhipkin and Nekludova, 1993; Gorny et al., 1993; Milton et al., 1993; Potts and Manooch, 1995).

Before proceeding, it is useful to restrict the scope of the question being considered. First, only the mean growth for a "species" is considered; therefore between-individual variability in growth is ignored. Second, I will assume that we have perfect knowledge about the growth of P and Q; i.e. statistical uncertainty is ignored. Third, I will consider only unqualified comparisons such as "P grows faster than Q," comparisons that apply only to a portion of the life history (e.g. "P grows faster than Q up to age 1") are excluded. The purpose of these restrictions is to allow for a simpler presentation. Without them, the picture is more complex, but the results given below will still apply, although not in precisely the same form.

Six methods of growth comparison

There are at least six plausible methods for comparing growth (Table 1). With method 1, we would say that P grows faster than Q if $L_{t,P} > L_{t,Q}$ for all t, where $L_{t,P}$ and $L_{t,Q}$ are the lengths at age t for species P and Q, respectively. The rationale behind this method is that $L_{t,P} > L_{t,Q}$ implies that P must have grown faster than Q (at least on average) over the period up to age t. Now, rather than comparing average growth rates over a period of time it may be more sensible to compare instantaneous growth rates. This is the reason for method 2. However, it may be argued that method 2 makes no sense when $L_{t,P}$ is very different from $L_{t,Q}$. For example, a growth rate of 10 cm/yr is fast for an animal of size 20 cm but slow for an animal of size 200 cm. There are two ways to deal with this difference: we can either insist that the comparison be made when the animals are of the same size (method 3), or we can standardize the growth rates by dividing by length (methods 4 and 5). (Method 5 is included here for completeness, but it is easy to show that it is exactly equivalent to method 3.) Method 6 could be appropriate where growth is asymptotic and the asymptotes for P and Q are different. Here the species that approaches its asymptote faster is said to grow faster. Of course, this method is not fully defined until we specify what we mean by "the rate at which the asymptote is approached."

To illustrate the difference between these methods we will assume that growth is adequately described by the von Bertalanffy equation with $t_0 = 0$, i.e.

$$L_t = L_\infty(1 - e^{-kt}).$$

Table 1

Six methods for comparing the mean growth of two species or populations. The absolute growth rate is the slope of the length-at-age curve (with dimension length/time) and the relative growth rate is this slope divided by the length (dimension 1/time).

Method 1:	compare lengths at each age
Method 2:	compare absolute growth rates at each age
Method 3:	compare absolute growth rates at each length
Method 4:	compare relative growth rates at each age
Method 5:	compare relative growth rates at each length
Method 6:	compare rates at which the asymptotic size is approached

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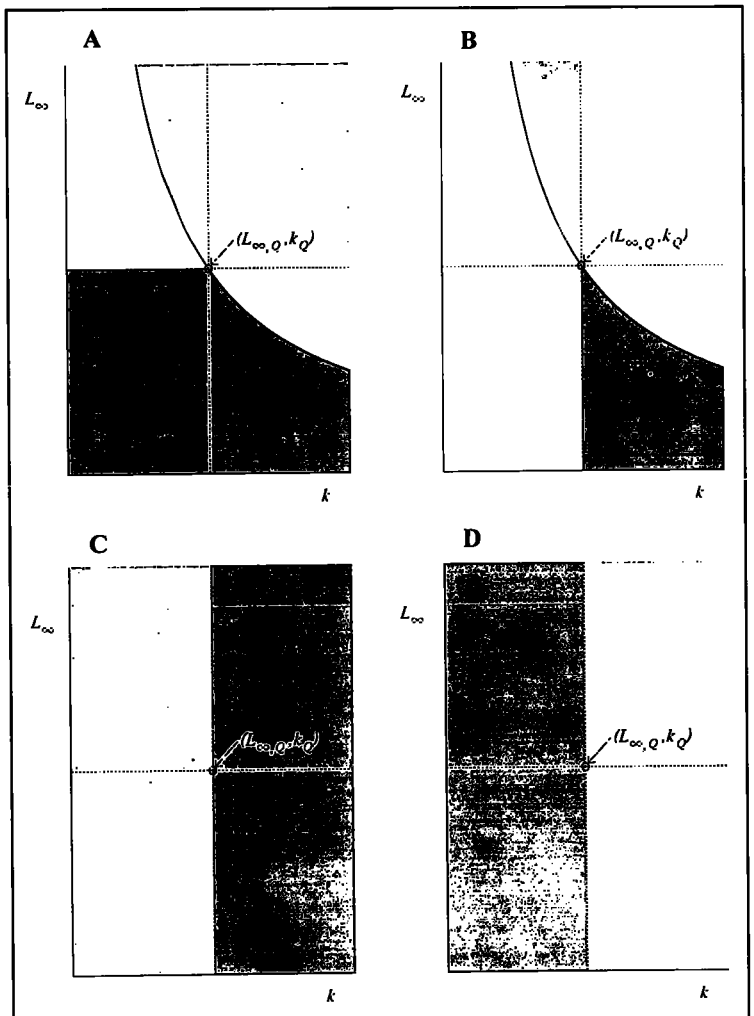

Figure 1

Illustration of the six methods of growth comparison in Table 1 when growth follows the von Bertalanffy equation. In each panel, the central point, 'o', represents the growth parameters for species Q, $(L_{\infty,Q}, k_Q)$. Species P is said to grow faster (or slower) than species Q if the point $(L_{\infty,P}, k_P)$ lies in the light (or dark) shaded area of the graph. In the unshaded areas, no comparison can be made over the whole life history (so P may be faster than Q at one age [or length] and slower at another). Comparisons are for (**A**) methods 1, 3, and 5; (**B**) method 2; (**C**) method 4; and (**D**) method 6. See Table 1 for definitions of methods. The curved line in panels A and B is $L_\infty = L_{\infty,Q}k_Q/k$. (Details of the derivation of this Figure are available from the author).

With this assumption, method 6 is fully defined because the parameter k determines the rate at which the asymptote is approached; the bigger k is, the faster the asymptote is approached. Thus, according to method 6, P grows faster than Q if $k_P > k_Q$.

Now, given growth parameters $L_{\infty,Q}, k_Q$ for Q, we are in the position to address the question, "What range of values can $L_{\infty,P}, k_P$ take if we are to say that P grows faster (or slower) than Q?". Figure 1 shows that the answer to this question depends strongly on which of the six methods of comparison is used. Methods 1, 2, and 5 give identical answers, but these are very different from the answers from the other methods. Methods 4 and 6 give completely opposite answers. For methods 4 and 6, we can always say either "P grows faster than Q" or "Q grows faster than P" (as long as the growth rates are not identical). However, for all other methods in Table 1, it will sometimes not be possible to make either of these statements without qualification. For example, in the unshaded areas of Figure 1A, P grows faster than Q at some ages (or lengths) and slower than Q at others (according to methods 1, 3, and 5).

Method 6: A comparison of rates at which the asymptotic size is approached

I suggest that method 6 is the most "natural" method of growth comparison, in the sense that it produces common-sense results. To see why, consider the question in the title of this paper. Orange roughy, *Hoplostethus atlanticus*, is described as "very slow-growing" (Fenton et al., 1991) and herring, *Clupea harengus*, is generally considered to be fast-growing; therefore the answer to this question should be "yes." Given growth parameters for orange roughy ($L_{\infty,Q}$=40 cm, k_Q=0.044/yr; Fenton et al., 1991) and any of the sets of herring parameters given by Pauly (1980) (range: $L_{\infty,P}$=19.4 – 36.0 cm, k_P = 0.21– 0.48/yr), the point $(L_{\infty,P}, k_P)$ would lie in the right-hand unshaded space in Figure 1A (and in the corresponding position in the other panels of Figure 1). This means that with methods 1, 2, 3, and 5 there would be no clear-cut difference in growth rates between these species and that with method 4 herring would grow slower than orange roughy. Only method 6 reaches the common-sense conclusion.

Another reason to prefer method 6 is that it ignores asymptotic size (L_∞). It seems to me that comparisons of this parameter determine only whether one species is bigger than another, not whether growth is faster or slower. In other words L_∞ describes size, not growth rate. But note that, for the methods covered by Figure 1, A and B, P cannot be judged to grow faster than Q unless $L_{\infty,P} > L_{\infty,Q}$. This confusion between measures of size and growth rate is illustrated by Figure 2. Method 6 ranks curve P

as the slowest-growing because it is the slowest of the three in approaching its asymptote; with methods 1, 2, 3, and 5, the ranking is reversed because of the influence of L_∞ (it is also reversed for method 4, but not because of L_∞).

So far, method 6 has been defined only where growth follows the von Bertalanffy equation with $t_0 = 0$. This definition works equally well even if $t_0 \neq 0$ (this parameter simply determines the horizontal position of the growth curve and is therefore irrelevant in describing the speed of growth). The definition also extends naturally to the Gompertz and logistic growth equations as long as growth is considered only to the right of the inflection point. Both these equations have a rate parameter precisely analogous to k (this is the parameter g in equations 3 and 4 of Schnute, 1981). However, more complex growth models (e.g. the four-parameter model of Schnute, 1981) are so flexible that it seems difficult to rank growth curves along a single dimension, from slower to faster. A simple solution, which is consistent with method 6, would be to determine the age at which a species reaches 90%, say, of L_∞. The younger this is, the faster-growing is the species.

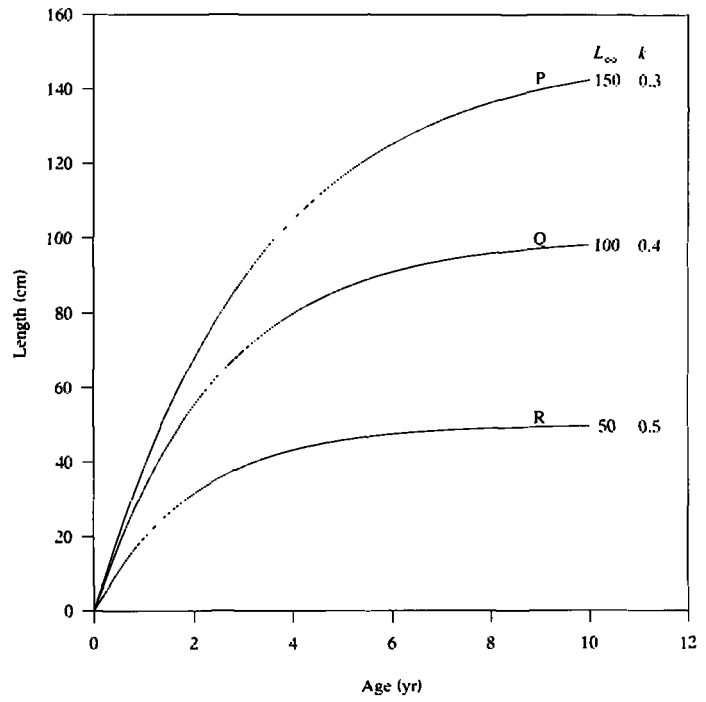

Figure 2

Example of three von Bertalanffy growth curves whose ranking, from slowest- to fastest-growth, is P, Q, and R for method 6 but the reverse for all other methods in Table 1.

Conclusions

The main conclusion of this paper is that statements like "P grows faster than Q" are ambiguous unless the method of growth comparison (e.g. one of the methods in Table 1) is specified. To some extent it does not matter which method is used as long as this is clearly stated. However, I have given some reasons to believe that method 6 is the most natural method. Amongst these reasons is the observation that, for von Bertalanffy growth, it is the parameter k that describes growth rate; L_∞ merely describes (eventual) size.

In order to make a point, the title of this paper refers to comparisons between disparate species. However, my main conclusion applies whether the growth comparison is made within or between species. I am happy to agree with an anonymous referee who asserted (forcefully) that some authors may not share my preference for method 6 (particularly for within-species comparisons).

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Announcement

The editorial staff of *Fishery Bulletin* would like to thank the following referees for their time and efforts in providing reviews of the manuscripts published in 1996. Their contributions have helped ensure the publication of quality science.

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Fishery Bulletin

Guide for Contributors

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